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THE BEHAVIORAL ECOLOGY OF THE AMERICAN WIGEON (*Anas americana*) OVER ITS ANNUAL CYCLE

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ABSTRACT

The behavioral ecology of the American Wigeon (Anas americana) was studied over its annual cycle in western Canada between 1974 and 1978. The objective of this work was to examine the cross-seasonal interactions of the biology and behavior of the wigeon as they underlie the evolution of its mating system.

The wigeon was more herbivorous than any other dabbling duck studied so far and spent a considerable amount of time feeding in upland habitats. Vegetation was important in the diet year round but particularly from late summer through the winter. Plant seeds were a rich source of protein and carbohydrate early in the spring. During breeding stages animal foods were selected by wigeons, particularly females. Wigeons usually did not feed on small crustaceans and gastropods but selected larger aquatic insect foods.

Relative to other Anas species, the wigeon has a goose-like bill whose structure facilitates feeding on upland and aquatic vegetation. With the evolution of this specialization, efficient surface-straining of small foods has been sacrificed. To increase food digestibility, wigeons altered gizzard grit composition and organ sizes. Through these mechanisms I have demonstrated how wigeons have been able to increase the efficiency of digestion.

Patterns of molt differed between sexes with females undergoing a heavy prealternate body molt in late winter and early spring. This molt continued through spring migration but was interrupted during breeding. The prebasic molt commenced near the end of brood rearing. Males underwent the prebasic and most of the prealternate molt in summer after breeding had ended. Unlike most females, males left the breeding area and migrated to large permanent marshes to molt. These sex-related differences in molt biology seem to be related to the greater parental investment by females and the different annual patterns of time and energy expenditure by the sexes.

The display and vocalization repertoires of the wigeon were described quantitatively. Male courtship displays highlighted the colorful plumages on the head, wings and rump and served to draw the female's attention and intimidate other males. Overt aggression and flight were important aspects of the competitive courtship process. Female displays indicated mate preferences and heightened competition among males. Once pairs formed, other mutual displays were performed over the winter and spring which tested and strengthened the bond between prospective mates. This process probably increased the chances of successful reproduction. Vocalizations, some of which seemed to be individually recognizable among individuals were important both in courtship and in maintaining pair integrity.

Wigeon displays were similar in many ways to those of other Anas species, but seemed most closely linked with blue-winged duck species.

The process of pair formation over the winter was examined in greater depth. Birds in the population did not court and pair concurrently as expected if photoperiod was the only proximate influence on this behavior. Rather, pair formation occurred gradually and spanned most of the winter. In general, adult males paired before juveniles, and plumage quality, body size, and body condition were related directly to pairing success. A similar pattern occurred in an experimental flock of captive wigeons at the Delta Waterfowl Research Station. During pairing, individuals of both sexes showed mate preferences and some bonds were ephemeral. It is likely that only the most vigorous and dominant males were successful in acquiring and keeping a mate. In this context the reproductive advantages of early pairing were discussed. I showed that the male qualities on which mate selection were based during winter courtship were the same as those important later during nesting.

Finally, all aspects discussed above were incorporated into a discussion of the evolution of the wigeon's reproductive biology and mating system.

Wigeons were strongly territorial and had long-lasting pair bonds similar to the Gadwall (Anas strepera) and blue-winged ducks. Males invested considerable time and energy in protecting their territory and mate from other conspecifics. Group Flights, forced copulation, and forced pair copulation were important aspects of wigeon reproductive biology. Unpaired males attempted to break existing pair bonds and one successful instance of this was documented. The varying reproductive

strategies of females, paired males and unpaired males were discussed in terms of net reproductive cost-benefits accruing to individuals. The dynamic nature of this relationship was also illustrated and it was shown how the selection by wigeons of environmentally stable and predictable habitats influences this pattern. The differential parental investment by the sexes, the need to leave breeding areas and migrate to winter habitats, the net advantages of winter pairing, the skewed sex ratio, ability of yearlings to breed and the homing behavior of females are all interrelated factors selecting for monogamy in the wigeon.

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4i Number of some waterbird species observed on the Moose Jaw study area, spring, 1977. 357

4ii Number of remaining waterbird species observed on the Moose Jaw study area, spring, 1977. 360

GENERAL INTRODUCTION

Much ornithological research has been directed toward the study of breeding birds. However, several authors (Fretwell 1972, Spurr and Milne 1976a,b, Raveling 1979, Heitmeyer and Fredrickson 1981, Myres 1981) have demonstrated a cross-seasonal influence on the biology of migrant species in particular. A recent workshop, on the ecology of wintering waterfowl, emphasized further this neglected concept (Anderson and Batt 1982).

I took this approach during an integrated study of the behavioral ecology of the American Wigeon (see Appendix 1 for scientific names of biota) over its annual cycle in British Columbia (wintering), Saskatchewan (breeding) and Manitoba (molting and fall staging). There are six chapters in the thesis, each with its own introduction, methods and discussion of results. Throughout the thesis I appraise the reproductive consequences of wigeons' adaptations to their environment. I have compared, where possible, the American Wigeon's behavior to other species of wigeons and other dabbling ducks of the genus Anas. In general, physiological adaptations are discussed first, and behavioral adaptations last. However, due to the inter-relatedness of these processes, some overlap exists between and among chapters, and cross-referencing occurs commonly.

The first two chapters examine how wigeons obtain foods that supply them with sufficient nutrients to survive and reproduce. The wigeon's

unique morphological, physiological and behavioral adaptations to a herbivorous diet are discussed. Although the wigeon is portrayed as a grazing specialist, I also emphasize its abilities to obtain food opportunistically.

In Chapter 3, I discuss the pattern of wigeon molt. A classical description of molt through the various feather tracts is not followed; however, I discuss variation in the pattern of molt of the sexes and of individuals. A link is drawn between scheduling of molt and reproductive cost-benefits that result.

The displays and vocalizations characteristic of wigeon social behavior are described in Chapter 4. Knowledge of the wigeon's display repertoire facilitates discussion of pair formation and mating system which are treated in Chapters 5 and 6, respectively. These final chapters draw on previous chapters to illustrate the continuity and inter-relatedness of events that occur during the wigeon's annual cycle. An appraisal of allocation of time and energy by individuals of known reproductive status is used to interpret the evolution of this cycle, and in particular, the wigeon's mating system and reproductive biology.

CHAPTER 1

FEEDING ECOLOGY OF THE AMERICAN WIGEON

INTRODUCTION

Early studies of the food habits of waterfowl were largely descriptive (McAtee 1918, Mabbott 1920, Cottam 1939) and were usually based only on gizzard contents of hunter-harvested birds. Therefore, these results did not accurately portray diets over the whole year (Swanson and Bartonek 1970, Danell and Sjoberg 1980).

More recent work by Perret (1962), Bartonek and Hickey (1969), Sugden (1973), Swanson et al. (1974a) and others attempted to reduce bias associated with differences in food digestion rates by considering material only in the upper digestive tract. In these studies consideration also was given to influences of habitat and the birds' status, to allow a more meaningful interpretation and application of the findings. This approach lead to current attempts to understand the evolution of waterfowl feeding strategies (Krapu 1974a,b, 1979, 1981, Serie and Swanson 1976, Siegfried et al. 1976, Reinecke and Owen 1980) and habitat selection (Siegfried 1976, White and James 1978, Eadie et al. 1979, Courcelles and Bedard 1979, Joyner 1980, Nudds 1980, Kaminski and Prince 1981a,b).

The American Wigeon is one of the most abundant waterfowl species in North America (Bellrose 1976). However, little quantitative information exists about its feeding ecology. Most published material indicates that wigeons are highly vegetarian (Mabbott 1920, Bent 1962, Bellrose 1976, Hirst and Easthope 1981). Johnsgard (1978) recognized that the structure of the wigeon's bill probably permitted it to be a

more proficient grazer than other Anas species (Chapter 2). However, Krapu (1979) showed that diets consisting of only plant material are insufficient to meet the demands of egg production by ducks (see also King 1973, Scott 1973). Many species respond at this time by shifting to animal foods that are high in protein (Swanson et al. 1979).

In this chapter I describe the feeding behavior and the food habits of the American Wigeon, and the nutritional quality of its diet over the annual cycle. Based on results from the early literature, I examine the hypothesis that this species is more vegetarian than other species of Anas.

METHODS

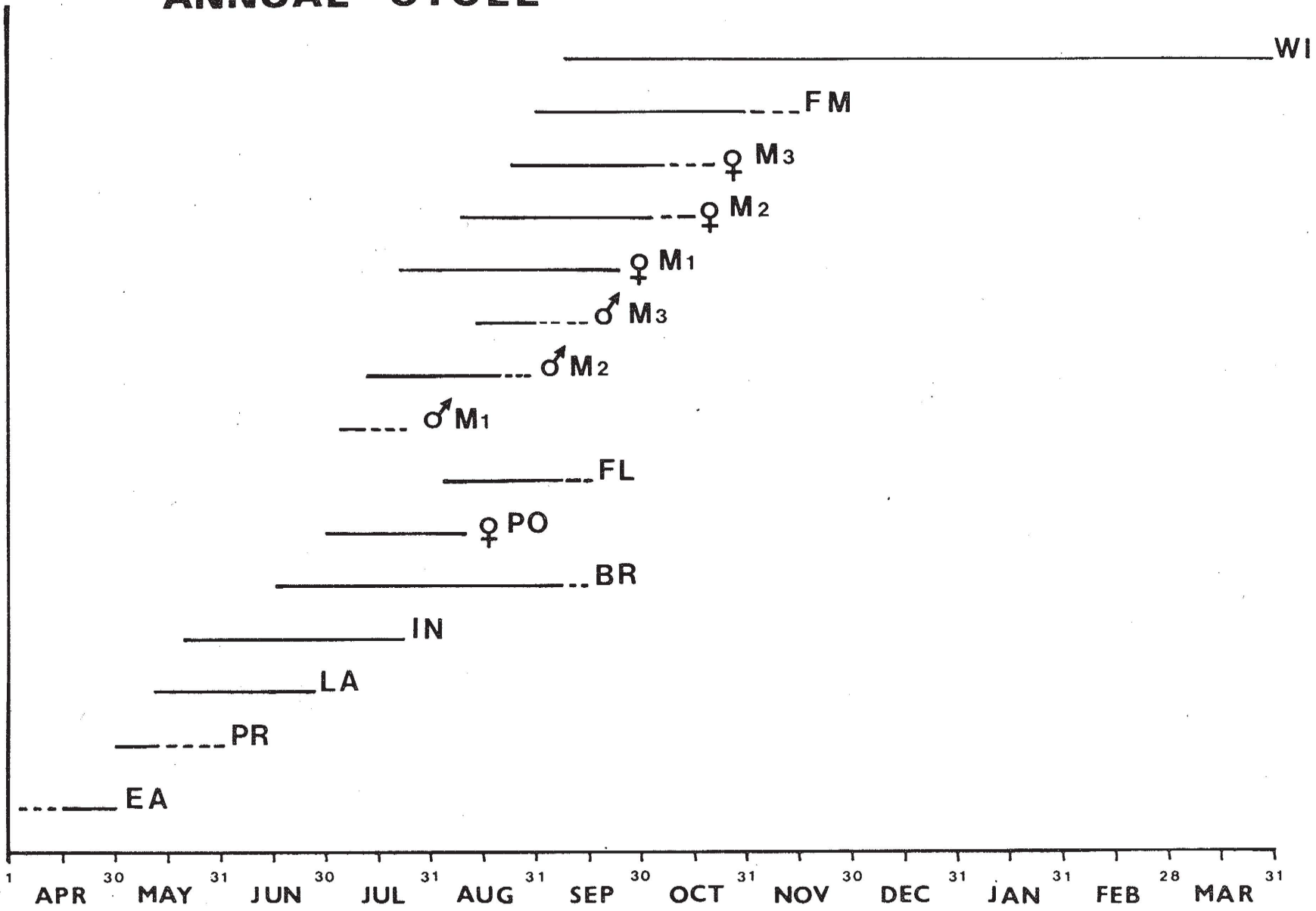
Wigeons were shot at all stages of their annual cycle (Fig. 1). During the Winter (stages capitalized), Postreproductive, and Fall Migration stages, feeding birds were usually wary and most were shot after being attracted to decoys. Some decoyed birds also were collected during Early Arrival in spring. Some molting birds were captured at night with a dip net from an air boat equipped with a spotlight. Some birds were obtained in fall from hunters. During the breeding season I observed birds feeding for at least 10 min before they were shot.

Only foods in the proventriculus and esophagus of birds were analysed. Gizzard contents were not used because of the possible bias associated with this material (Swanson and Bartonek 1970).

Fig. 1. Stages in the wigeon's annual cycle. EA=-Early Arrival, PR=Prelaying, LA=Laying, IN=Incubation, BR=Brood Rearing, PO=Postreproductive, FL=Ducklings Fledged, M1=Preflightless Molt, M2=Flightless Molt, M3=Postflightless Molt, FM=Fall Migration, WI=Winter. Dashed lines indicate the probable extension of stages for some individuals.

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ANNUAL CYCLE



On the breeding grounds where birds could be collected while they were feeding, I sampled the feeding site and adjacent areas to determine what foods were potentially available to wigeons. Sites were sampled immediately following collection, or where this was not possible, at the same time the following day. Three samples from the benthos were taken with a multiple corer (Hamilton et al. 1970) and plankton was sampled by passing 182 l of surface water (top 30 cm) through a sieve-bucket having 144 perforations/cm^2. All of this material was washed, preserved in formaldehyde and sorted later under a microscope. In most cases, invertebrates were identified to family (Pennak 1953, Ward and Whipple 1959, Edmunds et al. 1976, Wiggins 1977), and plant seeds (Martin and Barkley 1961) and vegetation (Fassett 1940, Budd and Best 1969, Prescott 1969, Hotchkiss 1972) to genus or species. Organisms, both ingested and sampled in the environment, were counted, dried in an oven at 60 C for 24 h and weighed to 0.1 mg.

At each feeding site water temperature, salinity, and conductivity were measured with a Yellow Springs Instrument model 33 meter. Water depth was measured, a representative plant collection made and each wetland classified (Stewart and Kantrud 1971).

Wigeon diets and the potential foods present at each feeding site were summarized for each sex by stage of the wigeon's annual cycle using frequency and aggregate percent dry weight (Swanson et al. 1974b, Reinecke and Owen 1980). An index of food electivity was calculated by comparing the proportion of each food in the diet with the mean of the aggregate percent of each in benthic and plankton samples:

$$E = (r-p)/(r+p)$$

where r=the aggregate percent dry weight in the diet and p=the aggregate percent dry weight for the same food at the feeding site. Values of E (electivity index) approximating zero indicate that a food was ingested in accordance to its presence. Values of 0 to +1 indicate that a food was in the diet in greater proportion to its estimated presence and negative values (0 to -1) the opposite (see Ivlev 1961, Serie and Swanson 1976).

An analysis was performed to compare the nutritional quality of the diets of males and females over their annual cycles. Where possible, data from the literature (Sugden 1973, Driver et al. 1974, Cummins and Wuycheck 1971, Krapu and Swanson 1975, Krapu 1979) were used. Using means so obtained, the few remaining unquantified seeds were assigned 9.8% protein, 4.8% lipid , 59.3% NFE (nitrogen-free extract), 6.4% ash, 18.7% fibre, 0.4% calcium and 4.5 kcal/g dry weight; vegetation (stems, leaves, roots) 13.9% protein, 1.0% lipid, 54.3% NFE, 16.1% ash, 14.7% fibre, 2.0% Ca and 3.8 kcal; animal foods 60.0% protein, 5.0% lipid, 10.0% NFE, 5.0% ash, 20.0% fibre, 0.6% Ca and 5.1 kcal (see Reinecke and Owen 1980). Mayfly larvae in their cases (cases primarily gravel but also vegetation, fruits and snail shells) were assigned values equal to those of snails in their shells (Sugden 1973) except for calcium which was set at 2.0%, similar to that of grit (Chapter 2). I assumed a conversion efficiency of 70% (King 1973), thus metabolizable energy (ME) was equal to:

$$ME = 0.7\ (\text{Gross Energy} - \text{Energy of Crude Fibre})$$

This value was expressed also on an ash-free basis. The crude fibre content of the diet, primarily cellulose, is indigestable and largely unavailable to waterfowl (Mattocks 1971). Therefore, the energy it holds (4.1 kcal/g dry weight) (Ricklefs 1974) was subtracted in the estimate of ME.

Individually marked birds (Chapter 6) were observed so that I could calculate a time budget for each sex over the breeding season (Early Arrival through Brood Rearing). Data were collected in all daylight hours (CST) as described in Chapter 6 and grouped into four time blocks (0500-0900 h, 0900-1300 h, 1300-1700 h and 1700-2100 h) (see Wishart and Sealy 1980). Some observations were continued after dark using a night vision scope.

Feeding behavior was divided into: 1) feeding below the water's surface (bill submerged), 2) feeding at the surface (bill not submerged), 3) tip feeding (head and neck submerged), 4) feeding on land (along shore or in uplands), 5) feeding on emergents (reaching up onto emergent plants to graze, glean insects or remove seeds) and 5) snatching insects out of the air. The percent of total feeding time spent by birds using each method was calculated. In addition I calculated the percent of total time that birds spent on the water, in flight, on the shoreline or in agricultural fields. Arcsin-transformed-percent data were analysed by one-way and two-way analyses of variance as described in Chapter 6.

STUDY AREAS

The study was conducted on three areas between 1974 and 1978 during different stages of the wigeon's annual cycle.

In winter, between 1 December and 31 March (1974-75, 1976-77) studies were carried out on the mudflats, farmland and tidal brackish marshes near Vancouver, British Columbia. Most of the work was performed on and around Westham Island in the Fraser River Delta, 30 km south of Vancouver (49°09'N, 123°01'W). The vegetation, climate, soils, glacial history and hydrological features of this and adjacent areas have been documented by Burgess (1970), Leach (1972), Taylor (1974), Vermeer and Levings (1977), Hirst and Easthope (1981), Bradfield and Porter (1982) and Hutchinson (1982). Behavioral studies were conducted at the north end of Westham Island in the George C. Reifel Migratory Bird Sanctuary (340 ha) and adjacent Alaksen National Wildlife area (231 ha) managed by the Canadian Wildlife Service. These areas have been described by Dawe and Davies (1975) and Vermeer and Davies (1978). Other data were collected at the Maplewood Mudflats intertidal zone in Burrard Inlet, 9.7 km north-east of Vancouver. The physical and biological features of this 81-ha area have been described by Vaudry and Land (1973).

The American Wigeon does not nest in lower mainland British Columbia but this area is an important overwintering location for this and other species of waterfowl between September and March (Munro 1949, Burgess 1970, Leach 1972). These birds nest in Alaska, the Yukon and inland in British Columbia (unpublished Canadian Wildlife Service banding data).

Between mid-April and mid-August, 1976-77, and in April, June and July, 1978, studies were conducted of breeding wigeons 32 km southwest of Moose Jaw, Saskatchewan (50°15'N, 105°50'W). This glaciated area lies within both the Old Wives Lake Plain and Missouri Coteau Upland in the Alberta High Plains physiographic region (Christiansen 1961). It is characterized by gently to strongly rolling grasslands with a total relief range of 244 m and an average of 32.2 wetland basins/km^2. On the 279.9 ha study area where most of the work was done, 80 wetland basins occupied 43.1 ha (15.4% of area). The remainder of the area consisted of 37.2% native pasture, 16.3% cultivated feed grains, 13.6% abandoned farmland, 10.2% planted hayland, 6.3% fallow, and 1.0% roads and farmyards. The proportions of cultivated habitats changed slightly from year to year with rotations of hay, feed grains and fallow.

Wetlands (classified as per Stewart and Kantrud 1971) in the area consisted of 3.8% ephemeral (Class I), 45.0% temporary (Class II), 17.5% seasonal (Class III), 13.7% semipermanent (Class IV), 17.5% permanent (Class V) and 2.5% intermittent alkali (Class VI). Over the season, surface water temperatures ranged from 10-24.5 C, salinity from 0.1-7.3 ppt and conductivity from 170-11,500 µmhos/cm^3. Of 58 wetlands in August, 1977 13.8% were classified as fresh (40-500 µmhos/cm^3), 63.8% slightly brackish (500-2000 µmhos/cm^3), 15.5% moderately brackish (2000-5000 µmhos/cm^3), and 6.9% brackish (5000-15,000 µmhos/cm^3) (Stewart and Kantrud 1971).

Climate, soils and wetland habitats of this area have been described by Leitch (1952), Walker and Coupland (1968, 1970) and Millar

(1976). Breeding American Wigeon in this area were more abundant than for any other area yet described (Bellrose 1976). Weekly waterfowl surveys (ground counts) in 1976 and 1977 showed that 10.7 and 7.1 pairs of wigeon per km^2, respectively, used the area prior to the peak of nesting in late May. Lesser Scaup, Mallard, Blue-winged Teal and Gadwall were all more abundant than wigeon, whereas Northern Pintail, Northern Shoveler, Redhead and Canvasback were less numerous. American Coots, Horned Grebes and Pied-billed Grebes were observed regularly and nested on wetlands on the study area. Potential waterfowl predators observed regularly in the area were Northern Harrier, Swainson's Hawk, Great Horned Owl, American Crow, Black-billed Magpie, Black-crowned Night-heron, Ring-billed Gull, Franklin's Gull, Red Fox, Coyote, Striped Skunk, Richardson's Ground Squirrel, Mink, weasel, and feral cat and dog.

To avoid affecting marked birds whose behavior was being studied, wigeons collected for food habits and physiological studies of body condition were taken from surrounding areas, at least 0.9 km from the borders of the study area. An area of 530 km^2 was used for these collections. Waterfowl from this area molted on Old Wives Lake, a bird sanctuary 12 km south of the main study area. Wigeon that breed in this area winter primarily in southern California and along the coast of the Gulf of Mexico (unpubl. Canadian Wildlife Service banding data).

Postbreeding wigeons were studied in July and August 1977, 1978 and in October and November, 1977, on the Delta Marsh, Manitoba (50°11'N, 98°19'W). Hochbaum (1944), Walker (1959, 1965), Anderson and Jones (1976) and Anderson (1978) have described the physical and biological aspects of this habitat. Wigeons nest uncommonly at Delta, but large numbers of molting adults and fledged offspring concentrate here after the breeding season prior to fall migration (Hochbaum 1944).

RESULTS

Of 192 wigeons collected over their annual cycle (Fig. 1), 84% (81 males and 81 females) had food in their upper digestive tract.

Diet

The diets of male and female wigeons were primarily leafy vegetation, except during Early Arrival and, in the case of females, during Laying (Figs. 2 and 3). Vegetation was eaten almost exclusively in the Fall and Winter. Birds made most use of invertebrates from Early Arrival until the start of Molt, but thereafter they were eaten in small amounts. During this period invertebrates made up double the proportion of females' diets compared to that of males. Plant seeds were important during most stages but were used the greatest from Early Arrival through the Molt. Seeds made up an average of 18% more of the diet of males than females, and males substituted vegetation for most of the invertebrates that females ate during Laying.

Fig. 2. Aggregate percent (dry weight) of each food type eaten by male wigeons over their annual cycle. Stages defined in Fig. 1. Information for several stages was not obtained.

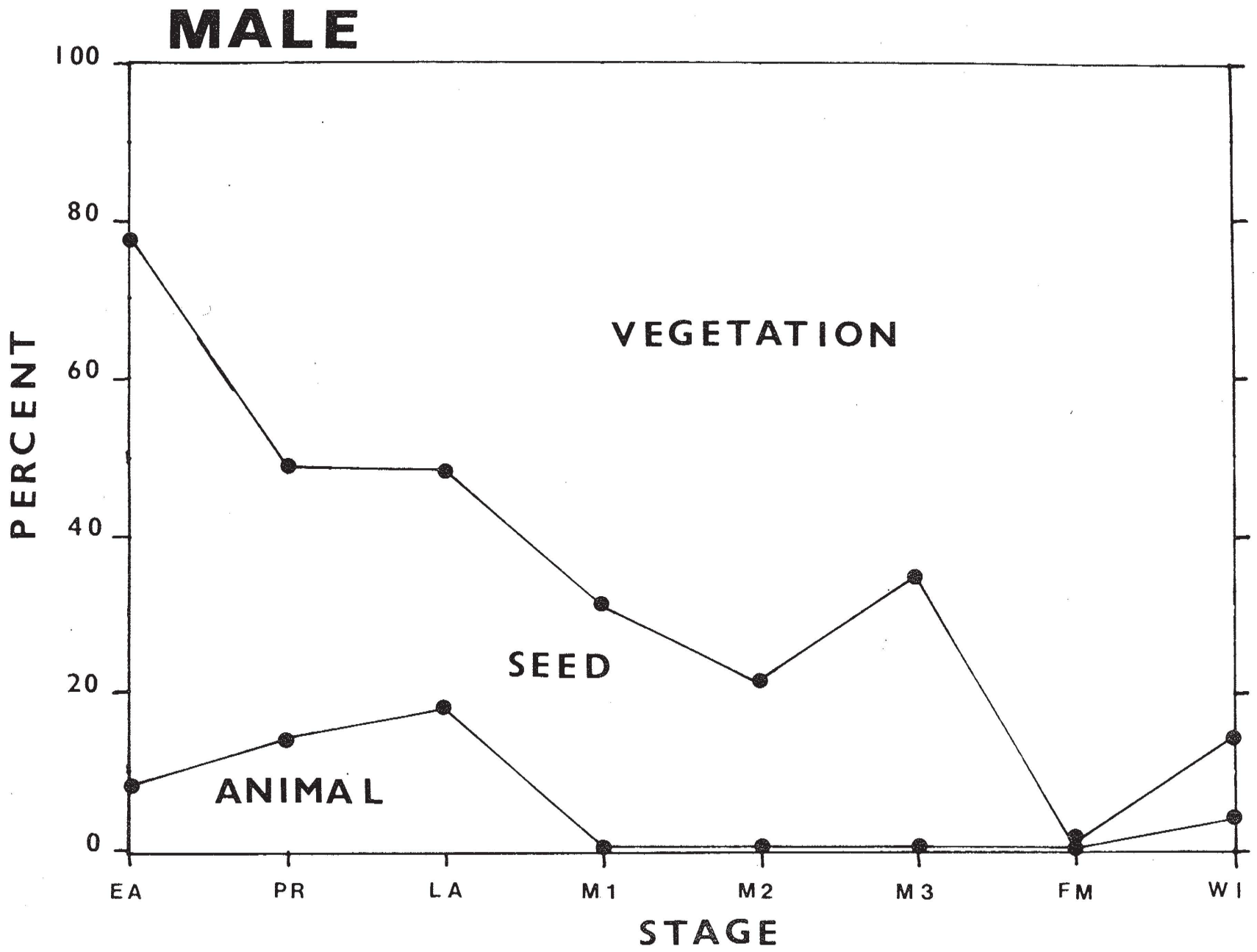
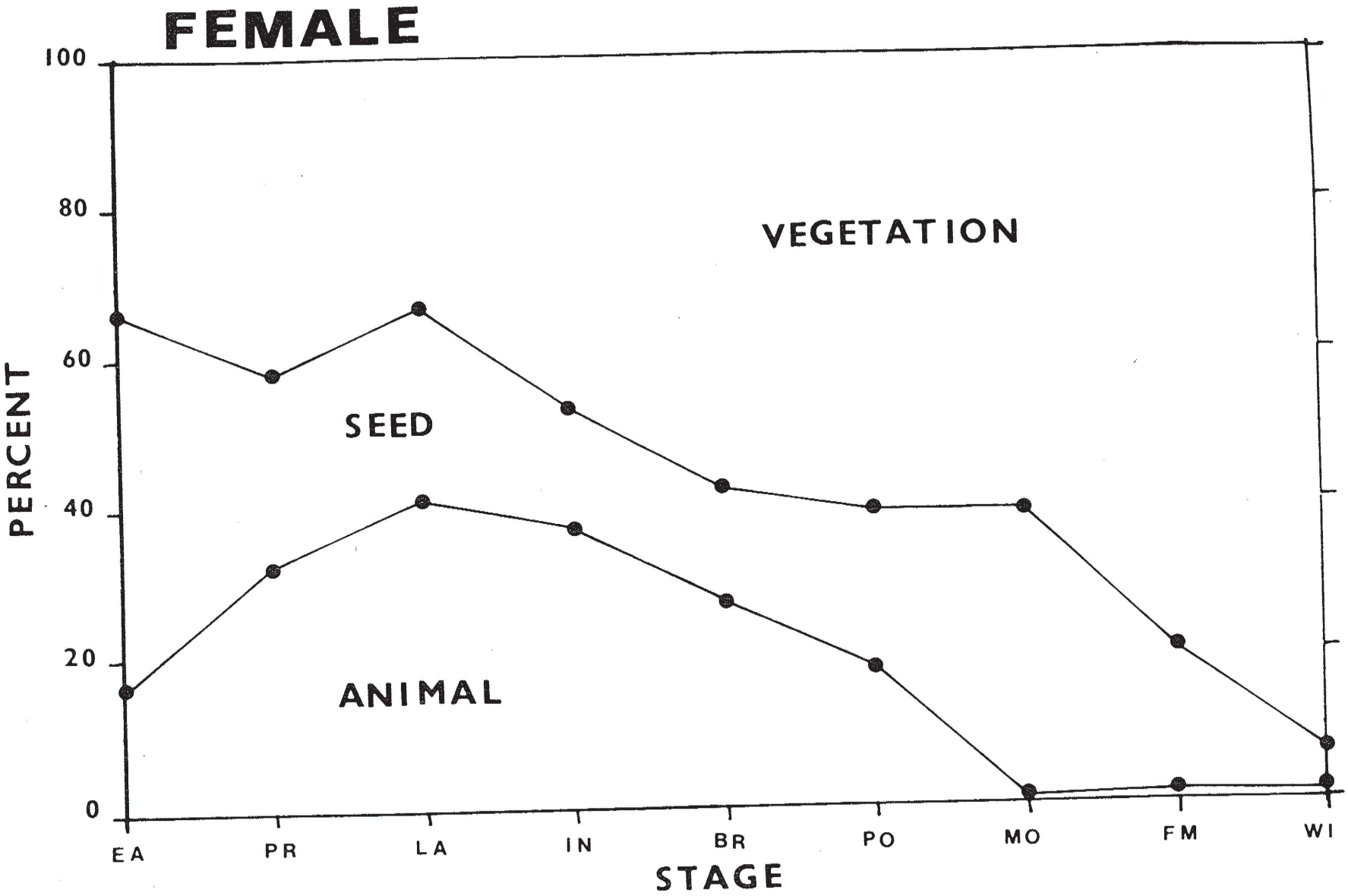

MALE
100
80
60
40
20
0
PERCENT
VEGETATION
SEED
ANIMAL
EA
PR
LA
M1
M2
M3
FM
WI
STAGE

Fig. 3. Aggregate percent (dry weight) of each food type eaten by female wigeons over their annual cycle. Stages defined in Fig. 1 (MO=all stages of molt combined).


FEMALE
100
80
60
40
20
0
PERCENT
VEGETATION
SEED
ANIMAL
EA
PR
LA
IN
BR
PO
MO
FM
WI
STAGE

Cultivated grains, primarily wheat (57% Durham, 43% common) but also oats and barley, were important wigeon foods during Early Arrival, Prelaying and to a degree, in Fall (Tables 1-4). The most important aquatic seeds eaten were those of pondweed (mostly Sago) and bulrush. Seeds of sedge, spike-rush, water buttercup and water milfoil also were often important, whereas those of arrowhead, grass, dock, and lamb's-quarters were seldom used.

Filamentous algae, pondweed, glumiforae (sedge, grass and bulrush), duckweed (90% Ivy-leaved, 10% Lesser) and water buttercup were the most important types of vegetation consumed through most stages until the Molt, and water buttercup was also eaten by females in Fall. Pondweed was a dominant food from Incubation through Fall Migration, whereas grass was important through the Spring and Winter. Water milfoil was consumed heavily only during Brood Rearing and aquatic moss, by females in Winter. For males, pondweed was a dominant food during the Preflightless Molt period and water celery was eaten in Winter, although it was found in just one bird.

In general, except for females during Prelaying and Laying, aquatic invertebrates, other than insects, made up only a small part of the diet. Dominant aquatic insect groups (primarily non-adult forms) were dragonflies (some adults eaten) (common skimmers, and narrow-winged damselflies), water boatmen, beetles (crawling water beetles, predaceous diving beetles, water scavenger beetles), caddisflies and biting midges. Females ate more snails, non-biting flies and crustaceans (seed shrimp, water fleas, fish lice) during Laying than did males. Round worms were also important at times.

Table 1. Foods of male wigeons (aggregate % dry weight) over their annual cycle, 1976-78.

Food	Stage[1] EA (19)	PR (4)	LA (11)	MI (3)	M2 (8)	M3 (4)	FM (4)	WI (28)
Seeds								
Barley	1.2	23.2						
Wheat	55.3						24.5	
Sago Pondweed					1.7	34.4		
Grass			9.1					
Sedge			19.0					
Spike-rush			1.5					
Bulrush	1.7	11.8		30.6	18.8	0.1		10.8
Dock	T[2]		T					
Lamb's-quarters	10.5							
Water buttercup	T							
Water milfoil	0.2							
Other	T		T				T	
Vegetation								
Algae (filamentous)	3.0	0.1	5.0	33.0	21.1			
Moss	1.9	0.5	4.0		0.5			T
Horned Pondweed				33.3				
Sago Pondweed					43.4	15.3		
Glumiflorae (unid.)							75.0	11.6
Grass	0.8	40.0						3.6
Sedge								1.3

Table 1. Cont'd.

Food	Stage[1] EA (19)	PR (4)	LA (11)	MI (3)	M2 (8)	M3 (4)	FM (4)	W1 (28)
Vegetation								
Duckweed	5.1		19.0					
Water buttercup		9.9	18.0					
Water milfoil	0.1							
Water celery								3.4
Other	12.8	0.1	6.1	2.8	14.5	48.8	0.5	64.8
Invertebrates								
Round worm	T							4.5
Snail[3]	T							T
Crustacean	T	T	3.0		T		T	T
Insect								
Dragonfly	2.5	T						
True bug	T					1.4		
Beetle	3.2	0.4	1.1					
Caddisfly[4]	T		9.1					
Fly	1.6	14.0	5.1	0.3				T
Other[5]	T	T						

[1]EA=Early Arrival, PR=Prelaying, LA=Laying, M1=Preflightless Molt, M2=Flightless Molt, M3=Postflightless Molt, FM=Fall Migration, W1=Winter. Sample size in parenthesis. [2]trace <0.1%. [3]In shell. [4]Larvae in case. [5]Hydra, segmented worms, mites.

Table 2. Foods of male wigeons (% occurrence) over their annual cycle, 1976-78.

Food	Stage[1] EA (19)	PR (4)	LA (11)	MI (3)	M2 (8)	M3 (4)	FM (4)	W1 (28)
Seeds								
Barley	5.3	25.0						
Wheat	57.9						25.0	
Sago Pondweed					12.5	50.0		
Grass			9.1					
Sedge			27.3					
Spike-rush			9.1					
Bulrush	15.8	25.0		33.3	37.5	25.0		21.4
Dock	10.5		9.1					
Lamb's-quarters	15.8							
Water buttercup	5.3							
Water milfoil	5.3							
Other	10.5	25.0					25.0	
Vegetation								
Algae (filamentous)	10.5	25.0	9.1	33.3	25.0			
Moss	15.8	25.0	9.1		12.5			3.6
Horned Pondweed				33.3				
Sago Pondweed					50.0	25.0		
Glumiflorae (unid.)							75.0	21.4
Grass	10.5	50.0						3.6
Sedge								3.6

Table 2. Cont'd.

Food	Stage[1] EA (19)	PR R(4)	LA (11)	MI (3)	M2 (8)	M3 (4)	FM (4)	WI (28)
Vegetation								
Duckweed	15.8		36.4					
Water buttercup		25.0	18.2					
Water milfoil	15.8							
Water celery								3.6
Other	52.6	25.0	18.2	33.3	37.5	75.0	25.0	78.6
Invertebrates								
Round worm	5.3							10.7
Snail[2]	10.5							3.6
Crustacean	21.1	25.0	18.2		12.5		25.0	3.6
Insect								
Dragonfly	5.3	25.0						
True bug	5.3					25.0		
Beetle	21.1	50.0	18.2					
Caddisfly[3]	5.3		9.1					
Fly	42.1	75.0	36.4					7.1
Other[4]	5.3	25.0						

[1]EA=Early Arrival, PR=Prelaying, LA=Laying, M1=Preflightless Molt, M2=Flightless Molt, M3=Postflightless Molt, FM=Fall Migration, W1=Winter. Sample size in parenthesis. [2]In shell. [3]Larvae in case. [4]Hydra, segmented worms, mites.

Table 3. Foods of female wigeons (aggregate % dry weight) over their annual cycle, 1976-78.

Food	Stage[1] EA (9)	PR (4)	LA (15)	IN (6)	BR (15)	PO (8)	MO (5)	FM (6)	WI (13)
Seeds									
Oats		21.2							
Wheat	42.1								
Sago Pondweed			0.8		0.1	0.4	38.2	0.6	
Arrowhead			5.2						
Grass			0.7		T[2]				
Sedge	8.8	3.3	7.8	0.2					
Spike-rush		1.4	0.2		T				
Bulrush		0.2	1.5	0.1			1.0	10.8	6.3
Dock				T	T			1.6	
Lamb's-quarters			0.2	T				1.2	
Water buttercup			4.2	15.5	13.1	13.2			
Water milfoil			5.5	0.2	1.4	1.4		4.4	
Other	0.1				T	6.6	0.4	0.1	
Vegetation									
Algae (filamentous)		0.1	4.5		12.4		17.5	T	3.4
Moss					T				7.4
Sago Pondweed				16.5	7.8	24.8	0.3	13.6	
Glumiflorea (unid.)								16.7	15.2
Grass	11.0	24.0	3.5		0.9				
Sedge									14.5
Bulrush							17.3		

Table 3. (cont'd)

Food	Stage[1] EA (9)	PR (4)	LA (15)	IN (6)	BR (15)	PO (8)	MO (5)	FM (6)	WI (13)
Vegetation									
Duckweed	11.0	1.1	11.2		26.2	12.9		0.7	
Water buttercup		14.5	9.7	17.2	0.2	10.2		13.5	
Water milfoil	0.1		0.2	0.1	7.4				
Other	11.1	2.4	3.5	12.7	3.3	12.3	25.3	35.2	52.5
Invertebrates									
Round worm	T				4.6			1.5	0.5
Leech						T			
Snail[3]	T	5.9	1.1	0.1	T	0.1		T	T
Crustacean		T	10.1	T	T	T		0.1	
Insect									
Dragonfly		8.2	4.5		9.6	5.4			
True bug	11.8				1.0	0.2			
Beetle	2.5	0.8	2.6	1.3	0.5	T			
Caddisfly[4]		4.6	14.3	33.2	9.9	12.5			
Butterfly					T				
Fly	1.5	11.9	8.7	0.1	1.6				0.2
Other[5]		0.3		2.8	T				

[1]EA=Early Arrival, PR=Prelaying, LA=Laying, IN=Incubation, BR=Brood Rearing, PO=Postreproductive, MO=Molt, FM=Fall Migration, Wl=Winter. Sample size in parenthesis. [2]trace <0.1%. [3]In shell. [4]Larvae in case. [5]Hydra, segmented worms, mites.

Table 4. Foods of female wigeons (% occurrence) over their annual cycle, 1976-78.

Food	Stage[1] EA (9)	PR (4)	LA (15)	IN (6)	BR (15)	PO (8)	MO (5)	FM (6)	WI (13)
Seeds									
Oats		25.0							
Wheat	44.4								
Sago Pondweed			13.3		6.7	12.5	25.0	16.7	
Arrowhead			6.7						
Grass			6.7		13.3				
Sedge	22.2	25.0	26.7	16.7					
Spike-rush		25.0	13.3		6.7				
Bulrush		25.0	20.0	16.7			20.0	16.7	23.1
Dock				16.7	13.3			16.7	
Lamb's-quarters			6.7	16.7				16.7	
Water buttercup			13.3	33.3	13.3	25.0			
Water milfoil			26.7	16.7	26.7	37.5		16.7	
Other	11.1				13.3	25.0	20.0	16.7	
Vegetation									
Algae (filamentous)		25.0	13.3		20.0		20.0	16.7	38.5
Moss					6.7				30.8
Sago Pondweed				16.7	13.3	12.5	20.0	16.7	
Glumiflorea (unid.)								16.7	15.4
Grass	22.2	25.0	6.7		6.7				
Sedge									15.4
Bulrush							20.0		

Table 4. (cont'd)

Food	Stage[1] EA (9)	PR (4)	LA (15)	IN (6)	BR (15)	PO (8)	MO (5)	FM (6)	WI (13)
Vegetation									
Duckweed	22.2	25.0	40.0		46.7	37.5		16.7	
Water buttercup		25.0	20.0	33.3	6.7	25.0		16.7	
Water milfoil	11.1		20.0	16.7	33.3				
Other	33.3	50.0	46.7	16.7	13.3	12.5	80.0	66.7	69.2
Invertebrates									
Round worm	11.1				13.3			16.7	23.1
Leech						12.5			
Snail[2]	11.1	25.0	26.7	16.7	20.0	12.5		16.7	15.4
Crustacean		25.0	33.3	16.7	40.0	12.5		16.7	
Insect									
Dragonfly		50.0	13.3		20.0	12.5			
True bug	33.3				20.0	12.5			
Beetle	22.2	50.0	46.7	33.3	33.5	12.5			
Caddisfly[3]		75.0	33.3	33.3	20.0	12.5			
Butterfly					6.7				
Fly	22.2	50.0	80.0	16.7	40.0				38.5
Other[4]		25.0		16.7	20.0				

[1]EA=Early Arrival, PR=Prelaying, LA=Laying, IN=Incubation, BR=Brood Rearing, PO=Postreproductive, MO=Molt, FM=Fall Migration, Wl=Winter. Sample size in parenthesis. [2]In shell. [3]Larvae in case. [4]Hydra, segmented worms, mites.

Electivity

In general, electivity indices for males were positive for seeds, algae, duckweed and water buttercup vegetation (Fig. 4). As a group, aquatic insects were positive throughout, but within this group indices were positive usually only for dragonflies, beetles and flies. Negative indices occurred during most stages for water milfoil, and during all stages for moss, snails and crustaceans. Pondweed was taken in accordance to its sampled presence.

Females in the Prelaying and Laying stages showed a pattern similar to males; seeds, insects and duckweed had positive electivity indices (Fig. 5). Water buttercup and caddisflies became positive as the season progressed. Again, aquatic moss and water milfoil had negative indices and pondweed was taken according to its presence. In Early Arrival, plant and animal foods had indices near zero but during Prelaying and Laying, animal foods were positive. In general, indices for molluscs and crustaceans were negative except during Prelaying and Laying, respectively. As the season progressed, indices for beetles and flies declined and after Brood Rearing, invertebrates were taken relative to their presence. Over the season, filamentous algae had inconsistent indices.

Fig. 4. Electivity indices of each food type eaten by male wigeons during the Early Arrival (EA), Prelaying (PR), and Laying (LA) stages. Food types are: SEED=plant fruits, ALG=filamentous algae, MOS=aquatic moss, PON=pondweed, DUC=duckweed, BUT=water buttercup, TOT PLANT=vegetation and plant fruits, SNA=snails, CRU=crustaceans, DRA=dragonflies, BUG=true bugs, BEE=beetles, CAD=caddisflies, FLY=flies, TOT INS=all insect orders combined (DRA to FLY), TOT ANIMAL=all animal foods combined (SNA to FLY).

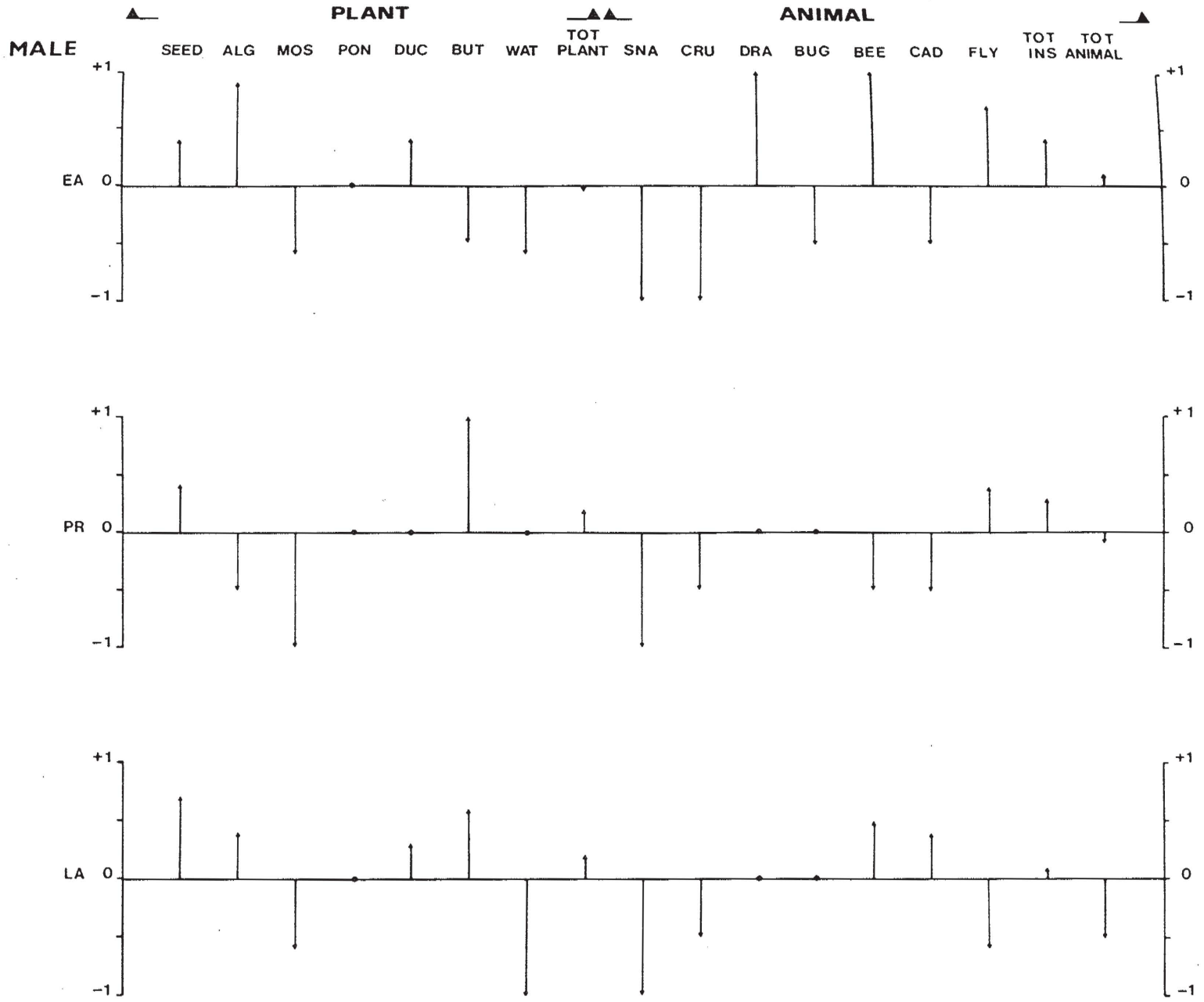
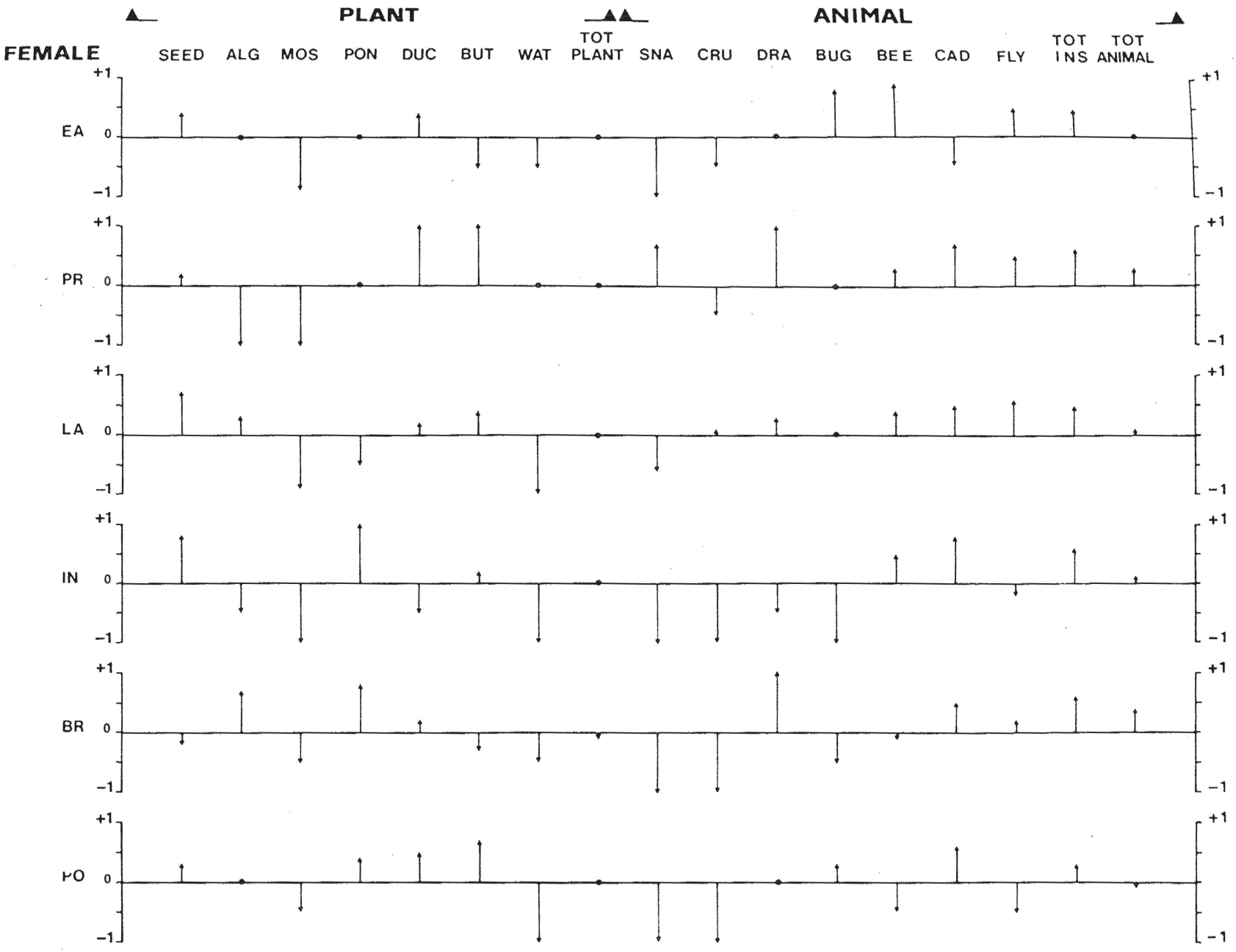

MALE
PLANT
ANIMAL
SEED
ALG
MOS
PON
DUC
BUT
WAT
TOT PLANT
SNA
CRU
DRA
BUG
BEE
CAD
FLY
TOT INS
TOT ANIMAL
EA
PR
LA
+1
0
-1

Fig. 5. Electivity indices of each food type eaten by female wigeons during the Early Arrival (EA), Prelaying (PR), Laying (LA), Incubation (IN), Brood Rearing (BR) and Postreproductive (PO) stages. See Fig. 4 for definitions of food types.


PLANT
ANIMAL
FEMALE
SEED
ALG
MOS
PON
DUC
BUT
WAT
TOT PLANT
SNA
CRU
DRA
BUG
BEE
CAD
FLY
TOT INS
TOT ANIMAL
EA
PR
LA
IN
BR
PO
+1
0
−1

Nutrition

Over the year, diets provided males with an estimated 2.3-3.1 kcal of metabolizable energy (ME) per g dry ash-free weight (Table 5). Highest energy levels were obtained during Early Arrival and Fall Migration, and lowest in the latter stages of Molt and over Winter. Dietary protein ranged from 12.8% in late Molt to 21.7% in Prelaying.

Females, over most stages, ingested a greater proportion of protein, Ca and ME than males. Protein levels were highest in the spring through Laying. Calcium peaked at 2.6% in Prelaying but dropped to 1.6% at Laying. Metabolizable energy was highest in Postreproductive females (3.5 kcals) but was high also through the spring until Laying. Incubating and Brood Rearing females ingested food low in energy, however, individuals in the latter group consumed high proportions of protein (Table 5).

Feeding Behavior

A sample of 392 observation periods was made of wigeons during 678.9 h from Early Arrival through Brood Rearing (Table 6). In Early Arrival, paired wigeons of either sex fed similarly (Figs. 6,7, Table 7). About 69% of feeding occurred at the water surface with most of the remainder below the surface or while on land. About 75% of feeding on land occurred along the shoreline and the remainder in agricultural fields nearby (Table 8). Tip feeding usually was of minor occurrence (10% of feeding time) as were feeding on emergents and snatching insects (5%), (Table 7). During Prelaying, an increase

Table 5. The nutrient quality of diets of male and female wigeons over their annual cycle, 1976-78.

		Composition on a dry basis (%)						ME[3]
Stage[1]	Sex	Protein	Lipid	NFE[2]	Ash	Fibre	Ca	(kcal/g)
EA	Female	22.9	3.3	55.6	8.1	9.2	0.8	3.0
PR		25.4	2.7	44.4	17.2	10.2	2.6	3.1
LA		23.5	4.2	37.3	21.3	13.7	1.6	2.9
IN		14.3	2.1	36.0	32.6	14.8	1.7	2.5
BR		22.2	2.6	40.7	20.4	14.0	1.6	2.5
PO		15.2	2.2	46.4	20.5	15.4	1.6	3.5
MO		17.0	6.1	47.0	12.5	17.4	1.5	2.9
FM		13.9	1.5	56.2	13.9	15.1	1.7	2.8
WI		13.9	1.0	54.5	15.6	14.7	1.9	2.9
EA	Male	19.1	2.9	63.4	6.5	7.9	0.6	2.9
PR		21.7	2.0	55.3	11.2	9.9	1.1	3.1
LA		16.7	2.7	47.0	18.6	15.0	1.5	2.7
M_1		15.1	3.6	52.2	16.3	12.8	1.6	2.8
M_2		12.9	0.9	55.5	13.7	17.0	1.9	2.5
M_3		12.8	2.1	47.2	10.7	27.3	1.4	2.3
FM		15.0	1.2	59.6	12.7	11.7	1.5	3.1
WI		15.3	1.2	53.9	14.6	15.9	1.8	2.8

[1]EA=Early Arrival, PR=Prelaying, LA=Laying, IN=Incubation, BR=Brood Rearing, PO=Postreproductive (lost clutch or brood), MO=stages of Molt, FM=Fall Migration, WI=Winter, M_1=Preflightless Molt, M_2=Flightless molt, M_3=Postflightless Molt. [2]Nitrogen-free extract. [3]ME=metabolizable energy on a dry, ash-free basis at 70% efficiency.

Table 6. Hours of observation and number of observation periods for wigeon time budget data collected in 1976-78, at Moose Jaw.

	Males					Females				
		Number[2]					Number[2]			
Stage[1]	Hours	I	II	III	IV	Hours	I	II	III	IV
EA	41.3	4	8	8	6	42.1	4	8	8	6
PR	114.3	15	19	14	19	112.1	14	18	14	20
LA	61.6	9	13	4	7	53.2	7	10	4	9
IN	101.2	12	16	7	32	19.6	3	2	1	11
B^1						22.4	1	2	3	5
B^2						62.9	6	6	7	6
B^3						25.8	5	2	3	1
PO						22.4	4	2	2	5
Total	318.4	40	56	33	64	360.5	44	50	42	63

[1]EA=Early Arrival, PR=Prelaying, LA=Laying, IN=Incubation, B_1=Brood Rearing young 1-2 weeks old, B_2=Brood Rearing young 3-4 weeks old, B_3=Brood Rearing young 5-6 weeks old, PO=Postreproductive.

[2]I=0500-0900h, II=0900-1300h, III=1300-1700h, IV=1700-2100h (CST).

Fig. 6. Upper graph depicts the percent of the total time budget that males spent in agricultural fields. Lower graph depicts the percentage of total feeding time that male wigeons spent using different feeding methods (see text for definition of methods) (OTHER=feeding on emergents plus snatching insects) over the spring (EA=Early Arrival, PR=Prelaying, LL=Laying while female absent, LP=Laying while female present, IP=Incubation while female present, IL=Incubation while female absent).

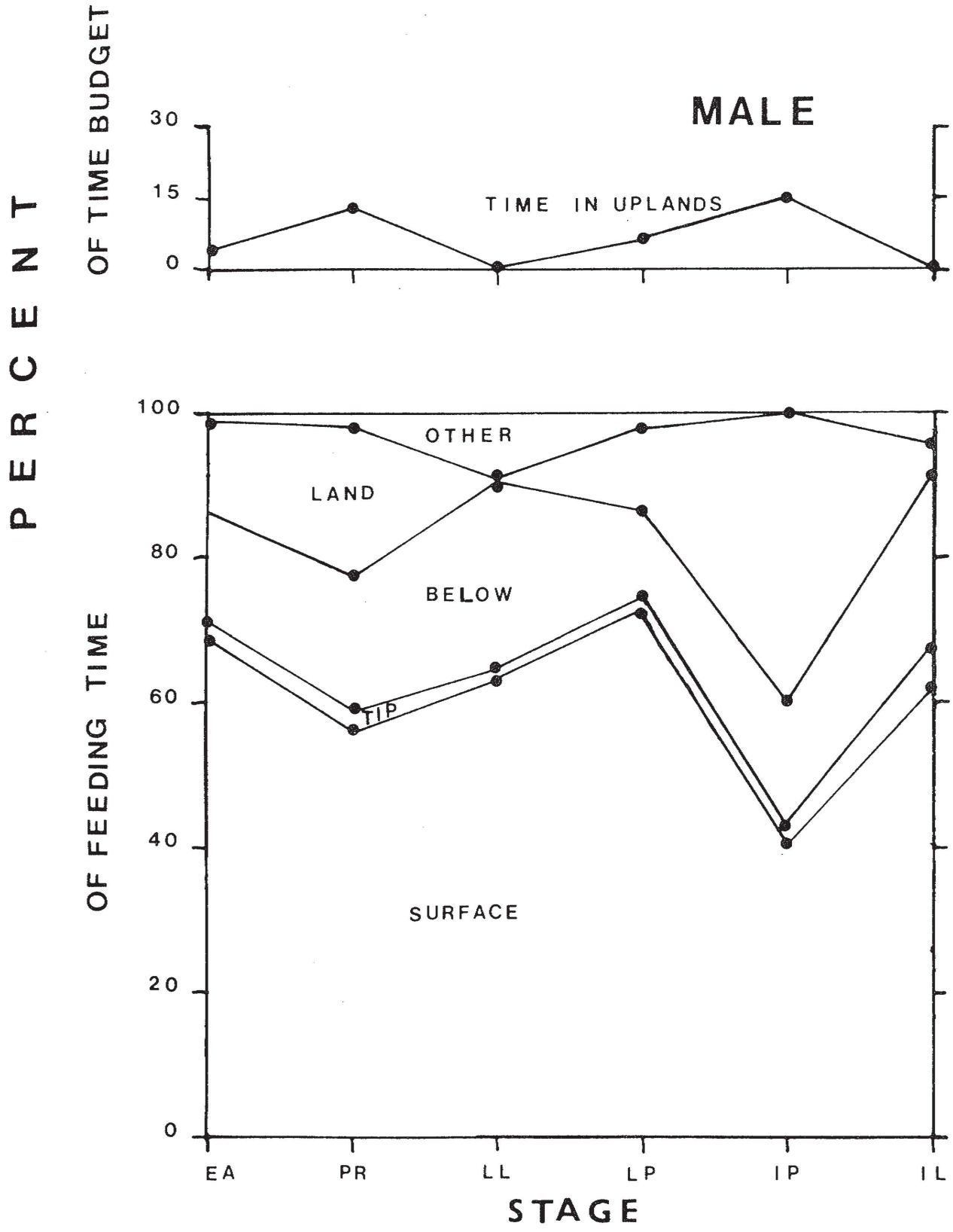

MALE
PERCENT
OF TIME BUDGET
30
15
0
TIME IN UPLANDS
OF FEEDING TIME
100
80
60
40
20
0
OTHER
LAND
BELOW
TIP
SURFACE
EA
PR
LL
LP
IP
IL
STAGE

Fig. 7. Upper graph depicts the percentage of the total time budget that females spent in agricultural fields. Lower graph depicts the percentage of total feeding time that female wigeons spent using different feeding methods (see text for definition of methods) (OTHER=feeding on emergents plus snatching insects) over the spring (EA=Early Arrival, PR=Prelaying, LA=Laying, IL=Incubation with male absent, IP=Incubation with male present, PO=Postreproductive, B1=Brood Rearing young 1-2 weeks old, B2=Brood Rearing young 3-4 weeks old, B3=Brood Rearing young 5-6 weeks old).

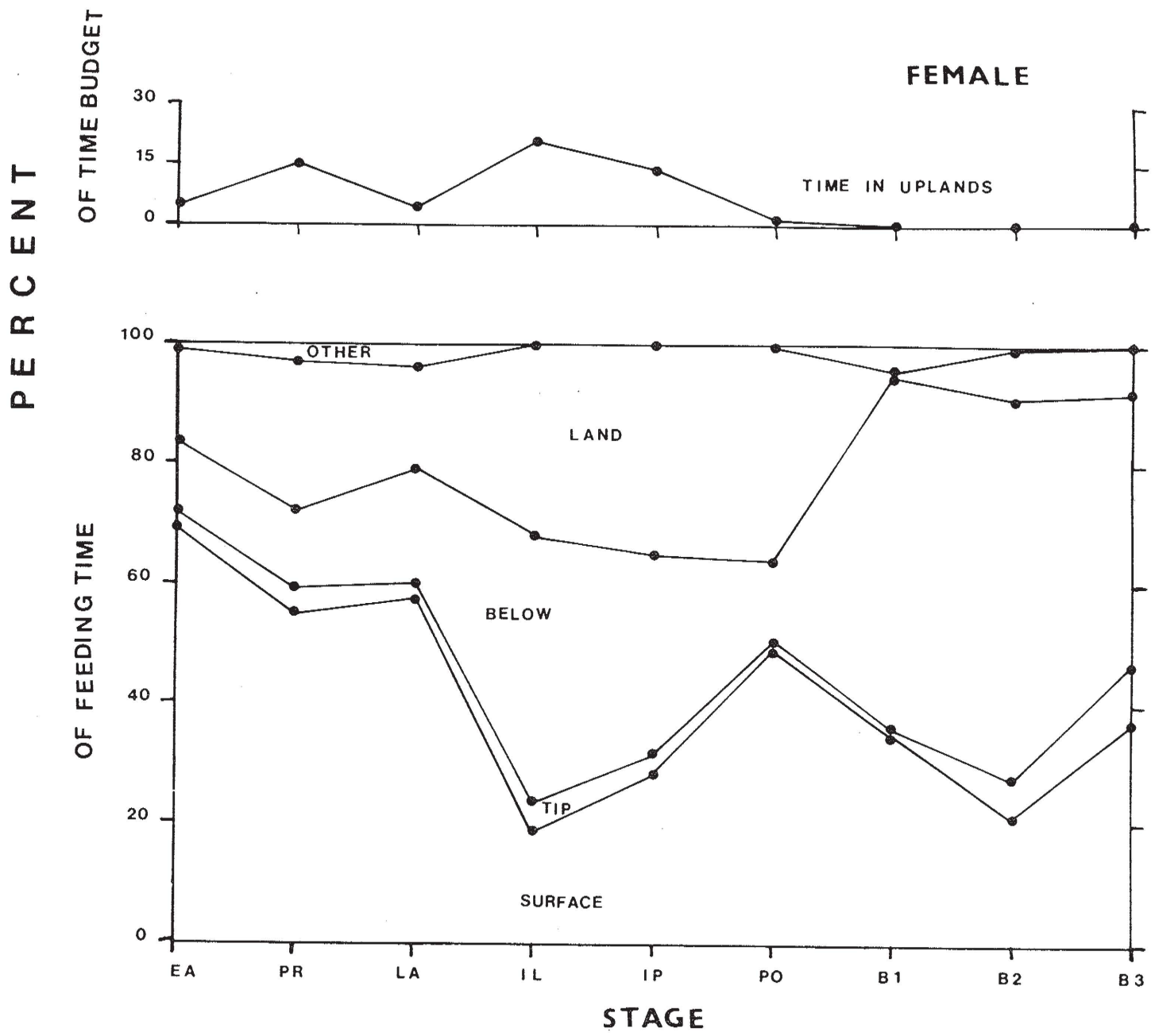

FEMALE
PERCENT
OF TIME BUDGET
30
15
0
TIME IN UPLANDS
100
80
60
40
20
0
OTHER
LAND
BELOW
TIP
SURFACE
OF FEEDING TIME
EA
PR
LA
IL
IP
PO
B1
B2
B3
STAGE

Table 7. The percent of time that male and female wigeons fed using various methods to obtain their food during the breeding season, 1976-78.

		Feeding methods (%)[2,3]											
		FB		FS		FL		TI		EM		HF	
Stage[1]	Sex	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
EA	Female	12.0	16.1	69.5	30.9	15.4	32.9	3.1	5.5	0.1	0.8		
PR		13.0	16.2	55.3	34.3	24.4	35.4	3.7	8.0	3.5	12.2	T	
LA		19.4	20.2[a]	58.3	33.3	17.3	29.0	1.9	3.9	3.0	12.5	0.2	0.5
IN		38.5	34.6	26.4	31.4[b]	34.8	38.3[c]	3.8	8.3				
PO		14.6	25.9	46.7	40.5	37.5	42.5	1.2	3.8				
B1		58.2	41.3	35.7	44.0	0.6	2.1	0.6	2.1	4.9	10.8		
B2		63.8	33.0	20.6	26.8	8.6	20.9	5.8	9.4	0.7	1.5		
B3		46.0	23.9	36.8	22.9	7.9	12.1	9.3	16.9				
IL		43.8	50.1	19.0	32.9	32.1	55.7	5.1	8.8				
IP		33.2	32.7	28.3	32.5	34.9	36.1	3.5	8.3				
EA	Male	15.6	18.6	68.4	32.4	13.5	33.2	2.2	3.8	0.3	1.2		
PR		20.8	27.2	55.9	35.3	18.7	32.8	3.1	7.0	1.5	5.8		
LA		12.6	19.0[a]	72.0	34.5	9.9	23.9	1.8	5.1	3.6	12.7	0.1	0.4
IN		21.0	27.2	58.5	39.0[b]	14.2	30.0[c]	3.5	6.3	2.7	14.4	T	

Table 7. (cont'd)

Stage[1]	Sex	Feeding methods (%)[2,3] FB $\bar{X}$	FB SD	FS $\bar{X}$	FS SD	FL $\bar{X}$	FL SD	TI $\bar{X}$	TI SD	EM $\bar{X}$	EM SD	HF $\bar{X}$	HF SD
LL		26.3	29.0	62.9	37.4			1.7	4.8	9.1	20.5		
LP		11.0	17.4	73.5	34.1	11.7	25.5	1.7	5.0	2.0	8.8	0.1	0.9
IL		23.8	28.5	63.5	36.2	4.4	12.5	4.4	7.0	3.8	17.2	T	
IP		19.2	31.5	40.6	43.0	38.6	44.7	1.6	3.6				

[1]Stages: EA=Early Arrival, PR=Prelaying, LA=Laying, IN=Incubation, IL=Incubation while mate absent, IP=Incubation while mate present, PO=Postreproductive (lost nest or brood), B1=Brood Rearing young 1-2 weeks old, B2=Brood Rearing young 3-4 weeks old, B3=Brood Rearing young 5-6 weeks old, LL=Laying while mate absent, LP=Laying while mate present. [2]FB=feeding below water surface, FS=feeding at water surface, FL=feeding while on land, TI=tip feeding, EM=feeding on emergent hydrophytes, HF=snatching insects. [3]Comparisons between sexes at same stage significantly different ($P<0.05$, analysis of variance) with same letter; comparisons within each sex between consecutive stages significantly different if joined by vertical bar. [4]Trace (<0.1%).

Table 8. Percent of daylight hours that male and female wigeons spent on various substrates at Moose Jaw, 1976-78.

		Time on substrates[2] (%)							
		Shore		Field		Water		Air	
Stage[1]	Sex	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
EA	Female	16.1	27.1	4.3	12.7	78.8	29.1	0.8	1.3
PR		24.5	29.0	14.9	24.9	59.7	31.2	1.0	2.5[a]
LA[3]		39.5	26.6	5.0	11.9	55.3	27.3[b]	0.2	0.4[c]
IN[3]		90.8	2.8[d]	1.8	2.5	7.2	3.4[e]	0.2	0.2[f]
PO		42.6	41.6	0.4	1.5	56.9	41.2	0.1	0.3
B1		22.3	20.6			75.4	23.0	0.1	0.3
B2		42.7	31.5			57.0	31.4	0.2	0.4
B3		49.7	28.1			50.1	27.8	0.2	0.4
IL[4]		17.2	16.0	21.1	36.6	59.8	39.5	1.9	1.1
IP[4]		26.4	24.4	13.1	16.8	58.9	26.6	1.9	1.6
EA	Male	12.2	25.3	4.4	12.8	82.2	27.1	1.1	2.6
PR		21.0	25.9	13.5	23.8	63.3	29.5	2.2	3.2[a]
LA		15.1	21.3	5.1	12.0	77.6	25.4[b]	2.3	3.7[c]
IN		22.5	30.2[d]	5.9	14.0	70.0	30.0[e]	1.6	2.2[f]
LL		3.6	7.9			90.0	9.9	6.5	3.8
LP		17.3	22.6	6.1	13.0	75.2	27.0	1.4	3.0
IL		26.9	32.3	1.2	4.1	70.5	31.3	1.4	2.0
IP		18.5	24.9	15.1	20.8	63.2	26.5	3.3	4.4

Table 8. (cont'd)

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[1]EA=Early Arrival, PR=Prelaying, LA=Laying, IN=Incubation, IL=Incubation while mate absent, IP=Incubation while mate present, PO=Postreproductive (lost nest or brood), B1=Brood Rearing young 1-2 weeks old, B2=Brood Rearing young 3-4 weeks old, B3=Brood Rearing young 5-6 weeks old, LL=Laying while mate absent, LP=Laying while mate present. [2]Comparisons between sexes at same stage significantly different ($P<0.05$, analysis of variance) with same letter; comparisons within each sex between consecutive stages significantly different if jointed by vertical bar. [3]Takes into account the time the female was at her nest. [4]Only the time females were on incubation recess.

occurred in feeding on land, particularly in fields. Total time that birds spent on the water declined at this time by almost 20% (Table 8). This was followed by a reversal during Laying. Paired males usually fed on land and spent time in fields during Laying and Incubation only when they were accompanied by their mate. When the female was at the nest, males spent 14.8% and 7.3% more time, respectively, on the water surface.

Female wigeons spent over 55% of their foraging time feeding at the surface from Early Arrival through Laying. This declined to less than 37% through Brood Rearing and 47% for Postreproductive females. For females after Laying, feeding below the surface was the most common method used. Brood Rearing females fed little on the shoreline and were never seen using agricultural fields. Tip feeding increased for the female as broods matured. Field-feeding was common from Early Arrival through Incubation even if the mate was absent.

There were some cyclic changes in feeding behavior over the day for both sexes (Tables 9, 10). Feeding was most common in early morning and late evening but the trend was significant only for females during Prelaying and Brood Rearing. Feeding continued after dark on the water until at least 0100 h. Feeding on land was most common, in all stages in which it occurred, during late evening. This pattern was significant for all stages except Prelaying males. For both sexes during Prelaying, feeding at the surface was most common in the early afternoon. A few other comparisons were significant but did not show consistent patterns (Tables 9, 10).

Table 9. Comparison of percent of feeding time that female wigeons used various feeding methods over the day during Early Arrival and Prelaying in the spring, 1976-77.

Feeding method[1]	Stage[2]	Percent of feeding time spent per time block[3,4]							
		I		II		III		IV	
		$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
FB	EA	16.0	18.1	22.7	20.3[a,b]	6.9	10.4[a]	5.8	5.4[b]
FS		45.2	36.3[c]	55.7	28.7	78.8	28.2[c,d]	41.5	33.2[d]
FL		28.0	40.8	17.2	27.6	10.0	25.3[e]	43.2	39.3[e]
TI		5.0	11.1	1.9	5.4	3.1	7.9	4.6	6.7
EM		5.8	20.2	2.6	8.2	0.8	3.1	4.8	10.3
HF								T	
TF		35.7	12.7[f]	30.2	14.1	22.0	11.6[f,g]	35.0	11.8[g]
FB	PR	11.5	13.7	16.1	26.7	14.7	12.0	5.8	8.2
FS		81.8	14.9	78.7	26.9	72.7	19.2	44.6	45.2
FL		6.5	11.2	0.1	0.3[h]	7.5	20.2	47.7	52.5[h]
TI		0.4	0.6	4.9	8.3	5.2	5.6	1.8	3.9
EM				1.5	0.5				
TF		40.8	30.5	38.0	16.1	41.2	11.5	39.9	7.6

[1]FB=feeding below water, FS=feeding at water surface, FL=feeding while on land, TI=tip feeding, EM=feeding on emergent hydrophytes, HF=snatching insects, TF=total feeding as percent of time budget. [2]EA=Early Arrival, PR=Prelaying. [3]T<0.1%, I=0500-0900h, II=0900-1300h, III=1300-1700h, IV=1700-2100h (CST). [4]Comparisons with same letter significantly different ($P<0.05$, analysis of variance).

Table 10. Comparison of percent of feeding time that male wigeons used various feeding methods over the day during Early Arrival and Prelaying in the spring, 1976-77.

Feeding method[1]	Stage[2]	Percent of feeding time spent per time block[3,4]							
		I		II		III		IV	
		$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
FB	EA	14.2	23.1	20.1	26.9	20.2	14.4	8.0	8.5
FS		85.8	23.1	74.7	26.9	70.6	18.1	42.5	45.6
FL			a		b	5.4	15.2[abc]	48.5	53.2[c]
TI				3.7	4.8	3.9	4.8	1.1	2.2
EM				1.0	2.2	T			
TF		38.8	27.1	36.8	13.0	40.6	12.7	41.9	9.6
FB	PR	30.2	29.9	21.8	19.3	14.0	26.6	17.4	30.7
FS		45.9	35.2	57.6	28.4	76.2	34.2[d]	44.2	35.9[d]
FL		16.6	34.6	17.1	30.7	7.2	18.0	33.8	40.4
TI		3.1	6.5	3.1	4.8	2.5	5.6	3.8	10.2
EM		4.1	10.4	0.9	3.9	0.2	0.8	0.8	2.2
TF		25.7	15.5	24.3	14.4	16.5	10.5	22.9	9.2

[1]FB=feeding below water, FS=feeding at water surface, FL=feeding while on land, TI=tip feeding, EM=feeding on emergent hydrophytes, TF=total feeding as percent of time budget. [2]EA=Early Arrival, PR=Prelaying. [3]T<0.1%, I=0500-0900h, II=0900-1300h, III=1300-1700h, IV=1700-2100h (CST). [4]Comparisons with same letter significantly different ($P<0.05$, analysis of variance).

DISCUSSION

The three species of wigeons have been characterized in the literature as vegetarians. Although little studied, the Chiloe Wigeon of South America is described as grazing preferentially on grass but also eating rush, water buttercup, and vegetation and seeds of water milfoil and bulrush (Phillips 1922-26). Owen and Williams (1976), and Owen and Thomas (1979) found that the Eurasian Wigeon in winter ate predominantly the leaves of fine grasses and aquatic vegetation. They also found birds flying regularly to agricultural fields to eat sprouting winter wheat, corn stubble and waste potato tubers. Palmer's (1976a) accounts indicate that some animal material is eaten, although vegetation predominates. A summer study by Danell and Sjoberg (1980) and winter work by von Kanel (1981) further documented the preference for vegetation by this species.

More information is available for the American Wigeon at specific stages of its annual cycle. Sugden (in Palmer 1976a) observed that wigeon spent much time ashore grazing and that it was the most terrestrial of Anas species. Studies by Mabbott (1920), Munro (1949), McGilvrey (1966), Stewart (1962) and Burgess (1970), based on gizzard contents, indicated that the wigeon in the fall and winter was almost totally vegetarian. In winter in British Columbia, Munro (1949) found the wigeon feeding on aquatic vegetation to a greater extent than other dabbling ducks. Birds commonly grazed on grass and clover in pastures and city parks and ate Brussels Sprouts in cultivated fields. Hirst and Easthope (1981) analyzed the upper digestive tracts of 17 wigeons

wintering in the Fraser River Delta of British Columbia and found only one that had ingested invertebrates. They found wigeons preferred to graze in pastures on green leafy vegetation or uprooted plants. Bellrose (1976) noted that in California, the wigeon does considerable damage to crops of lettuce, alfalfa, clover and barley.

Wigeons commonly associate with diving waterbirds in spring and summer but more frequently in fall and winter (Munro 1949, Bent 1962, Hellyer 1977, Bailey and Batt 1974, Knapton and Knudsen 1978, Bayer 1980). In these associations they pick up dropped or uprooted vegetation opportunistically or actively pirate food from other birds as they surface after dives. I also observed a small number of adult and juvenile wigeons of both sexes pirating sea lettuce regularly from American Coots at the Maplewood study area (Wishart unpubl. data).

This method of feeding may be advantageous to wigeons where certain nutritious foods are inaccessible (Knapton and Knudsen 1978). It may be more important for northern populations of wintering birds where freezing temperatures periodically may restrict food supplies. Although its occurrence is uncommon, it demonstrates the opportunistic and aggressive nature of foraging wigeons (see also Chapter 6).

There is little information dealing with the diets of adult wigeons on breeding and molting habitats. Bartonek (1972) provided some evidence that animal foods are taken during the spring and summer but his sample sizes were small. Sugden (1973) found that animal foods dominated the diet of wigeon ducklings (82% aquatic insects) until three

weeks of age. Thereafter, they shifted to plant material (90%). Young birds did not strain for small items and crustaceans were consumed in only trace amounts. Flies, beetles and bugs predominated but snails occurred in just 3 of 129 birds (Sugden 1973).

My study, while supporting earlier evidence that vegetation is important in the diet of the wigeon during the autumn and winter, has added new information for other times of the year. Wigeons spent a considerable portion of their time in spring, feeding on cultivated grain in agricultural fields. In the fall I also observed small numbers of them accompanying Mallard and Pintail flocks on flights to stubble grain fields. Their ability to learn to exploit this rich artificial food source is further evidence of the flexibility of the wigeon's feeding strategy (Bossenmaier and Marshall 1958, Bellrose 1976).

I was unable to measure food selectivity of wigeons feeding in fields and so birds collected in uplands were not included in the calculation of electivity indices. In addition, the procedures used to measure food availability probably did not sample all foods and feeding zones used by the wigeon on an equal basis (Sugden 1973). The presence of a food does not necessarily mean it is available to a forager because this is influenced by its distribution and conspicuousness (Dirschl 1969). However, despite these limitations, comparisons made between the diets of males and females at the same stage and over the year, do provide an index of selectivity for broad categories of food types (Serie and Swanson 1976).

Contrary to Keith's (1961) findings, plant seeds were important to the wigeon throughout the year. During Early Arrival in spring, before invertebrate food was abundant and before the new vegetative growth, seeds were taken most heavily. At this time, benthic seeds were at their maximum but with germination, decomposition and consumption they would have declined thereafter (see also Perret 1962, Dirschl 1969, Baldassarre 1979). Casual observations indicated that seed production peaked in early July and Incubating, Brood Rearing and Postreproductive females exploited this food.

Crustaceans and snails were abundant in the environment, but did not constitute consistently a significant proportion of the wigeon's diet. In some instances water scuds (amphipoda) were so numerous that they adhered thickly to the plumage of collected birds. Yet, as for Mallard (Perret 1962), Gadwall (Serie and Swanson 1976), Northern Pintail (Krapu 1974b) and Northern Shoveler (Swanson et al. 1979), they did not make up a significant part of the wigeon diet. Only Blue-winged Teal (Swanson et al. 1979) and Lesser Scaup (Bartonek and Hickey 1969) consume scuds heavily.

As has been shown for other species of waterfowl, male and female wigeons increased their use of animal food from Early Arrival to a peak at Laying followed by a decline to almost zero by the Molt. Although invertebrates were abundant during this period, they (particularly aquatic insects) were taken in proportions greater than their measured abundance in the environment. Females consumed almost twice the proportion of invertebrates as males, which indicated their stronger selection for this type of food.

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Wigeons fed on invertebrates at a lower level than the 70-90% rate characteristic of other dabbling ducks during Laying (Swanson et al. 1979). However, comparisons are difficult because, except for recent work done by Reinecke and Owen (1980), most other workers have presented food habits data as wet volumes. As Reinecke and Owen (1980) pointed out, this method is biased because foods do not contain equal amounts of water. Thus, the dry weight method I used probably is the more accurate means of representing food habits data.

Many authors have noted that waterfowl switch to a diet dominated by animal foods during reproduction. They have discussed this switch in terms of the quantity of protein it provides for egg production relative to that obtained from vegetation (Swanson et al. 1974a, 1979, Krapu 1974a,b, 1979, 1981, Serie and Swanson 1976, Drobney and Fredrickson 1979, Reinecke and Owen 1980). However, if foods are considered on a dry weight basis, this conclusion is not accurate. Insects do indeed provide the greatest weight of crude protein, but plant seeds, due to their low water content, are second and are followed by crustaceans, snails in the shell and vegetation, respectively (Table 11). Thus, seeds potentially are a high quality food that if abundant (Baldassarre 1980), can be important in the diet of some species of egg-laying waterfowl (Keith 1961, Swanson et al. 1979).

Krapu and Swanson (1975) and Sugden (1973) noted that protein quality is as important as its quantity. If any essential amino acid is lacking in the diet, then the individual must ingest more food, catabolize body reserves or reduce its egg production (Scott 1973).

Table 11. The relative values of dry matter, protein and energy of various waterfowl foods.[1]

Food	Type	Wet (g)	Dry (%)	Dry (g)	Protein[2] (%)	Protein[2] (g)	Energy[2] (kcal/g)	Total energy (kcal)
White-top Grass	seeds	100	90	90	8.8	7.92	4.43	398.7
Slough grass	seeds	100	90	90	8.9	8.01	4.73	425.7
Duckweed	foliage	100	23	23	15.2	3.50	2.47	56.8
Pondweed	foliage	100	14	14	13.3	1.86	3.74	52.4
Water boatmen	adults	100	20	20	71.5	14.30	5.31	106.2
Midges	larvae	100	16	16	56.0	8.96	4.30	68.8
Water fleas	instars	100	13	13	31.8	4.13	2.71	35.2
Scuds	instars	100	15	15	47.0	7.05	4.02	60.3
Snails	in shell	100	17	17	16.9	2.87	0.92	15.6

[1]Data from Sugden (1973).

[2]On a dry weight basis.

In general, animal foods provide the richest assortment of most easily mobilized amino acids (Krapu and Swanson 1975). The high fibre content and resistant cellulose coat on seeds and vegetation makes the protein they hold, potentially less available. These characteristics may also increase the time required for plant foods to be digested (Swanson and Bartonek 1972) and introduce a physiological constraint on the time available to a bird for feeding. This could be critical during egg-laying (Afton 1979) when there is a need for rapid mobilization of nutrients (Krapu 1979).

In addition, waterfowl eggs hold high levels of lipid (Ricklefs 1977) and females rely on their body energy (lipid) reserves to see them through incubation (Siegfried et al. 1976, Korschgen 1977, see also Chapter 6; but see Drobney 1980). Energy is also required to allow Prelaying and Laying females to move between feeding sites. Thus, energy as well as protein is needed during reproduction, and plant foods are the richest sources of energy (carbohydrate) (Table 11). Thus, a balance in needs must be met. Because no waterfowl foods meet all of the requirements of breeding birds (Krapu and Swanson 1975) a mixed diet is necessary. Wigeon, and possibly other species of waterfowl are capable of adapting grit intake and digestive organs to changes in diet (Chapter 2). This permits them to increase their rate of digestion and the efficiency of nutrient absorption.

Krapu (1979) and Krapu and Swanson (1975) found that female dabbling ducks during egg-laying operate on a diet of about 28% protein. Krapu (1979) found that Mallards fed on a wheat-only diet providing 14%

protein were less productive. Holm and Scott (1954) believed that 18% protein was sufficient for domestic waterfowl. North (1972) and Schaible (1976) observed that chickens must ingest 18 g of protein/day to maintain egg production and Drobney (1980) estimated that female Wood Ducks required 5.1 g of protein/day for gonadal recrudescence and egg production. However, Drobney did not consider the additional requirements of activity and maintenance. Schaible (1976) estimated that chickens need at least 3.0 g of protein/day for body maintenance. Therefore, active wild ducks likely would require considerably more.

On an ash-free dry basis the estimated proportions of ME and protein provided by the diet of laying wigeon females were more than adequate to meet the needs of production (Scott 1973). However, protein levels were about 5% lower than the 28% of total diet found for other species of Anas (Krapu 1979, Reinecke and Owen 1980). After the breeding season, use of vegetation increased to a point where adequate amounts of protein for egg production were no longer consumed. Diets of males held 3-7% less protein than those of females during the breeding season, but were similar at other times. This supports the contention that breeding females needed additional protein.

Krapu (1979) showed also that ducks fed a diet low in calcium were unable to produce sufficient egg shell, and egg production in general declined. North (1972) determined that laying chickens required 2.8% Ca in their diet and Krapu (1979) estimated that 2.0-3.2% was needed by ducks. Snails and crustaceans have a high Ca content (Driver et al. 1974, Krapu and Swanson 1975) and this may be one reason for their

(d) enter into an agreement with the owner of any land for the carrying out of any works considered necessary for the implementation and operation of a scheme;
(e) issue, subject to provisions of The Forest Act, permits for cutting of forest from protected areas;
(f) issue, subject to provisions of The Water Rights Act, permits to alter surface water courses;
(g) recommend the acquisition by the Crown, of any real or personal property necessary for a scheme;
(h) sell, subject to the provisions of The Water Rights Act, water from reservoirs constructed or operated by the board;
(i) require the municipality to furnish to the board information pertinent to a scheme.

These powers of a district board may be directly linked with the authority of the Lieutenant Governor in Council proclaimed in section 24 of the Act:

The Lieutenant Governor in Council may

(a) authorize a board to abandon in part or in whole any works or operations of a district; or
(b) authorize or require a board to repair, maintain or operate any additional works of a district; or
(c) abolish or amend the boundaries of any district; or
(d) consolidate two or more districts; or
(e) make such orders as may be necessary to give effect to any abolition or amendment.

In summary then, the administrative hierarchy of conservation districts in descending order is: (1) the Lieutenant Governor in Council (through the Minister and the Conservation Districts Commission); (2) the Conservation Districts Commission; (3) the Conservation District Board; and (4) the Sub-district Committees.

(e) finances

The total cost of operating a conservation district is shared between the board and the Provincial Government.

In conclusion, although the wigeon is an opportunistic omnivore and has a diverse diet, it depends on aquatic and upland vegetation to a greater extent than its congeners. As in other species, it shifted to animal foods during the breeding season which helped females meet the nutritional demands of egg-laying, but this shift was relatively less pronounced than in other Anas. Outside of the breeding season, and to a degree during it, there is an advantage for waterfowl to be efficient herbivores. Vegetation and plant fruits are energy-rich and abundant, making them important for waterfowl survival and production. Geese, similar to wigeons, are unable to digest cellulose (Mattocks 1971) but can subsist almost entirely on plant foods (Ogilvie 1978, see Chapter 2).

CHAPTER 2

THE MORPHOLOGICAL AND PHYSIOLOGICAL ADAPTATIONS OF THE AMERICAN WIGEON TO ITS DIET

INTRODUCTION

Eadie et al. (1979), White and James (1978), Nudds (1980) and Nudds et al. (1981) found that individuals feeding in multi-species flocks partitioned food resources by foraging selectively in different habitats. Others have found that variability in bill morphology is another means by which food niche overlap is reduced in birds (Schoener 1965, Bedard 1969, Burton 1974). Schoener (1965) did not consider anatids in his analyses because he believed that their bill dimensions were not correlated with variation in prey size. However, Goodman and Fisher (1962) and Nudds et al. (1981) demonstrated that such a system probably operates in this group.

The American Wigeon breeds and overwinters sympatrically with up to eight other species of Anas. In Chapter 1 I indicated that among these species, the wigeon is most vegetarian in its diet. In this chapter I examine the morphological and physiological adaptations which have evolved in wigeon to allow it to fill this niche.

Also in Chapter 1 I showed that wigeons shifted their diet cyclically during the year in response to changing nutrient requirements. Here I examine the hypothesis that birds are able to synchronize changes in their digestive organ and gizzard grit characteristics with these dietary shifts, thereby maintaining digestive efficiency.

METHODS

Bill Morphology

Six bill measurements were made on 70 museum specimens of 13 species of Anseriformes. These were: 1) length from commissural point to tip,

2) width at commissural point, 3) width at base of the nail, 4) proportion of the bill (measured from the base) up to the widest point, 5) maximum nail width, and 6) height at commissural point. Additional measurements made on the duck specimens were: 1) total number of lamellae on both sides of the upper mandibular tomia, and 2) length of the upper tomia that holds lamellae. Bill length and lamellae/cm were standardized by dividing by mean wing length for each sex-age group as provided in Bellrose (1976). Body length (Wishart 1979) was not used in this structural index because neck length in Anseriformes may vary differentially by species relative to foraging strategy, rather than only structural size. Standardized variables were: 1) LENGRAT (bill length/species wing length, 2) WIDSHP (bill width at commissure/bill width at base of nail), 3) NAILAREA (bill width at base of nail/nail width), 4) HTLENG (bill height at commissure/bill length). These variables were log transformed and stepwise discriminant analyses (Dixon and Brown 1977) were used to identify combinations of variables that were useful in differentiating among groups.

Grit and Body Characteristics

American Wigeons were collected over their annual cycle at study areas in British Columbia, Saskatchewan and Manitoba (Chapter 1). Food habits data were analyzed (Chapter 1) and the carcasses were frozen for later analysis.

Grit was removed by mixing gizzard contents in water and decanting the organic material. Particle sizes of grit (<0.25->5.00 mm) were separated by washing through a series of eight standard screens. For

each bird, the grit in each size category was dried in an oven at 105 C for 24 h and weighed. The gross mineral content of grit from each study area was estimated qualitatively under a miscroscope by personnel of the University of Manitoba Geology Department (P. and I. Cerny, pers. comm.).

In the laboratory, total body and wing lengths were measured on thawed carcasses. Body length plus wing length (mm) was used in computing each bird's structural index (Wishart 1979). Carcasses were then dissected and the digestive organs were measured. Lengths of unstretched large and small intestines and ceca were measured with a ruler. Wet weights were taken of the large intestine, ceca, pancreas, left kidney, liver and gizzard after accompanying lipid depots and digesta had been removed. Dry weight (g) was measured for the gizzard after it had been chopped and dried in an oven at 105 C for 24 h.

Organ and grit measurements were log transformed and compared for each sex by stage of the annual cycle (Chapter 1) using analysis of covariance. The structural index was used as a covariate to correct for size differences among individuals. Stepwise multiple regression was used to test if changes in grit and digestive organ characteristics were correlated with changes in diet over the year.

RESULTS

Bill Morphology

In the first discriminant analysis, using species as groups, LENGRAT and WIDSHP were the only two useful discriminating variables (Table 12).

Table 12. Mean (± SD) values of bill structure variables measured for waterfowl species and groups used in discriminant analyses.

Species	Group[1]	N	WIDSHP[2]		NAILAREA[2]		HTLENG[2]		LENGRAT[2]	
			$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
Lesser Snow Goose	A	7	1.67	0.08	1.25	0.08	0.50	0.02	0.12	0.01
Ross' Goose	A	4	1.63	0.11	1.22	0.05	0.51	0.03	0.10	0.01
White-fronted Goose	A	3	1.60	0.12	1.22	0.05	0.44	0.04	0.12	0.01
Lesser Canada Goose	A	3	1.39	0.07	1.43	0.15	0.44	0.02	0.12	0.01
Mean/Total	A	17	1.60	0.13	1.27	0.11	0.48	0.04	0.12	0.01
American Wigeon	B	8	1.33	0.19	2.28	0.33	0.38	0.02	0.15	0.01
Gadwall	C	3	1.22	0.08	2.40	0.17	0.32	0.01	0.18	0.01
Blue-winged teal	D	9	0.99	0.08	2.70	0.30	0.33	0.03	0.24	0.01
Green-winged teal	D	5	1.01	0.08	3.47	0.35	0.31	0.03	0.23	0.01
Cinnamon Teal	D	4	0.97	0.06	3.28	0.28	0.31	0.02	0.24	0.01
Mallard	D	5	0.99	0.03	2.64	0.22	0.31	0.01	0.22	0.01
American Black Duck	D	4	0.95	0.03	4.26	3.23	0.30	0.04	0.22	0.01
Northern Pintail	D	7	0.92	0.05	3.02	0.47	0.31	0.01	0.21	0.01
Mean/Total	D	34	0.97	0.07	3.14	1.15	0.31	0.03	0.23	0.02
Northern Shoveler	E	8	0.61	0.04	4.41	0.60	0.24	0.02	0.28	0.01

[1]A=Geese, B=Wigeon, C=Gadwall, D=Other Dabblers, E=Shoveler. [2]Variable names described in text.

Using the jackknife method of reclassification of cases (Dixon and Brown 1977, Lachenbruch and Mickey 1968) only 56.5% were assigned correctly to species. All errors occurred among the 4 species of geese (8 wrong) and among 6 species of Anas (22 wrong). Ordination using the first two cannonical variables illustrated the degree of overlap (Fig. 8). Groups that were distinct, without errors of classification, were Wigeon, Shoveler and Gadwall.

Based on this, a second discriminant analysis was performed using Geese, Wigeon, Gadwall, Shoveler and Other Dabblers as groups. LENGRAT and WIDSHP were again selected as useful discriminators as well as HTLENG (Table 13). Ninety-seven percent of the cases were correctly assigned. The only cases in error were two of three Canada Geese which were classified as Wigeon. Ordination using the first two cannonical variables showed distinct separation (Fig. 9). Geese and Shovelers were at the extremes. Wigeon were closely allied with Geese but separated from Shovelers by Gadwall and Other Dabblers.

Wigeon had a mean spacing between adjacent lamellae of 1.07 mm, similar to Pintail (Table 14). Within the ducks, Mallard and Northern Shoveler were at extremes. Gadwall were similar to Blue-winged Teal and along with Green-winged Teal, had intermediate spacings. When the number of lamellae/cm was standardized by wing length, wigeon were still similar to Pintail but significantly differed from all other species (Table 14).

Grit Characteristics

Grit in winter consisted primarily of quartz and rock fragments of basalt, schist and quartzite. Other less common minerals (<1% by

Fig. 8. Discriminant function ordination based on the bill morphology of Anseriforme species. Points indicate individual birds. Lines encompass individuals of each species.

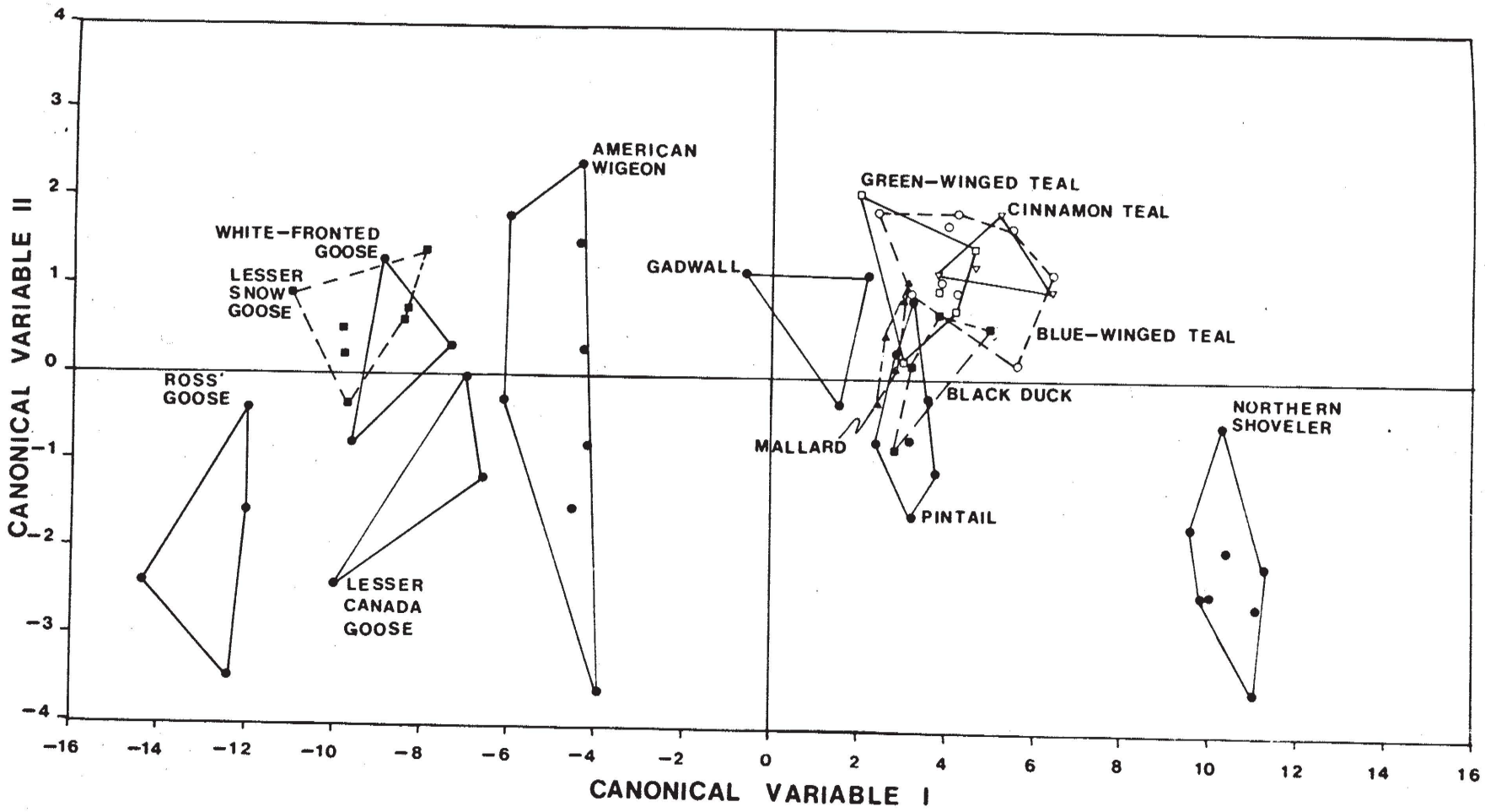

AMERICAN WIGEON
GREEN–WINGED TEAL
CINNAMON TEAL
WHITE–FRONTED GOOSE
LESSER SNOW GOOSE
GADWALL
BLUE–WINGED TEAL
ROSS' GOOSE
BLACK DUCK
NORTHERN SHOVELER
MALLARD
PINTAIL
LESSER CANADA GOOSE
CANONICAL VARIABLE II
CANONICAL VARIABLE I
4
3
2
1
0
−1
−2
−3
−4
−16
−14
−12
−10
−8
−6
−4
−2
0
2
4
6
8
10
12
14
16

Table 13. Discriminant function coefficients from the analysis of bill structure for waterfowl species and groups. The absolute value of each variable coefficient represents its relative contribution to the discriminant function.

Variable[1]	Species	Groups
LENGRAT	35.5	19.7
WIDSHP	-14.9	-16.1
HTLENG		- 5.5

[1]Variable names described in text.

Fig. 9. Discriminant function ordination based on the bill morphology of groups within the Anseriformes. Groups were selected based on overlap depicted in Fig. 8. Points indicate individual birds and lines encompass individuals of each group.

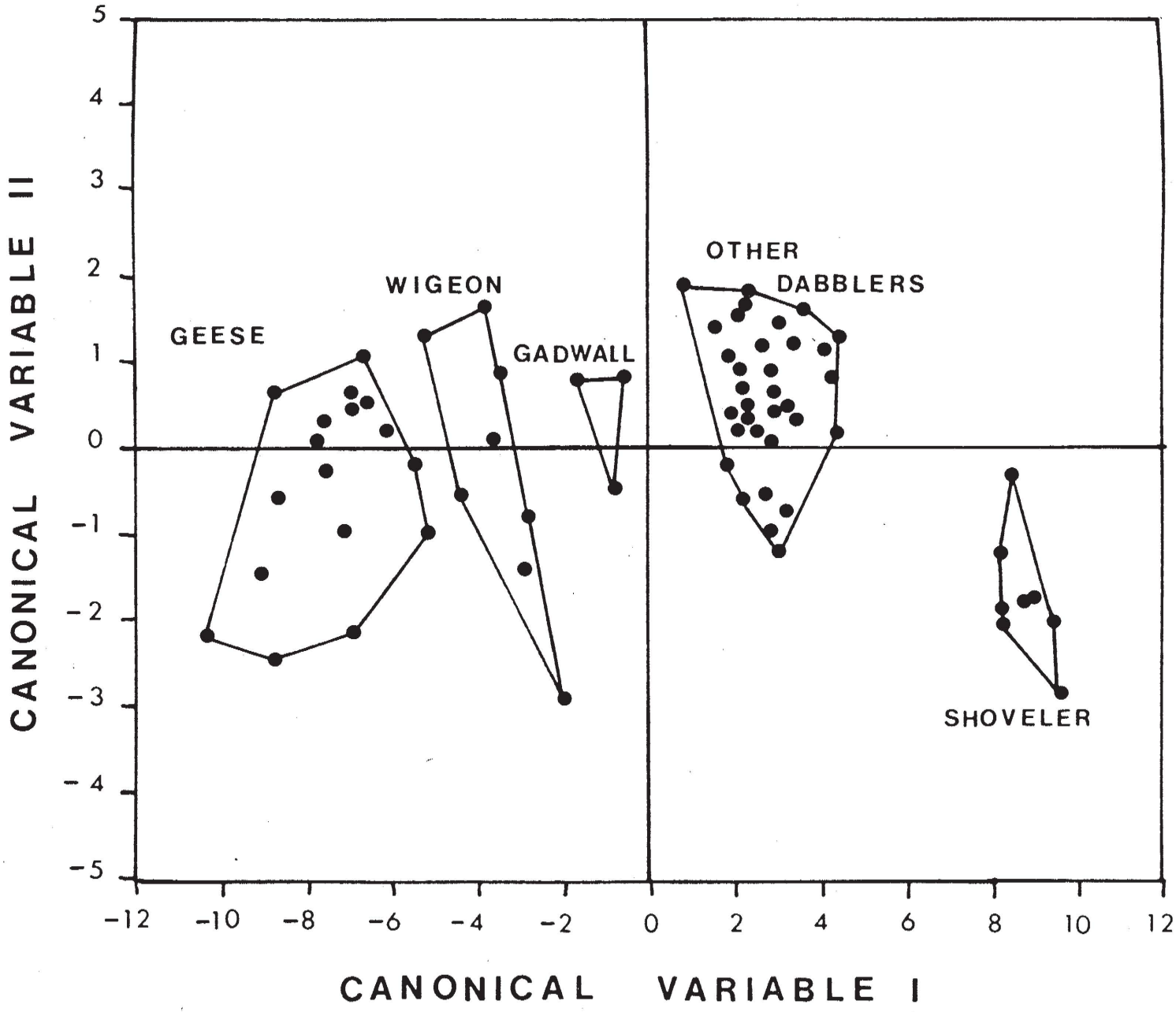

CANONICAL VARIABLE II
CANONICAL VARIABLE I
GEESE
WIGEON
GADWALL
OTHER
DABBLERS
SHOVELER
5
4
3
2
1
0
-1
-2
-3
-4
-5
-12
-10
-8
-6
-4
-2
0
2
4
6
8
10
12

Table 14. The mean space (mm) between successive lamellae, the number of lamellae per cm of bill tomium and the standardized number of lamellae for seven species of Anas.

Species	N[1]	Spacing $\bar{X}$	Spacing S.D.	Number[2] $\bar{X}$	Number[2] S.D.	Standardized[3] $\bar{X}$	Standardized[3] S.D.	Sig.[4]
American Wigeon	5	1.07	0.04	9.36	0.35	0.38	0.03	a
Mallard	3	1.25	0.14	8.29	0.54	0.31	0.02	c
Northern Pintail	3	1.07	0.03	9.39	0.28	0.36	0.01	a
Gadwall	3	0.87	0.06	11.59	0.78	0.45	0.03	b,c, d,e
Blue-winged Teal	6	0.87	0.06	11.22	1.07	0.61	0.05	b
Green-winged Teal	3	0.74	0.04	13.64	0.63	0.75	0.02	d
Northern Shoveler	4	0.47	0.07	21.73	3.17	0.91	0.15	e

[1]Number of specimens of either sex.

[2]Number of lamellae per cm of bill.

[3]Number of lamellae per cm of bill/mean wing length (cm).

[4]Species without the same letter have standardized values significantly different ($P<0.05$, Mann-Whitney U test).

volume) included magnetite, muscovite and hematite. On the breeding and molting grounds, quartz comprised over 80% of grit fragments. Other less common minerals (1-4%) at this time were feldspar, schist, jasper, hematite, hornblende and garnet. By treating with dilute HCl, limestone fragments were found to comprise 1-2% of this grit but no limestone was found in winter grit.

Only two gizzards contained grit fragments larger than 5 mm in diameter (9 x 5 mm and 7 x 8 mm). Most birds (61.2%) held no grit larger than 1 mm in diameter. Those having stones 2-3 mm (19.1% of birds), 3-4 mm (18.0%) and 4-5 mm (0.5%) usually had only 1-5 fragments of these sizes. Only two birds (1.1%) did not have any grit less than 0.25 mm.

In consecutive sequence (<0.25 mm, 0.25-0.50 mm, 0.50-1.00 mm, 1.00-2.00 mm, 2.00-3.00 mm, 3.00-4.00 mm, 4.00-5.00 mm, >5.00 mm) most grit sizes were positively correlated with one another (Table 15). Only at either ends of the continuum were there negative correlations.

Male and female wigeons had the same proportion of the various grit sizes during most stages of the annual cycle (Appendix 2, Figs. 10 and 11). Overall, males averaged more grit than females (4.8$\pm$1.7 g, N=92 vs 3.7$\pm$1.2 g, N=83) but when adjusted for sexual differences in structural size, this was not significant ($P>0.05$).

Grit composition changed for both sexes over the annual cycle (Figs. 10 and 11). Total grit weight was generally greatest during Molt and through Winter and was least during the Prelaying, Laying and Brood

Table 15. Correlation coefficients between grit, digestive organ and diet variables for wigeons collected over their annual cycle, 1976-78.

Variable[1]	G125	G25	G0.5	G1	G2	G3	G4	Gg4	Gtot	Sml1	Lrgw	Lrgl	Cecw	Cecl	Liv	Panc	Gizz	Kid	Seed	Veg	Plnt	Anim
G125																						
G25	.35																					
G0.5	-.37	.50																				
G1	.21	.23	.26																			
G2	-.38	-.65	-.21	.19																		
G3	-.20	-.58	-.46	-.01	.68																	
G4	-.07	-.07	-.12	-.23	-.12	.02																
Gg4	-.01	-.09	-.10	.19	.44	.52	-.05															
Gtot	.24	.87	.77	.51	-.45	-.56	-.17	-.05														
Sml1	.18	.67	.30	.14	-.63	-.54	.10	-.06	.53													
Lrgw	.18	.55	.28	-.13	-.58	-.61	-.07	-.17	.42	.57												
Lrgl	.30	.38	.17	-.03	-.64	-.48	.10	-.05	.32	.58	.82											
Cecw	.10	.78	.45	.08	-.63	-.61	.01	-.12	.64	.59	.70	.55										
Cecl	.37	.74	.29	.22	-.65	-.69	.02	0	.62	.71	.64	.60	.73									
Liv	-.20	.41	.49	.14	-.19	-.05	-.04	.32	.45	.51	.54	.51	.52	.26								
Panc	-.07	.74	.62	.19	-.44	-.53	-.07	.01	.71	.58	.72	.54	.88	.70	.60							
Gizz	.17	.84	.65	.31	-.46	-.63	-.08	-.03	.86	.56	.67	.44	.84	.66	.55	.85						
Kid	.05	.69	.58	.09	-.58	-.52	-.00	-.04	.67	.65	.74	.70	.82	.70	.62	.92	.76					
Seed	-.35	-.10	.16	.04	.44	.39	-.05	.45	-.02	.07	.27	.16	-.03	-.21	.60	.22	.09	.14				
Veg	-.39	.34	.34	-.22	-.23	-.31	.03	-.27	.20	.13	.17	-.11	.57	.22	-.03	.51	.36	.39	-.13			
Plnt	-.46	.41	.53	-.11	-.08	-.20	-.07	.03	.36	.15	.47	.13	.63	.21	.45	.72	.58	.54	.48	.75		
Anim	.46	-.41	-.53	.11	.08	.20	.07	-.03	-.36	-.15	-.47	-.13	-.63	-.21	-.45	-.72	-.58	-.54	-.48	-.75	-1.00	

Table 15. Cont'd

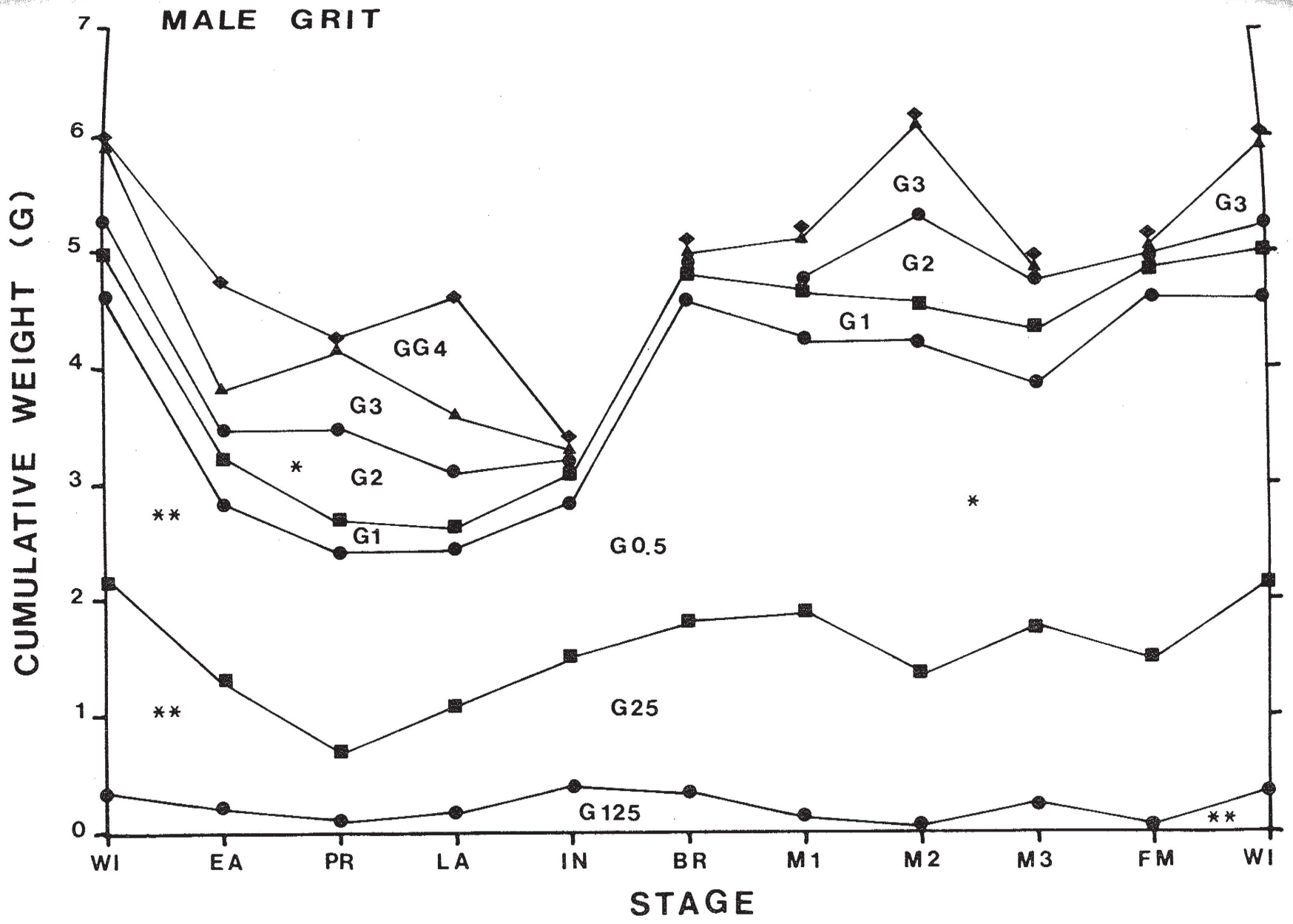
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[1]G125=aggregate mean weight of grit <0.25, G25=aggregate mean weight of grit 0.25-0.50 mm, G0.5=aggregate mean weight of grit 0.50-1.00 mm, G1=aggregate mean weight of grit 1.00-2.00 mm, G2=aggregate mean weight of grit 2.00-3.00 mm, G3=aggregate mean weight of grit 3.00-4.00 mm, G4=aggregate mean weight of grit 4.00-5.00 mm, Gg4= aggregate mean weight of grit >5.00 mm, Gtot=aggregate mean total weight of grit, Sml1=log of aggregate mean small intestine length, Lrgw=log of aggregate mean large intestine weight, Lrgl=log of aggregate mean intestine length, Cecw=log of aggregate mean ceca weight, Cecl=log of aggregate mean ceca length, Liv=log of aggregate mean liver weight, Panc=log of aggregate mean pancreas weight, Gizz=log of aggregate mean dry gizzard weight, Kid=log of aggregate mean left kidney weight, Seed=arcsin of aggregate mean percent of dry weight of plant fruits in diet, Veg=arcsin of aggregate mean percent of dry weight of vegetation in diet, Plnt=arcsin of aggregate mean percent of dry weight of total plant material in diet, Anim=arcsin of aggregate mean percent dry weight of total animal material in diet.

Fig. 10. Change in grit of various size classes for female wigeons over the annual cycle (1976-78). See Fig. 1. for definition of stage abbreviations. See Table 15 for definition of grit abbreviations. Sample sizes, means, 95% C.I. and statistical comparisons between sexes provided in Appendix 2. Stars (*) indicate significant differences between adjacent stages for a particular grit size (*=$\underline{P}$<0.05, **=$\underline{P}$<0.01, ***=$\underline{P}$<0.001, analysis of variance).

FEMALE GRIT
CUMULATIVE WEIGHT (G)
STAGE
WI
EA
PR
LA
IN
BR
PO
M1
M2
M3
FM
WI
G4
G2
G3
G1
G2
G0.5
G 25
G 125

Fig. 11. Change in grit of various sizes for male wigeons over their annual cycle (1976-78). See Fig. 1 for definition of stage abbreviations. See Table 15 for definition of grit abbreviations. Sample sizes, means, 95% C.I. and statistical comparisons between sexes provided in Appendix 2. Stars (*) indicate significant differences between adjacent stages for a particular grit size (*=$\underline{P}<0.05$, **=$\underline{P}<0.01$, ***=$\underline{P}<0.001$, analysis of variance).


MALE GRIT
CUMULATIVE WEIGHT (G)
STAGE
WI
EA
PR
LA
IN
BR
M1
M2
M3
FM
WI
0
1
2
3
4
5
6
7
GG4
G3
G2
G1
G0.5
G25
G125
*
**

Rearing stages. Smaller grit sizes (<0.50 mm) were at their greatest weights during Molt, Fall Migration and Winter. Large grit (>2 mm) increased in relative weight during Early Arrival and Prelaying.

Organ Sizes

Adult (>1 year old) male wigeons averaged structurally larger than females (structural index=759.6±21.3 mm, N=95 males *vs* 708.3±20.0, N=84 females) ($P<0.001$, *t*-test). Concommitant with this, males over most stages had heavier and longer organs than did females (Appendix 2, Figs. 12 and 13). However, when subjected to covariance analysis most differences were related only to structural size and were not significant ($P<0.05$). Most differences occurred during Prelaying and Laying when some female organs were larger ($P<0.05$) than those of males (Figs. 12 and 13). In general for both sexes, the kidneys, pancreas, gizzard and intestinal tract were largest during Molt, Fall and Winter (Figs. 12 and 13). Largest sizes usually occurred during Molt (gizzard, ceca length, large intestine and small intestine) with Winter sizes being smaller than those in Fall (gizzard, large intestine and ceca). Liver size followed a slightly different pattern. Its weights were extreme during spring and fall with a pattern similar to that of other organs at other stages.

Diet In Relation To Grit and Organ Characteristics

Changes in diet and nutrient intake for wigeon over the annual cycle have been described in Chapter 1. Birds fed most frequently on seeds during Early Arrival and on vegetation following Incubation and through the Winter. Invertebrates (primarily aquatic insects) were an important

Fig. 12. Change in wet weights and lengths of large and small intestines, and the ceca in male (solid line) and female (dashed line) wigeons over their annual cycle (1976-78). See Fig. 1 for definition of stage abbreviations. Sample sizes, means, 95% C.I. and statistical comparisons between sexes provided in Appendix 2. Stars (*) indicate significant differences between adjacent stages for a particular organ (*=$P<0.05$, **=$P<0.01$, ***=$P<0.001$, analysis of covariance).

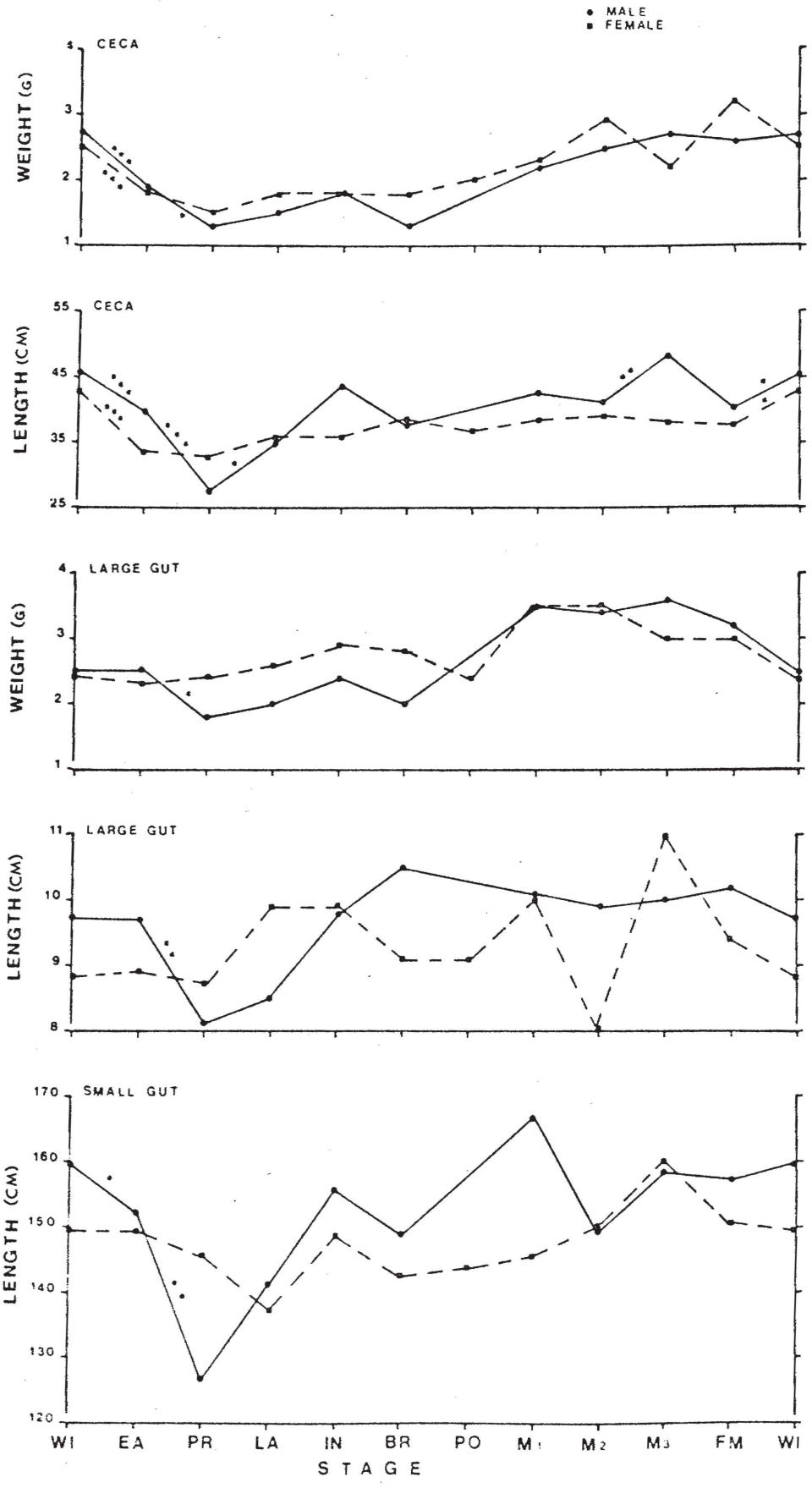
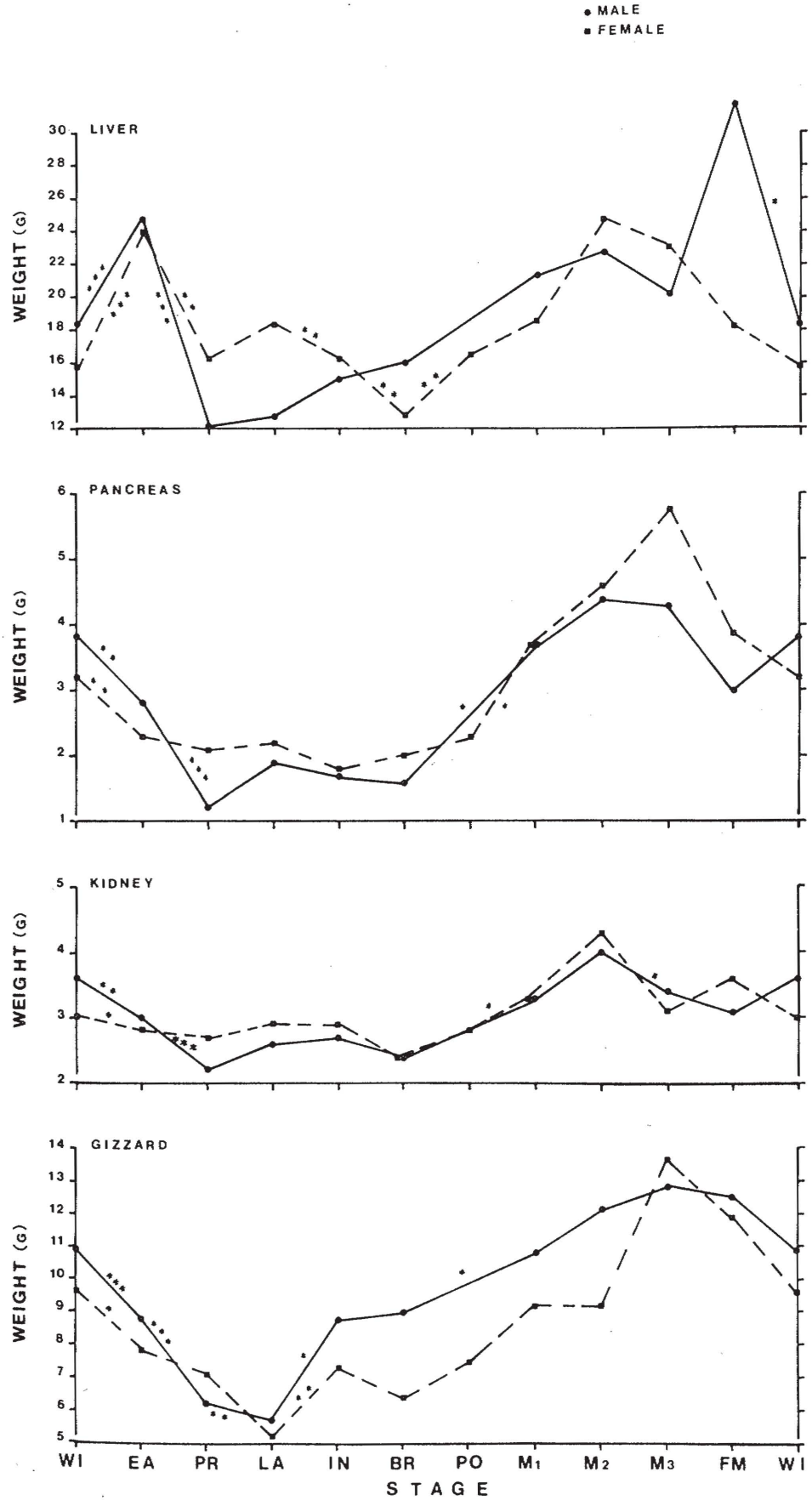

MALE
FEMALE
CECA
WEIGHT (G)
4
3
2
1
CECA
LENGTH (CM)
55
45
35
25
LARGE GUT
WEIGHT (G)
4
3
2
1
LARGE GUT
LENGTH (CM)
11
10
9
8
SMALL GUT
LENGTH (CM)
170
160
150
140
130
120
WI
EA
PR
LA
IN
BR
PO
M1
M2
M3
FM
WI
STAGE

Fig. 13. Change in wet weights of liver, pancreas and left kidney, and dry weight of gizzard for male (solid line) and female (dashed line) wigeons over their annual cycle (1976-78). See Fig. 1 for definition of stage abbreviations. Sample sizes, means, 95% C.I. and statistical comparisons between sexes provided in Appendix 2. Stars (*) indicate significant differences between adjacent stages for a particular organ (*=$\underline{P}<0.05$, **=$\underline{P}<0.01$, ***=$\underline{P}<0.001$, analysis of covariance).


• MALE
▪ FEMALE
LIVER
PANCREAS
KIDNEY
GIZZARD
WEIGHT (G)
WI EA PR LA IN BR PO M1 M2 M3 FM WI
STAGE

food from Prelaying through Incubation. Animal foods made up twice the proportion in female diets as in those of males (see Chapter 1).

A correlation matrix of diet, digestive organ and grit variables indicated that many were highly correlated (Table 15). After removing one variable of an intercorrelated pair (those with $R^2>0.80$), multiple regression analyses were used to see if I could explain variation in diet makeup. Using 3-5 grit and organ variables 67-87% of this variation was accounted for (Table 16).

The importance of plant seeds in the diet was directly proportional to weights of large grit (>2 mm in size). Other important variables were the wet weight of the large intestine, weight of the liver and of grit 0.50-1.00 mm in size. The importance of vegetation in the diet was most directly related to the weight of the ceca, and indirectly to the length of the large intestine and weight of intermediate sized grit (0.25-1.00 mm). Large grit (>1mm) was negatively correlated, whereas organ sizes (ceca, pancreas, gizzard and kidney) were positively correlated with vegetation (Tables 15 and 16).

The proportion of animal foods in the diet was linked positively with small grit (<0.25 mm) and negatively with intermediate grit (0.25-1.00 mm) and total grit weight. Negative correlations also existed between animal foods and the sizes of all digestive organs, particularly weight of ceca, gizzard, pancreas and kidney (Tables 15 and 16).

Table 16. Regresssion of diet variables against grit and digestive organ variables for wigeons over their annual cycle.

Dependent variable[1]	R^2	Equation[2]
Seed	0.87	$\hat{Y}$=34.8Gg4+124.5Lrgw+248.5S2+431.4G3+9.5G0.5-56.2
Vegetation	0.67	$\hat{Y}$=151.2Cecw-253.7Larg1-23.9G125+269.4
Plant	0.83	$\hat{Y}$=274.8Panc-161.5Cec1-282.6Kid-48.0G1+383.9
Animal	0.83	$\hat{Y}$=161.8Cec1-274.6Panc+282.2Kid+48.2G1-294.3

[1]Arcsin of aggregate percent dry weight of each type of food in the diet. Note that Plant=Seed+Vegetation.

[2]Variables defined in Table 15. All equations significant ($P<0.001$).

DISCUSSION

Bill Morphology

Huxley (1942) and Lack (1944) suggested that differences in bill morphology among species reflect differences in their preferred foods. Hutchinson (1959), Schoener (1965) and others have found differences in bill characteristics in closely related sympatric species related to reduced food niche overlap among them. Goodman and Fisher (1962) linked waterfowl bill shape and structure with foods and foraging methods.

American Wigeons spent a considerable amount of their time grazing in upland habitats, particularly in winter and spring (Chapter 1). Although they ate some invertebrates, vegetation and seeds were the dominant foods (Chapter 1).

Goodman and Fisher (1962) identified bill characteristics that were correlated with the tendency of a species to feed, either by grazing or by straining (see Table 17). The characteristics I measured for wigeon and other species reflect these opposing capabilities. WIDSHP and HTLENG are directly related to increased strength that can be exerted at the tip of the bill, and thus to the ability to pluck vegetation. In contrast NAILAREA and LENGRAT are directly related to a greater commissural length and therefore, to a greater tendency to strain for food (see Goodman and Fisher 1962).

Table 17. Waterfowl bill morphology related to grazing or straining capability (adapted from Goodman and Fisher 1962).

Bill character	Strainers	Grazers
Length	Long: more surface area for straining.	Short: more power at tip, less surface area for straining.
Shape	Swollen tip: more surface area for straining	Tapered: greater force directed at bill tip.
Nail	Small: weaker at tip	Large: stronger at tip.
Lamellae	Many, hair- or blade-shaped	Fewer, thick and harder.

The tendency for the wigeon to feed more consistently on vegetation than other Anas species and its regular habit of grazing in uplands (Chapter 1) correlate with its bill structure. In all four bill variables the wigeon was at extremes with the shoveler, a straining specialist (Bellrose 1976), and most closely associated with the geese that also obtain most of their nutrition by grazing (Ogilvie 1978).

Wigeon rarely fed on small invertebrates, however, several ingested large numbers of seeds indicating that they were capable of straining small food items (Chapter 1). Lamellar spacings were small enough to allow wigeons to trap most species of macroscopic invertebrates I recorded on the study area (Chapter 1). I believe that the wigeon's short bill (i.e., reduced tomia length) and not lamellar spacings limit its ability to feed efficiently by filtering. Even the Green-winged Teal that is only 0.69 times the size of the wigeon (based on wing length) has a slightly longer culmen (38.1 vs 37.4 mm) (see Godfrey 1966). The Gadwall, nearest to the wigeon in body size has a bill that is 1.16 times longer, with 1.24 times more lamellae per cm (Table 14). In addition, the wigeon is the only Anas species observed that, like geese, has a bill that narrows from its base to the tip which enhances the closing strength at the tip. All other species have bills with swollen ends that increase their commissure length for added straining efficiency (Table 17). Therefore, it is likely that wigeon could not compete successfully with other dabblers if they exploited a limited food supply accessible only by straining.

Grit Characteristics

The grinding action of grit in the gizzard increases the surface area of food on which digestion can act and thus, increases its nutrient and energy conversion ratios (Smith 1960, Titus 1961, Oluyemi et al. 1978). Keith (1961) found that 90% of the grit ingested by breeding wigeons was less than 1 mm in diameter. This contrasted with all other waterfowl species he studied (except Gadwall) at the same location that had 47%-72% of their grit greater than 1 mm in size. My data for wigeon agree closely with Keith's.

The proportion of seeds in the wigeon's diet correlated with large grit. May and Braun (1973) also found that the size of grit increased for White-tailed Ptarmigan eating harder foods and decreased when softer foods were more commonly eaten. Larger stones may be more effective in scarifying hard material.

The proportion of invertebrate foods eaten by wigeons was positively correlated with very small grit (0.25 mm) and negatively with intermediate sizes, and with total weight of grit. Invertebrate foods are generally soft and require less mastication (Swanson et al. 1974b). Mathiasson (1972), Norris et al. (1975), Schaible (1976) and Trost (1981) found that total grit weight decreased with increased ingestion of softer foods. This pattern was most clearly illustrated in wigeon during Laying when females ate twice the proportion of invertebrate food as males and concomitantly held less grit, which was smaller than in males. Porkert (1972) found that grit was lost when birds fed on soft foods. This is adaptive in that carrying unnecessary weight is eliminated.

As the proportion of leafy vegetation in the wigeon diet increased, total grit weight and weight of intermediate sizes (0.25-1.00 mm) also increased. Both very small and very large grit sizes declined at this time. Vegetation has a cellulose coat but this is thinner than that surrounding seeds. Intermediate grit sizes likely scarify most efficiently this highly fibrous, bolus-forming type of food. Grit elimination rates are high when leafy vegetation is eaten (Porkert 1972) and therefore, more grit must be ingested then to ensure that the gizzard does not congest (Schaible 1976).

Positive correlation between most successive grit sizes indicated that wear by grinding (Vance 1971) was not the most important factor which explained the seasonal variation I found in grit characteristics. The ability of some species to select calcium during egg laying was found by Jones (1976), Kopischke (1966), Harper (1964), and Sadler (1961). Trost (1981) also has demonstrated experimentally that Mallards are capable of selecting grit based on stone size and mineral composition.

Digestive Organs

Since Leopold's (1953) analysis there have been many studies linking changes in the sizes of birds' digestive organs with changes in their diets. Several workers have dealt with waterfowl but none has done so over the annual cycle.

The wigeon's intestinal tract was largest in the summer through winter which corresponded to periods when vegetation predominated in its

diet (Chapter 1). The decline in size during spring probably was related to the increased consumption of seeds and the lower fibre content of diets then (Chapter 1). The size of the intestines has been related in many other studies to the proportion of vegetation, seeds or fibre ingested (Moss 1972, 1974, Miller 1975, 1976, Pendergast and Boag 1973, Paulus 1982).

The size of the wigeon's intestinal tract also seemed to be influenced by the amount of food ingested. Although males ate a greater proportion of vegetation than females during Prelaying and Laying, female tracts remained longer at these times. This corresponded to a period when females were spending 10.3-11.6% more time feeding than males (Chapter 6). When hyperphagia prior to fall migration coincided with a period when vegetation also was dominant in the diet, sizes of ceca and intestines for both sexes reached maxima. In winter, feeding rates probably declined but vegetation still comprised most of the diet. This was a stage when the tracts declined in size only slightly. Work on the Wood Duck (Drobney 1977), Lesser Snow Goose (Ankney 1977a) and Spruce Grouse (Fenna and Boag 1974) has also demonstrated a direct relationship between the rate of food intake and the size of the intestines.

Mattocks (1971) showed that waterfowl, unlike ruminating mammals, do not support microflorae that can digest cellulose. Thus, they are relatively inefficient herbivores. However, larger and longer intestines and ceca may decrease the loss of nutrients.

The function of the ceca is obscure. Sauer et al. (1979) found that cecectomized horses had lower food digestability. Gasaway et al. (1975, 1976) and Gasaway (1976a,b) demonstrated in ptarmigan that the ceca are involved in absorption of water, minerals and vitamins, and the digestion of carbohydrate and protein. Gasaway et al. (op. cit.), Miller (1976) and Thompson and Boag (1975) found that the ceca produce volatile fatty acids which contribute 5-7% of mean daily energy requirements. Fenna and Boag (1974) found that indigestable fibre was diverted into the large intestine and the remaining nutrient-rich residue into the ceca where further digestion and absorption occurred.

There is little information on the relative lengths of ceca among bird species. Miller (1976) showed that Galliformes have long ceca; 14-24% of mean body weight ((length of combined ceca in mm/body weight in g) x 100). Captive Mallards that Miller maintained on a high fibre diet, developed ceca of just 2.5-3.2% of body weight. I found the mean values for wigeons of both sexes were 5.2%. This is well below that of gallinaceous birds but may reflect the greater potential of wigeon to digest plant material compared to the Mallard. More data for other species of wild waterfowl are needed to see if there is an overall relationship between relative cecal size and diet.

Kidney and pancreas weights followed a pattern similar to that of the intestinal tract. Larger organs would allow a greater intake and faster processing of food. This would be important when there was a need for quick mobilization of nutrients (e.g., during egg formation) (Krapu 1979). Contrary to this, when feeding rates decline, or less

fibrous foods are ingested, it would be inefficient to maintain unnecessarily large digestive organs (Moss 1974). Catabolism of nutrients from excess tissue would further reduce the amount of food required (Ankney 1977a).

Shah and Panicker (1976) asserted that gizzard weights changed in direct relation to body weight, regardless of the nutrient composition or amount of food. However, Sturkie (1976) showed that seed-eating species had large muscular gizzards, whereas those feeding on soft foods had weak, sack-like organs. Miller (1975), Pendergast and Boag (1973) and Moss (1972) also found a direct relationship between gizzard size and fibre content of the diet of the species they studied. Wigeon gizzard size correlated with the texture and apparent intake rate of food. The only variation it showed from the pattern exhibited by the intestinal tract was that the gizzards of females at Laying were smaller, and at Incubation were larger than expected. However, although females fed more than males at Laying they also ingested at that time a greater proportion of soft invertebrate foods (Chapter 1).

Digestion rates for invertebrate foods are shorter than those for vegetation (Swanson et al. 1974) and thus would require less storage space and mastication (Anderson 1972, Drobney 1977). As Ankney (1977a) suggested, the catabolism of gizzard tissue might also have been an important source of amino acids for egg production. Lower feeding rates by the males during Laying and Prelaying (Chapter 6) may have resulted in disuse atrophy of their gizzards. The contention that there is a direct relationship between gizzard size and food characteristics is supported

by the increase in gizzard size that occurred in post-breeding wigeons. In this light the increase in female gizzard size during Incubation is difficult to understand. Invertebrates continued to make up a large part of the diet and feeding time declined to 3.5% of the day (Chapters 1 and 6). In species such as the Lesser Snow Goose (Ankney 1977a) and Common Eider (Korshgen 1977), that depend on body reserves and feed little during incubation, gizzard size declines steadily. Wigeon females also depended heavily on their body reserves at this time (Chapter 6) but these were insufficient, without regular supplementary feeding, to see them through incubation (Wishart, unpubl. data). Afton (1979) concluded that the Northern Shoveler was too small to carry sufficient nutrient stores to complete its incubation without taking feeding recesses, and he found that gizzard size also did not decline during this stage. A large gizzard may be important for female wigeons during incubation as a food storage organ and to ensure fast and efficient digestion of food eaten during their short recesses. This could reduce the length of time of recesses and their frequency.

The liver is important in intermediary metabolism because it converts glucose to glycogen, stores glycogen and transforms excess glucose and amino acids to storable lipid. The opposite process occurs there during periods of negative nutrient balance (Sturkie 1976).

Liver weights were at their maxima during spring and fall. The reason for smaller livers in females in Fall is unclear, but may be due to sex-related differences in feeding, times of molt, etc. Liver weight

seemed to be related directly to food intake and so is probably a reflection of greater glycogen storage at these times rather than to only increased lipogenesis or lipolysis. Ankney (1977a), Young (1977), and Drobney (1977) reported similar correlations of liver size with feeding rate in other species of waterfowl.

CHAPTER 3

CHRONOLOGY OF MOLT IN THE AMERICAN WIGEON

INTRODUCTION

The pattern of molt in birds is highly variable. Operating under a variety of selection pressures, feather replacement occurs one to several times annually (Palmer 1972, King 1974). Because there is an increase in metabolic rate and the consumption of nutrients during molt, its scheduling has evolved in relation to other energy demanding processes (Payne 1972, Dolnik and Gavrilov 1979, Bailey 1982).

Young ducks may undergo almost continuous feather replacements through their first year of life (Oring 1968). However, some individuals molt earlier than others. This may influence their ability to compete for and obtain food, mates and/or breeding space (Chapter 5).

In general, North American Anas species undergo much of their molt in summer following nesting (Bellrose 1976). However, several studies (e.g., Oring 1968, Billard and Humphrey 1972) have shown that some ducks undergo a partial molt in late winter and that patterns differ between the sexes. In this context I examine here the general pattern of molt in American Wigeon over the annual cycle. Where differences occur between males and females the adaptability of these are discussed in relation to their reproductive strategies.

METHODS

A sample of 191 American Wigeons was shot between January and November in 1976 to 1978 at study areas (see Chapter 1) in British Columbia, Saskatchewan and Manitoba (Table 18). Plumage of each bird was examined for feather replacement and then plucked prior to other carcass

Table 18. Number of wigeons studied for feather molt, by sex, age, month and location.[1]

Month	Study area[2]	Collected				Live-trapped				Museum specimens[3]				Total
		Males		Females		Males		Females		Males		Females		
		HY-SY	ASY-AHY	HY-SY	ASY-AHY	HY-SY	ASY-AHY	HY-SY	ASY-AHY	HY-SY	ASY-AHY	HY-SY	ASY-AHY	
Jan	A		2		1					2	3	2	2	12
Feb	A		9		4					2	4	2		21
Mar	A	2	21	2	7					3	3			38
Apr	B	6	13		10	2	3				6	2		42
May	B	1	12	6	7	6	18	4	2					56
Jun	B		8	3	12	1	1	5	5					35
Jul	B-C	2	12	3	15		1	9	5					47
Aug	B-C	3	6	3	7				1					20
Sep												2	1	3
Oct	C	5	1	4	3						1			14
Nov	C		1							5	9	4		19
Dec	A					6	18	12	17	12	4	3		72
Total		19	85	21	66	15	41	30	30	24	30	15	3	379

Table 18. Cont'd.

[1]HY-SY=juveniles, ASY-AHY=adults (see text).

[2]Study areas referring only to captured or collected specimens. A=Fraser River Delta, British Columbia (49°09'N, 123°01'W), B=Moose Jaw, Saskatchewan (50°15'N, 105°50'W), C=Delta Marsh, Manitoba (50°11'N, 98°19'W).

[3]Of 72 museum specimens, 51 from British Columbia, 4 from Manitoba, 8 from Ontario, 1 from New York, 6 from California, 1 from Utah and 1 from Louisiana. Specimens from Manitoba Museum of Man and Nature, University of Manitoba Zoology Museum, British Columbia Provincial Museum, Cowan Vertebrate Museum, National Museum of Canada and Royal Ontario Museum.

analyses (Wishart 1979). The incidence of molt, as indicated by presence of blood-filled feather papillae, was recorded. Because flat skins could not be made (see Wishart 1979) the standard molt score procedures (Billard and Humphrey 1972, Young and Boag 1981) were not employed. The stage of wing and tail molt was noted and the extent of body molt on other pterylae described as heavy (>50 papillae), moderate (10-50 papillae) or light (<10 papillae). The length of ensheathed primaries was also measured.

In addition, 116 wigeons were live-trapped on these study areas (Chapters 4 and 6) and examined for molt before they were marked and released. The plumage of 72 museum specimens was also examined for months (September to March) with insufficient data for live birds. Forceps were used to fold back feathers of each pteryla to check for the presence of papillae.

Birds were aged using techniques described by Carney (1964) and Wishart (1981). Standard banding terminology (see Sealy 1979) was used to describe each age class (i.e., hatching year=HY, second year=SY, after-second year=ASY and after-hatching-year=AHY).

RESULTS

Juveniles

In late August, HY birds were molting heavily on the body (prebasic I). Southwick (1953) described the downy plumage of wigeon and the prejuvenal molt. Palmer (1976a) described the juvenal plumage and its replacement, which usually began by the time the birds fledged.

Some birds I studied shed rectrices in October but most did not begin to do so until December and January. Even by March three SY males had only replaced the four middle tail feathers and in April one female still had all notched juvenal rectrices (see Carney 1964).

The timing of the prealternate I molt varied considerably among individuals. Several acquired alternate I plumage by October, except for a few basic I papillae conspicious on the flanks, sides and crissum. Others did not reach this stage until six months later (Chapter 5). Males (drab coloration of females made them difficult to study) achieved full alternate I plumage first on the head and neck, followed by the breast and flanks, and then the rump. Molting of feathers of the back, scapulars, and tail finished last. By the time birds returned to the breeding grounds in April, all I examined had attained alternate I plumage. However, as Wishart (1981) pointed out, the wing remained in juvenal plumage until mid-summer.

Adult Males

By October, AHY males had largely completed the prealternate molt (Table 19). However, as late as January some still retained a few basic feathers on the upper and lower back, the flanks and rump. From February through April a light to heavy molt occurred on the breast, tail coverts, back and scapulars. Plumage coloration was not altered by this molt and Billard and Humphrey (1972) called it a continuation of the prealternate in Greater Scaup. In May there was no evidence of molt but in June as females began to incubate, the prebasic molt began on head, breast, belly, flanks, rump, tail and scapulars.

Table 19. Incidence of molt by adult male wigeons over their annual cycle.[1]

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep[4]	Oct	Nov	Dec
Plumage [2]	A	A	A	A	A	A	B	B	A	A	A	A
Molt[3]		A	A	A	B	B	B	A	A	A	A	A
Head							+++	+++				+
Neck							+++	+++			+	
Breast		+	++	+	+	++	+++	+++			+	
Flanks						++	+++	+++		+	+	+
Rump						+	+++	+++				+
Tail						+	+++	+++				
Upper back			+	+			+	+++		+	+	+
Lower back			+	+			+	+++		+	+	+
Scapulars		+	+			+	++	++		+		
Tertials							+++	+++			+	
Tertial coverts								+++				
Primaries							+++	+++				
Secondaries							+++	+++				
Wing coverts							+++	+++				

[1]Rating based on the intensity of molt on individuals (+=light, ++=moderate, +++=heavy).

[2]Dominant plumage presently held by the bird. A=alternate, B=basic.

[3]Molt underway. A=prealternate, B=prebasic.

[4]No males examined.

In July once pair bonds had broken, the prebasic molt continued as males congregated in small groups on larger bodies of water. Within a week, these birds moved away from the breeding area (see Hochbaum 1944, Salomonsen 1968, Bellrose 1976) to larger lakes and marshes where their molt continued. This may be a long movement for wigeons using such molting areas as Swan Lake (Bergman 1973) and the Delta Marsh (Hochbaum 1944) in Manitoba, which are not near important breeding areas. In contrast, Old Wives Lake, Saskatchewan (106°00'W, 50°07'N), which was selected by molting wigeons in preference to other adjacent waterfowl molting areas (e.g., Pelican Lake and Chaplin Lake), was surrounded by a dense breeding population (Chapters 1 and 6), and movements there may involve only a matter of several kilometers. Wigeon concentrations increased on these areas in June and July and then declined through August as the autumn migration began (see also Hochbaum 1944). Timing of this movement was delayed for males attending late-nesting or renesting females (Chapter 6).

The prebasic molt was completed on freshwater lakes. Before remiges were shed, birds attained almost full basic body plumage. However, rectrix molt was still incomplete by the time that birds became flightless. The rectrices were not replaced in a fully consistent pattern, although central feathers usually were replaced first. Back feathers also were not molted by this stage.

The first flightless male was collected on 11 July with the peak of flightlessness for the population occurring between 15-31 July. One flightless male was collected as late as 20 August. Tertials were already ensheathed when the primaries, secondaries and their coverts were shed. Underwing coverts were lost last.

The tenth primary was first to reappear as were the proximal secondaries. On average $P_{8, 7, 6,}$ and 5 were slightly longer than inner and outer ($P_{1, 2, 3, 4, 9}$ and 10) primaries at early stages of feather growth (N=7 males). However, because distal primaries ($P_{9, 10}$) are longer than proximal when full grown, they (and occasionally also P_5) were last to have blood-free calami. By this stage the birds could already fly.

While primaries were growing, some rectrices were still ensheathed and molt on the spinal tract began. By the time flight was regained, spinal and body down molt was heavy and molt of rectrices was complete.

The prealternate molt began on the body in mid-August after the wing feathers were almost fully grown. This proceeded first on the head, breast, rump, scapulars and flank.

Adult Females

In January, adult females showed light molt on the upper spinal tract and scapulars (Table 20). Through February and March the incidence of molt increased dramatically. Again Billard and Humphrey (1972) identified this as a continuation of the prealternate molt in Greater Scaup. In contrast to males, females underwent heavy molt on neck and head, and light molt on flank, rump and scapulars. This continued in March with heavy molt on breast, back and scapulars and a moderate molt on the rump and tail of some birds.

After returning to the breeding grounds in April, adult females were still in light to heavy contour molt on the head, neck, breast, back and

Table 20. Incidence of molt by adult female wigeons over their annual cycle.[1]

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov[4]	Dec
Plumage[2]	AB	AB	AB	AB	A	A	B	B	AB	AB	AB	AB
Molt[3]	A	A	A	A		B	B	A	A			
Head		+	+++	+++			?					
Neck		+	+++	+++			?	+++				
Breast			+++	+++		+++	+++	+++	+++			
Flanks		+					++	++				
Rump			+				++	++				
Tail		+	+	+++		+	+	++	+			
Upper back	+		++	++			++	++	++			
Lower back			++	++			++	++	++			
Scapulars	+	+	+	++		+	++	+	+			
Tertials							+	++				
Tertial coverts								++				
Primaries								+++				
Secondaries								+++				
Wing coverts								+++				

[1]Rating based on the intensity of molt on individuals (+=light, ++=moderate, +++=heavy).

[2]Dominant plumage presently held by the bird. A=alternate, B=basic.

[3]Molt underway. A=prealternate, B=prebasic.

[4]No females examined.

scapulars. A medium to heavy down molt also occurred at this time. Rectrices and their coverts were also in full molt, although this ended during the breeding period in May and June.

No noticeable molt occurred in May when females were laying eggs. In June, females that lost nests began to replace down and contour feathers on the breast and abdomen (i.e., brood patch).

In July, the females I examined were in a variety of reproductive stages (i.e., Laying, Incubating, Postreproductive and Brood Rearing) (see Fig. 1). Laying and Incubating birds and those in early Brood Rearing showed little evidence of molt except for the replacement of two to eight median secondary coverts. Postreproductive females began the prebasic molt on breast, flanks, back, scapulars and sides as well as on tail and tail coverts. A similar degree of molt occurred in late Brood Rearing (young more than two weeks old) females, particularly for those collected in August.

After six to seven weeks, wigeon females usually abandon their broods (see Beard 1964). At Moose Jaw these females formed small flocks on larger ponds and ranged more widely over the area. Some then departed, presumably for the same molting lakes used by males. Several molting adult females were collected at the Delta Marsh although the concentration of males on this molting area was much greater. Not all females left the nesting area to molt. One flightless bird was captured with a six week old (age estimated using Gollop and Marshall (1954)) brood on a permanent breeding pothole in Saskatchewan on 11 August 1976. But because the birds were not marked I could not tell if the offspring were hers or those abandoned by another female.

When the primaries were shed, the pattern of replacement was similar to that of males with middle primaries longer than those most proximally and distally. Again P_{10}, 9 and 5 were last to have calami clear of blood (N=1). When secondaries, coverts and primaries were ensheathed, molt was also heavy on body pterylae. All rectrices and tail coverts were replaced also at this time. Prealternate molt was resumed and feather replacement was heavy on breast, tail, and back into September. No apparent signs of molt occurred in adult females between October and December.

DISCUSSION

Most northern Anatini males, including the American Wigeon, molt into alternate plumage (nuptial) in the late summer and fall. This contrasts with many other nonpasserine and passerine species (see Dwight 1900, Palmer 1976a,b) which do not initiate this molt until just before spring migration and pairing. However, unlike most other species that renew their pair bonds annually, wigeon and most other North American ducks court and pair over the winter (Weller 1965, Chapter 5).

In wigeon, sex ratios favor males and some juvenile birds paired and reproduced successfully (Chapter 5). Thus, there was competition for females, and adult wigeon males that had completed the prealternate molt were more successful in mate acquisition. Later-molting adults and juvenile males that only progressed gradually through the prealternate I molt rarely took part in courtship and frequently did not obtain mates (Chapter 5).

Even those males that completed the prealternate I molt were not in definitive plumage because juvenal wing feathers were not replaced until the prebasic II molt. Thus, during their first courting and breeding season these birds did not have the white upper wing coverts which were displayed in courtship and antagonistic situations (Chapter 4, Wishart 1981). Males with this particular plumage fared poorly in competition for mates (Chapter 5).

Adult males underwent a light molt in late winter. Oring (1968) believed that male Gadwalls that molt at this time were replacing only a few feathers that were lost accidentally. However, feather replacement was too heavy for this to be a plausible explanation for wigeons (see also Billard and Humphrey 1972).

Compared to females, the winter molt by males was light and did not continue through migration. Visually, the alternate plumage color patterns were not disrupted by this molt.

It is not adaptive for males to molt during the breeding season. Added nutrient requirements due to molt would reduce the amount of time and energy available for the male to invest in defense of his mate and territory. Plumage coloration and flying ability would also be important for the male to fulfill these needs. Molt or any other processes that reduced the chances of successful reproduction would be selected against (Chapter 6).

Males replaced most of their alternate plumage, starting in June when it was badly worn and after the energy demands of reproduction had ended. Molt at this time is advantageous. By replacing badly worn and even broken feathers the individual could thermoregulate and fly more efficiently (Bailey 1981).

Once males were flightless they were almost completely in the dark cryptic basic plumage. Birds are inactive and secretive at this time (Hochbaum 1944, Young 1977) and it is assumed that this reduces their vulnerability to predators (King 1974). Bailey (1982) suggested there may also be a thermal advantage to wearing a dark plumage when papillae are highly vascularized and the body is subject to rapid heat loss.

With flight resumed, vulnerability to predators would be lower and at this stage the prealternate molt began to replace the dull eclipse plumage. Although this feathering was still relatively unworn there are several advantages for its early replacement.

Molt occurring in the warm weather of late summer when food was abundant (Bergman 1973) would be less costly energetically and there would be sufficient time for molt to end before fall migration (King 1974). Once males completed the molt they could begin competing for potential mates and have a greater chance of acquiring one for the next breeding season (Chapter 5).

Unlike males, wigeon females completed much of the prealternate molt (including down and most rectrices) in late winter and early spring. Little noticeable change was evident because the basic, like the alternate plumage was dull. However, molt in winter and through migration would be energetically very demanding (King 1974). The adaptability of this pattern in female wigeon is unclear but seems to be related to the high energy costs of reproduction and the extended period of brood care. Waterfowl depend on open water for survival and in the short interval between molt initiation and fall freeze-up a rapid molt is important. This would be facilitated by an interrupted molt in which part of the prealternate molt was accomplished after migration.

The winter molt by adult female ducks seems to be widespread. It has been documented in Gadwall (Oring 1968, Paulus 1980), Mallard (Jorde 1981), Redhead (Weller 1957b, 1970) and Greater Scaup (Billard and Humphrey 1972). Jorde (1981) found that usually only after female Mallards paired did they undertake this molt.

The prealternate molt of female wigeon extended through April. Most females had not begun to nest before late May, or two to six weeks after the first birds had returned to the breeding grounds. Possibly this interval was necessary to renew reserves used in molt prior to breeding (Chapter 6).

Molt in the wigeon female was interrupted prior to egg-laying and was not resumed until after the young were several weeks old. Through this interval, females stored nutrient reserves and then invested them in the production and care of offspring (Chapter 6). By the end of incubation

females were close to starvation body weights (Wishart 1979, Chapter 6) and even a small increase in nutrient demand at this time due to an earlier onset of molt could be critical to the survival of the female and her young (see Korschgen 1977, Ankney and MacInnes 1978).

Females that have successfully reared broods may begin the prebasic molt no earlier than late August, up to two months behind the schedule of males. However, because much of the prealternate molt was apparently carried out in late winter, the time and energy required to molt before fall migration would have been reduced. Despite this, females still lagged well behind males. Most males departed on fall migration in late August and early September at a time when females and juveniles were still molting and building up pre-migration nutrient reserves (see also Bellrose 1976).

The extent to which either the migrant or sedentary molt strategy was followed by females could not be established. Gilmer et al. (1977) found that 42% of female Wood Ducks and 39% of female Mallards remained to complete the molt on breeding areas. Salomonsen (1968) believed that female dabbling ducks did not undergo a true molt migration as did males, but acknowledged that some did leave the breeding areas to molt. Chabreck (1966) reported some female Gadwalls underwent the prebasic and prealternate molts after they had apparently completed migration to the wintering grounds in Louisiana. The variability of this molt may be related to the breeding chronology and condition of females and possibly also to changes in weather and food conditions in different years (see Billard and Humphrey 1972).

Females that migrated to molt may have been early or failed breeders that had sufficient nutrient reserves to undertake this extended movement. They then would be able to take advantage of the security and reliable food and water resources available in these large molting habitats. Females that nested successfully and had insufficient reserves or time to migrate may have been forced to molt on the breeding area where conditions were less suitable. Late renesters or diseased birds in poor condition might delay molt until after fall migration. Weather conditions on the breeding grounds such as drought or early freeze-up in some years might induce some birds to migrate before completing the molt.

Differences in time-energy budgets, particularly related to pairing, nesting and brood care (Chapters 5 and 6) between male and female wigeons seem to be related to differences in their molt pattern. Although waterfowl are secretive and wide-ranging outside of the nesting period, further study of their biology at this time is necessary to understand the coexistence and chronology of events in their annual cycle.

CHAPTER 4

SOCIAL DISPLAYS AND VOCALIZATIONS OF AMERICAN WIGEON

INTRODUCTION

The wigeons, including the American, Eurasian, and Chiloe, are a closely related group within the Anatini (Johnsgard 1965, 1978). Males possess distinct tracheal anatomy and females, unlike other congeners, lack conspicuous flank markings (Johnsgard 1965). Downy young, like those of most diving ducks, lack facial stripes and are distinctive in having rust-tinted heads (Johnsgard 1965, Palmer 1976a, C. Nelson, unpubl. data). Adults have a specialized goose-like bill adapted for upland and aquatic grazing (Johnsgard 1961, 1965, Chapters 1 and 2).

Despite these unique anatomical features and their interesting phylogeny the wigeons have been little studied. There is sparse and often conflicting information about their breeding biology (see Chapter 6) and incomplete documentation of displays and related vocalizations (Johnsgard 1965, 1971, Cramp 1977).

Displays are ritualized behavioral responses used to communicate information. They are genetically controlled and thus, ultimately are subject to natural selection as are most other individual physical and behavioral traits. McKinney (1973) recognized that the behavior of a species has evolved as a compromise among a number of competing selection pressures. He (1975) speculated that changes in signalling behavior probably evolved in relation to ecological adaptations.

In this Chapter I describe quantitatively most of the major displays and vocalizations of the American Wigeon. The behavioral contexts in which the displays occur are examined and their probable adaptive functions discussed in relation to this species' mating system and ecology.

METHODS

American Wigeon social behavior was studied between December and March in 1974-75 and 1976-77 on the British Columbia study area (Chapter 1). Birds were observed from a plastic tee-pee blind on the shore of an impoundment in the George C. Reifel Migratory Bird Sanctuary. Displays were filmed at a distance of 10-60 m with an 11 power super 8 mm Nizo movie camera at 19 frames per second.

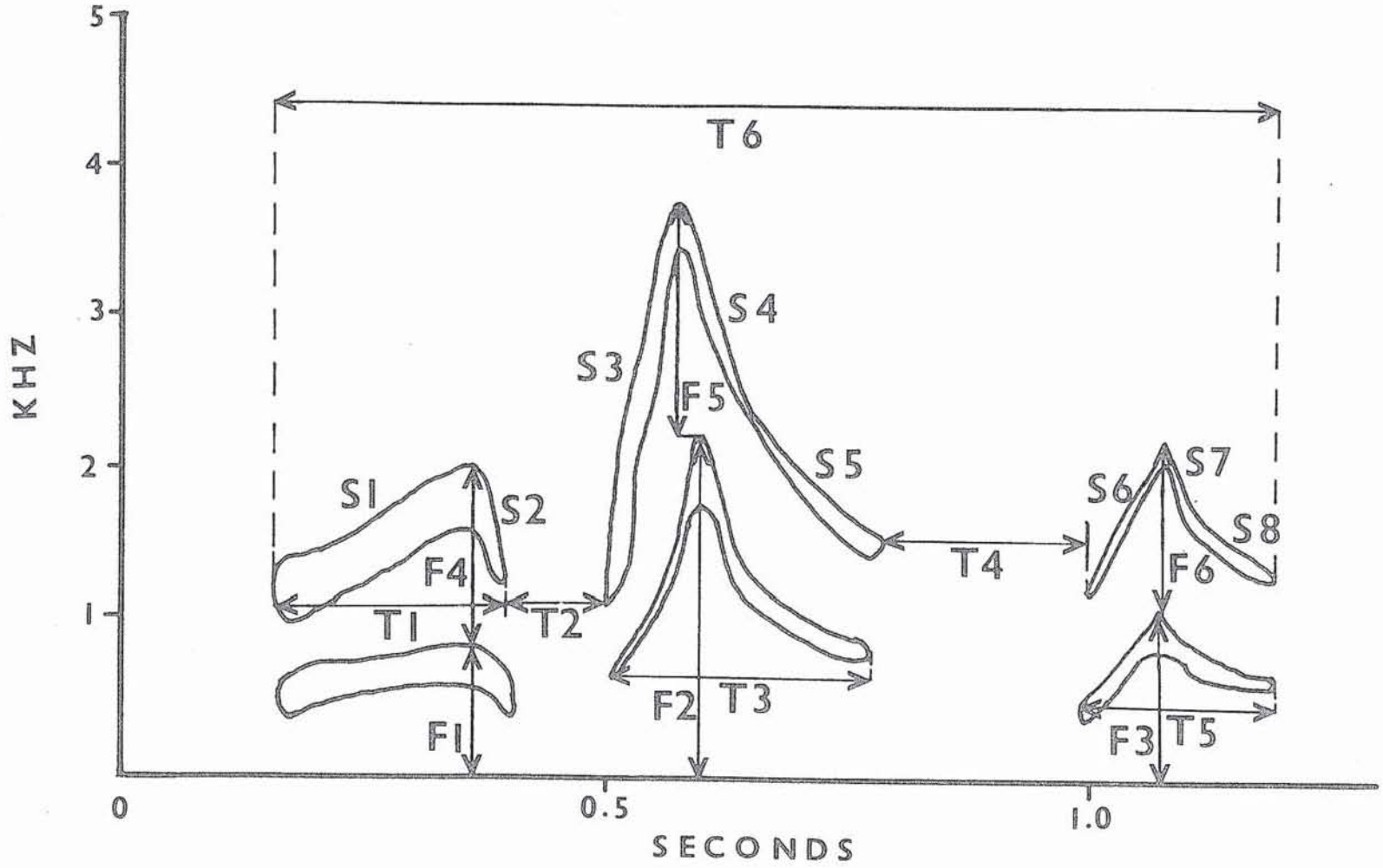
Movie films (395 m) were analyzed frame by frame on a Goko editor-viewer. A series of frames for each display was traced directly from projections. Display intervals were calculated by counting frames on the viewer. Orientation of displaying birds was recorded and inter-bird distances were estimated in relation to known bird body lengths. Display nomenclature is derived from Johnsgard (1965), McKinney (1970) and in some cases from Cramp (1977).

Wigeon breeding biology was studied at the Saskatchewan study area (Chapter 1) between April-August in 1976 and 1977 and in April, June and July, 1978. Birds were captured and marked as described in Chapter 6. Individuals were observed from blinds with a 20-45 power spotting scope

during all daylight hours. Displays and vocalizations of marked birds of known breeding status were described into a continuously running tape recorder. Times of some events were later measured from the tape with a stop watch.

Two to four pairs of individually marked wigeon were placed in an enclosed flight pen at the Delta Waterfowl Research Station, Manitoba, on 4 May 1978. These birds were observed daily from a blind set outside the pen where I filmed their behavior. Vocalizations of two of these males and one female, as well as two wild males at Delta, were tape recorded at 19 cps with a Uher 4000 Report-L tape recorder and a Gibson parabola. A sequence of 4-9 calls, several up to two days apart, was recorded for each male. All calls were analyzed on a Kay Elemetrics Missilizer 675. The calls of the males were analyzed further to see if individual characteristics could be detected. Twenty call variables, 14 spectral and 6 temporal, were measured for each call (Fig. 14). Factor analysis (Dixon and Brown 1977) identified variation of vocalization parameter means between birds (Beightol and Samuel 1973). Factor scores were calculated for each vocalization using computer generated standardized data and variable coefficients. Factor scores were tranformed and a one-way analysis of variance performed to see if variation between birds was greater than intra-individual call variation (Van Valen 1978). Discriminant analysis (Dixon and Brown 1977) was used to determine whether the individual that uttered a particular vocalization could be identified.

Fig. 14. Sonogram of male American Wigeon three syllable Slow Whistle. F=frequency, T=time, S=slope. F1, F2 and F3 measured from base of sonogram plus 50 hz. S1, S3 and S6 are slopes of Up-slopes. S2, S4 and S7 are slopes of Down-slope tops. S5 and S8 are slopes of Down-slope-bottoms. Similar measurements were taken of the fourth syllable of four syllable Slow Whistles.


5
4
3
2
1
KHZ
T6
S1
S2
S3
S4
S5
S6
S7
S8
F1
F2
F3
F4
F5
F6
T1
T2
T3
T4
T5
0
0.5
1.0
SECONDS

RESULTS

Pair Formation

An Overview of Courtship Behavior

Pair formation in a population of American Wigeon in British Columbia proceeded gradually over the winter (Chapter 5). Each pair formed at the culmination of competitive social courtship (Gesellschaftsspiel) in which males and females performed ritualized displays.

Aggression among males was common. At the height of courtship there usually occurred a mass chase of the female. This led to a series of short, wing-flapping rushes in which males attempted to grab or mount the female. During this activity the female usually responded by diving or by taking flight. If the female flushed, the courting males followed and a rapid, Group Flight Associated with Social Display (GFASD) ensued (see below). On landing, chasing and courtship usually resumed until either a pair formed, the group disbanded or the males shifted their attentions to another female.

Male Displays

Swimming-shake (SS)

This movement is a ritualized form of the swimming-shake (McKinney 1965a) performed frequently by wigeons as a comfort movement. In many dabbling duck species it is given as a preamble to sequences of other displays, thus, the term "Introductory-shake" was coined by Lorenz (1953). In wigeon, however, it is a major display with no introductory function.

This movement usually was preceded by rapid Tail-wagging (TW). Prior to completion of the TW the head and neck were thrust forward and upward. As the anterior portion of the breast was elevated out of the water the head was extended further up and forward and several rapid body shakes and head rotations were performed. As these shakes ended, the neck was pulled into the body and the breast lowered back forward onto the water. The neck and bill were then tucked into the breast with the crown erected. The display was terminated with another rapid TW (Fig. 15). The full display including TW averaged 3.50±0.87 s (N=19) ($\bar{X}$±S.D.) with the portion exclusive of TW averaging 1.17±0.21 s.

This display was most often performed within 1 m of the female (70.2%, N=104) while the male was aligned parallel (side-on) to her (62.5%) (Fig. 16). Swimming-shakes at times seemed infectious among a group of courting males. On 25 occasions at least 3 males performed this display concurrently or consecutively. Although usually occurring on water, I saw several males perform this display while courting in an agricultural field on 21 February 1977.

Although wigeons did not perform the Grunt-whistle display characteristic of many other Anas species (Johnsgard 1965), one male did perform a highly exaggerated SS with much accentuated arching and little evidence of body shaking. However, the bill did not touch the water and no vocalization was given. Thus, this movement could not be classified as a Grunt-whistle.

Fig. 15. Male wigeon Swimming-shake. Numbers of film frames are indicated at the bottom.

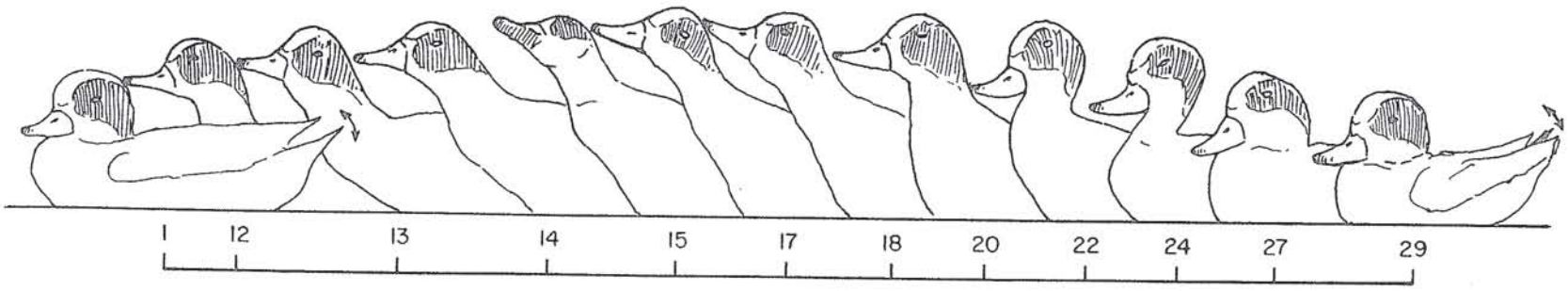
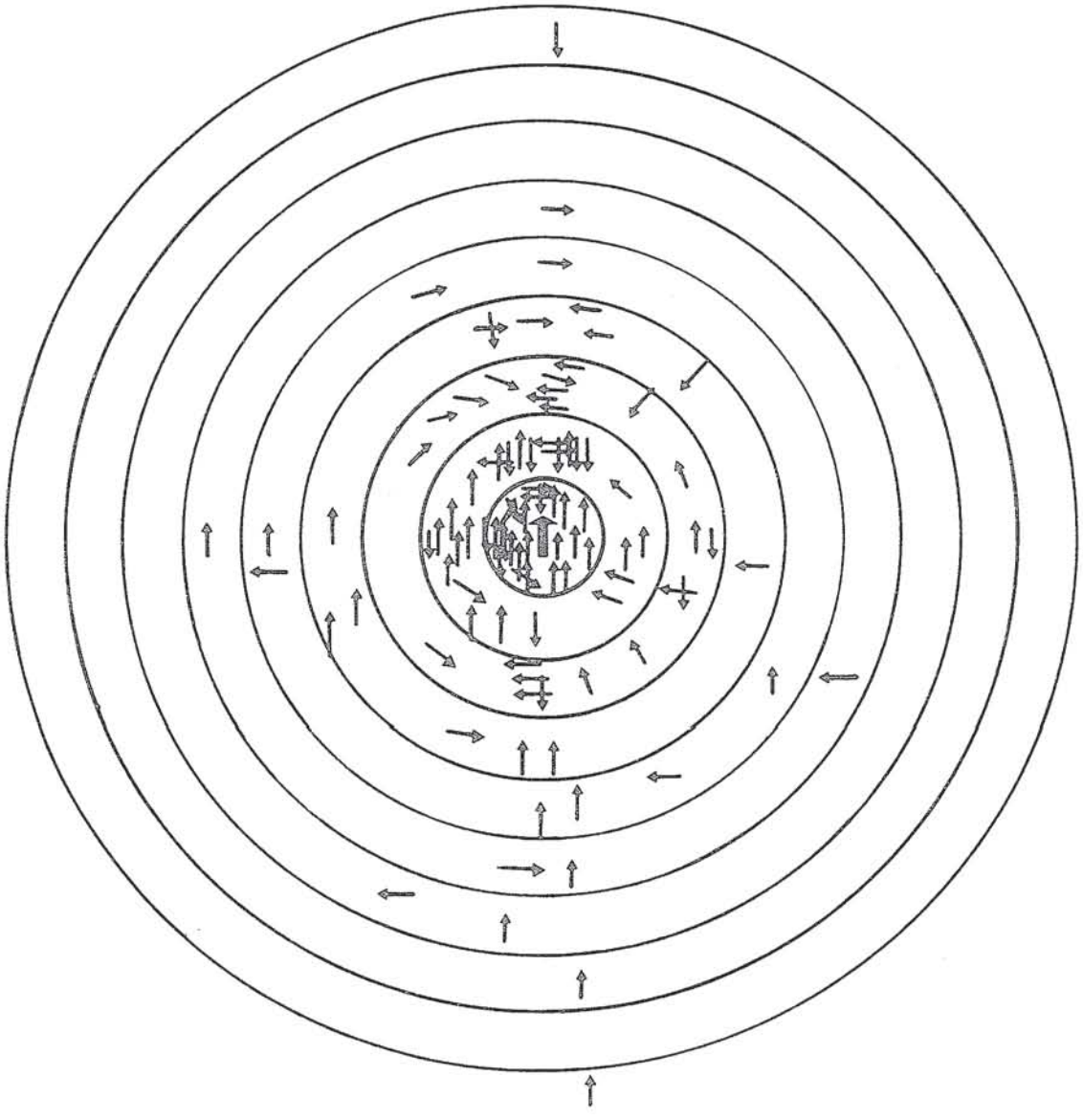

1
12
13
14
15
17
18
20
22
24
27
29

Fig. 16. Position of male wigeons performing Swimming-shake. Dark arrow in centre indicates female's position. Distance between adjacent circles is 0.3 m. The male outside the rings is 4.3 m from the centre.

Swimming-shake



The SS apparently functioned to draw the female's attention. Shaking movements accentuated the black and white bands on the rump and the colorful bill and head markings of the adult male in full alternate plumage (see Palmer 1976a for a complete morphological description of the wigeon). Occasionally males finished this display with Preening or with an attempt to lead the female away from the group (Turn-back-of-head).

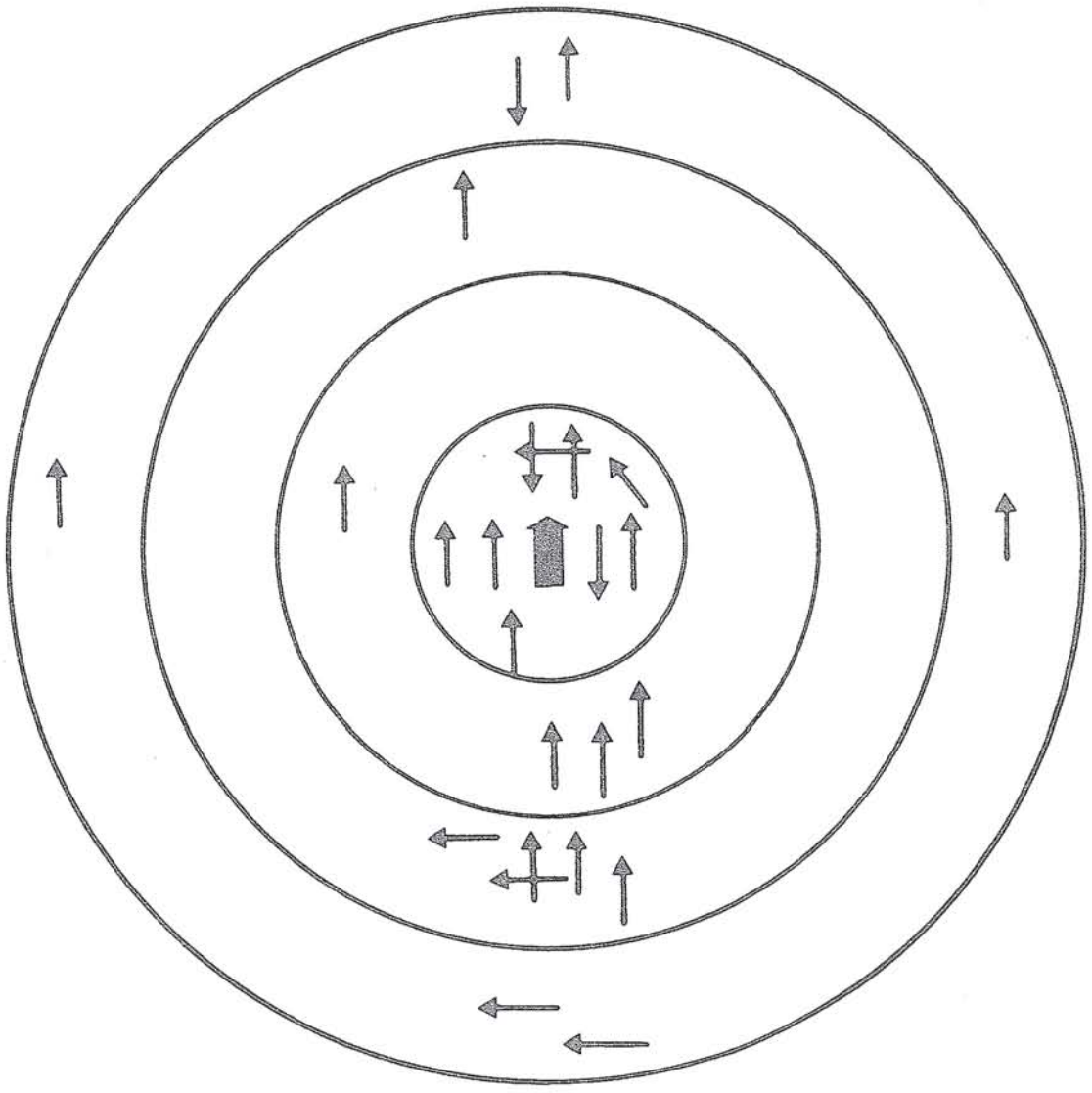
Bathe and Wing-flap (BAWF)

As in the preceding display, Bathe and Wing-flap (BAWF) also occurred regularly as comfort movements in wigeons. Tinbergen (1952) noted that it was difficult to determine whether these are simply functional responses to disordered plumage. Indeed, these movements usually occurred after aggressive encounters while courting, and McKinney (1965a) believed that in these situations BAWF was probably a comfort movement rather than a signal. However, a secondary function of this behavior is suggested in that males performed 76% of WF within 1 m of the female and 60% (N=25) were performed side-on to her (Fig. 17). McKinney (1965a, 1970) also noted that shoveler males performed exaggerated WF while oriented sideways with respect to the female, during courtship.

Bathing consisted of a series of 2-6 head-dippings usually with rapid wing-shuffling. These bouts averaged 6.08±2.70 s (N=10). Following 96.4% of BA (N=28), males also performed WF movements. However, only 71.1% of WF were preceded by BA. Wing-flap also directly followed Head-shakes (three times), Preening (once), Burp (once) and inter-male aggression (six times). Wing-flap required 2.16±0.57 s (n=31) and the number of wing

Fig. 17. Position of male wigeons performing Wing-flap. Dark arrow in centre indicates female's position. Distance between adjacent circles is 0.3 m.

Wing-flap



beats in a sequence averaged 5.3±1.5 (N=23). Ten times pronounced tail-wags followed WF and these averaged an additional 1.69±0.57 s.

This behavior drew attention to the performer both visually and acoustically (splashing and wing-beating). While open, the white upper wing patch denoting age (Wishart 1981) was visible. Vigorous movements like BAWF may advertise the condition of the displayer as well as reveal his ability to fly. Rearing up out of the water and opening the wings increased the apparent size of the individual and may have assisted in establishing dominance. It seems, therefore, that these displays may serve dual secondary functions; i.e., in attracting the female's attention and establishing dominance.

Burp (B)

This display was recorded on film 664 times. The male revealed his intention of Burping (B) by stretching his head and neck up in alert posture, erecting the crown feathers and opening the bill (Fig. 18). While performing B, the male emitted a Slow Whistle vocalization (see below). Burp was often repeated 2 or 3 times by a courting individual and 75.2% were given concurrently by other males in the group. Prior to 27 of the B in which observable behavior occurred, 4 were preceded by Head-shakes, 2 each by Wings-up and Wing-flap, 1 each by Head-flick and Tail-wag and the rest by B. Other behaviors followed 42 B, including, 17 B, 15 Head-shakes, 3 Swimming-shakes, 3 Preen, and 1 each of Wing-flap, Bathe, aggression and Tail-wag.

Fig. 18. Male wigeon performing Burp. Note the alert posture, raised crest and white wing patch. The bill is opened as the Slow Whistle is given.



Of 143 B, 28.7% took place within 0.3 m of the female. Another 62.2% were recorded between 0.3-1.3 m and the remainder (9.1%) between 1.3-2.3 m. Of 74 B performed ahead of or beside the female, 50 were side-on to her field of view and 24 head-on (Fig. 19). Of 69 B behind the female, 13 were side-on and 56 head-on. Those behind averaged 0.96 m away from the female while those ahead or beside her averaged 0.64 m.

While B, the striking head and bill colors were exhibited and this appeared to be primarily an attention-getting display. The auditory component appeared to be individually distinctive (see below). This increased the impact of the display and made it appropriate even when the male was behind the female and out of her view. As with Wings-up and Swimming-shake, this display was frequently performed concurrently or consecutively by other competing males. This indicates the importance of these displays in influencing female behavior.

Turn-back-of-head (TBH)

Johnsgard (1960) noted that Turn-back-of-head (TBH) is a display characteristic of many duck species. It is performed by the male and apparently is a means of leading the female away from other courting males (McKinney 1975).

Contrary to findings by Johnsgard (1965, 1978) and Cramp (1977) for Eurasian Wigeon, TBH was often performed by American Wigeon males. During this display the male swam alertly ahead of the female (Fig. 20).

Fig. 19. Position of male wigeons performing Burp. Dark arrow in centre indicates female's position. Distance between adjacent circles is 0.3 m.

Burp

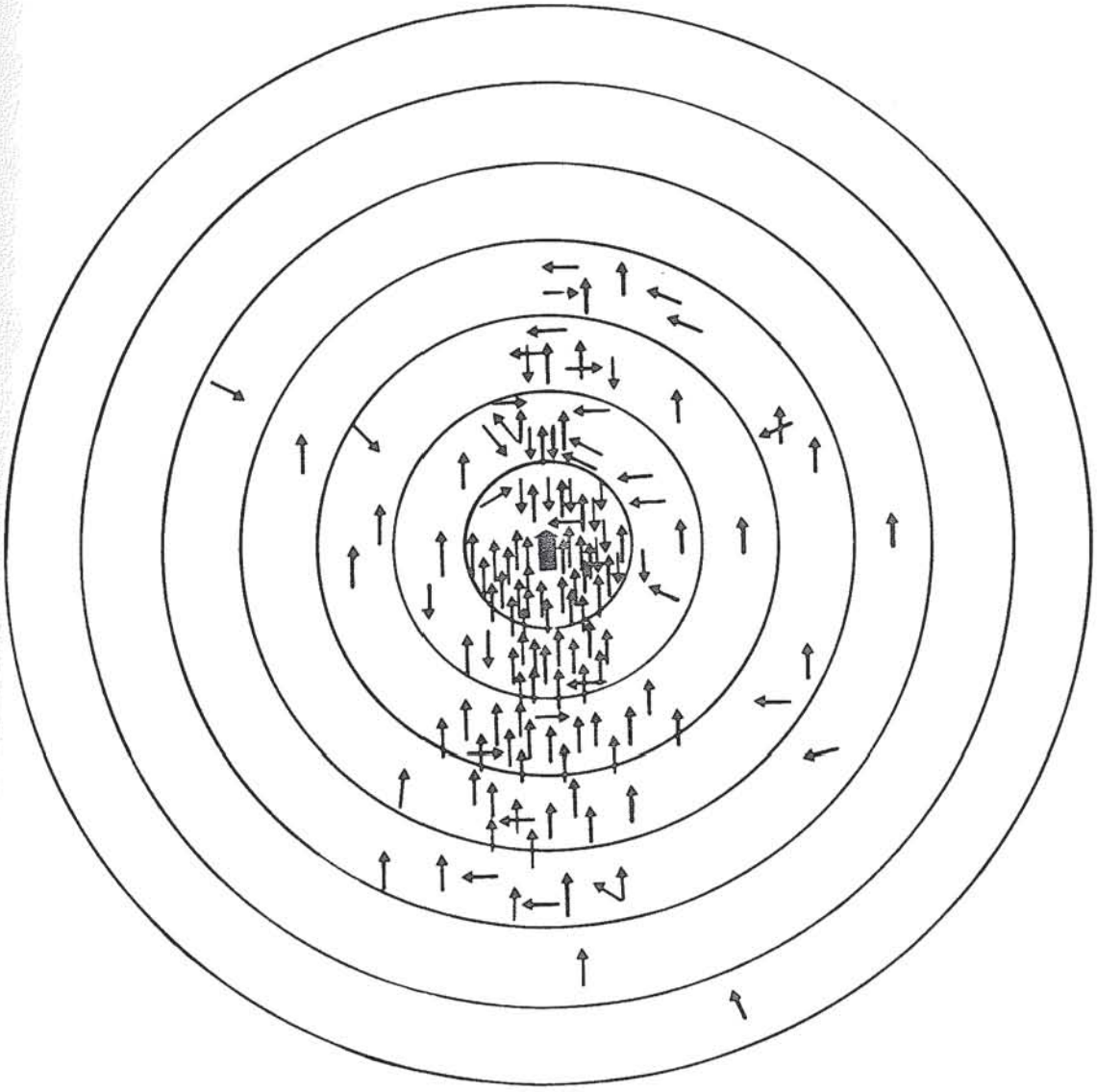
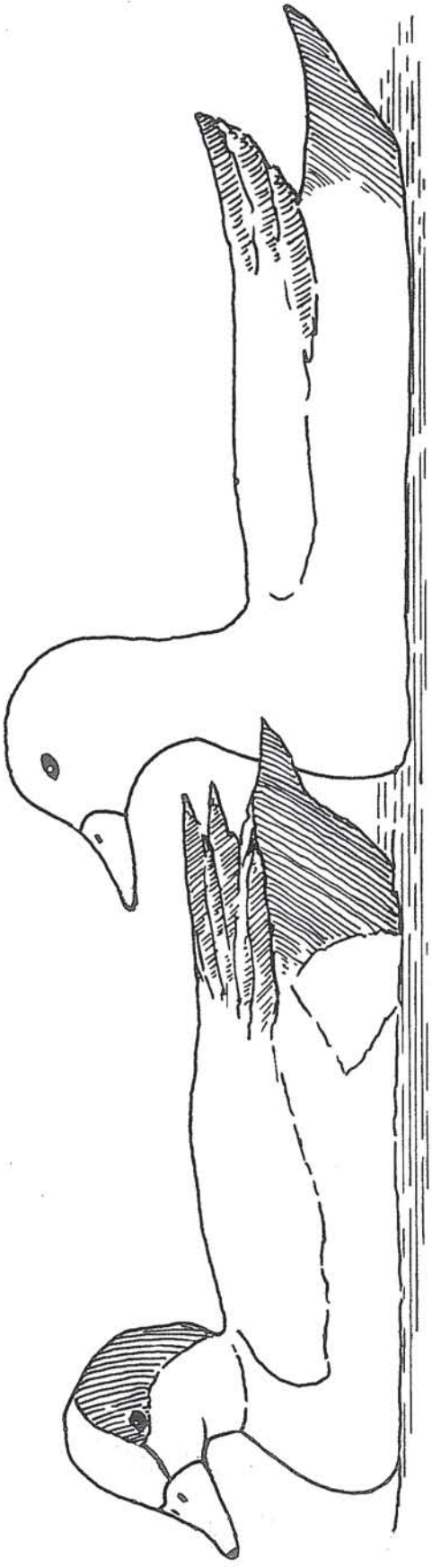


Fig. 20. Male wigeon performing Turn-back-of-head and leading female.



As she followed, his head was often tilted to one side. This may have allowed him to observe her movements, as well as those of the other males while advertising his own striking head plumage.

While following, the female frequently Incited (INC) and Chin-lifted (CL) over her shoulder at other males that followed. This was contrary to Cramp (1977) who reported that TBH was rarely associated with female INC in Eurasian Wigeon. If the female did not follow, or other males impeded her, the male ended TBH and swam back toward her. Aggression or fighting then began among the males.

Occasionally a male performed TBH to a female that already appeared paired with another male. This usually resulted in both pair members threatening the male.

Turn-back-of-head normally occurred on water. However, on 21 February 1977 I saw it several times on land as a group of birds courted. The female followed a male performing TBH and while doing so she repeatedly CL and INC over her shoulder at the other males that walked behind.

Jump-flight (JF)

Jump-flights (JF), characteristic of Mallard (Lebret 1958, 1961) and Northern Shoveler (McKinney 1970), have been described for wigeon by Soutiere et al. (1972). I observed them only six times, usually during vigorous courtship activity. In all cases, a male that had been on the water left behind by the courtship group, flew up and landed ahead of the

swimming female. McKinney (1970) concluded that these displays functioned in attracting the female's attention in a way similar to TBH. The flights were short (3-5 m) and apparently lacked the pronounced ritualized posturing and wing noise characteristic of the JF of the Shoveler (McKinney 1970).

Males performing JF usually elicited Inciting displays from the female and aggressive threats from other nearby males. Vigorous courtship activity associated with JF frequently ended in a courtship flight.

Facing (FA)

Facing (FA) was a common display performed mutually by both sexes during courtship but was usually initiated by the male. Termed the Forehead-turning-display by Cramp (1977), it has been described by Lorenz (1953), Johnsgard (1965) and others for Eurasian Wigeon as resembling the Triumph Ceremony of geese.

The display often followed Turn-back-of-head when the female did not continue to follow the male or was prevented from doing so by other courting males. The male performing Turn-back-of-head responded by swimming back to the female and FA her alertly breast-to-breast (Fig. 21). From this position he frequently attempted to herd the female away from the other suitors. As a result, their breasts occasionally came into contact. This strongly directional display (Simmons and Weidmann 1973) seemed to be a direct assertion of a male's choice of mates and on some occasions appeared aggressively motivated in that the male physically impeded a female's attempt to swim away.

Fig. 21. Wigeon pair Facing. Male with Wings-up and Bill-dipping, female Chin-lifting.

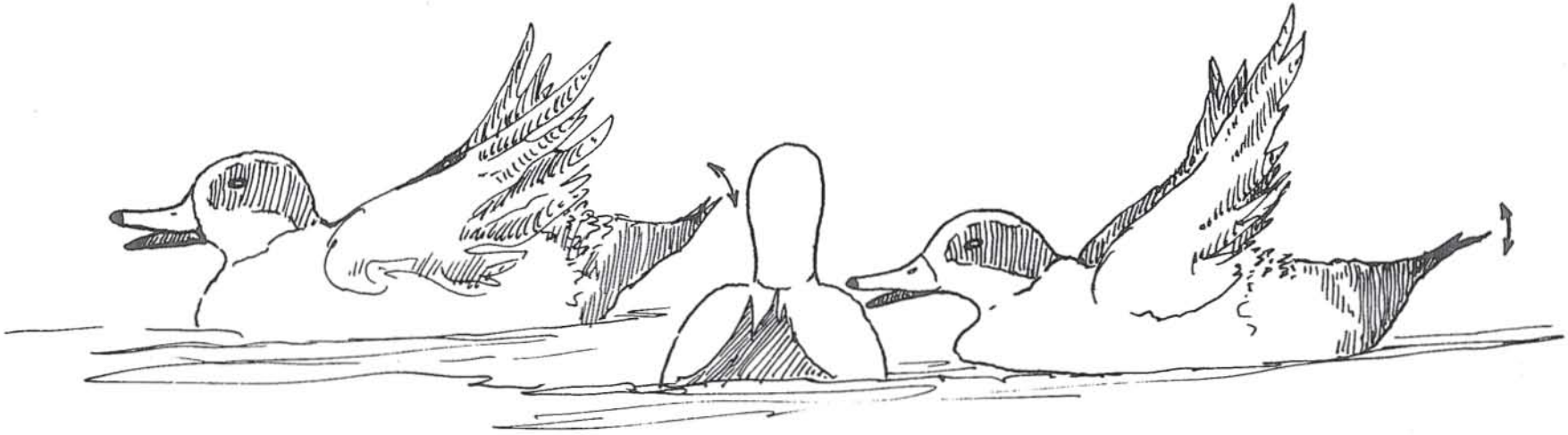
Although the female frequently performed Chin-lifting and Inciting movements at other males from this position, contrary to observations of Eurasian Wigeon (Lorenz 1953, Johnsgard 1965, Cramp 1977), males did not perform Chin-lift while FA. They did, however, often perform Head-shake and Bill-dip and regularly rotated around quickly to threaten or make aggressive head-out-bill-open attacks at other males. This activity usually ended with a bout of Preening or with the male resuming Turn-back-of-head and leading the female away.

Wings-up (WU)

The Wings-up (WU) was one of the most frequently occurring displays given by males during courtship in winter, and was seen 184 times. In this display the wings were arched over the back with the primaries crossed. The degree of arching seemed related to the intensity of the display as did the rapidity of Tail-wagging which occurred concurrently. Usually during this display the head was held out and compressed back against the neck (Fig. 22). Fast Whistle vocalizations (see below) were given repeatedly.

This display usually occurred in an aggressive context during the most vigorous stages of social courtship. Cramp (1977) and Johnsgard (1965) also ascribed an aggressive function to this behavior in American and Eurasian Wigeons, but apparently it is uncommon in the Chiloe Wigeon (Johnsgard 1965). On 18 January 1977 a single male Eurasian Wigeon participating in an American Wigeon courtship party performed this display three times in response to other males doing WU.

Fig. 22. Two male wigeons performing Wings-up in front of a female. Arrows indicate Tail-wagging. Both males are emitting Fast Whistle vocalizations.



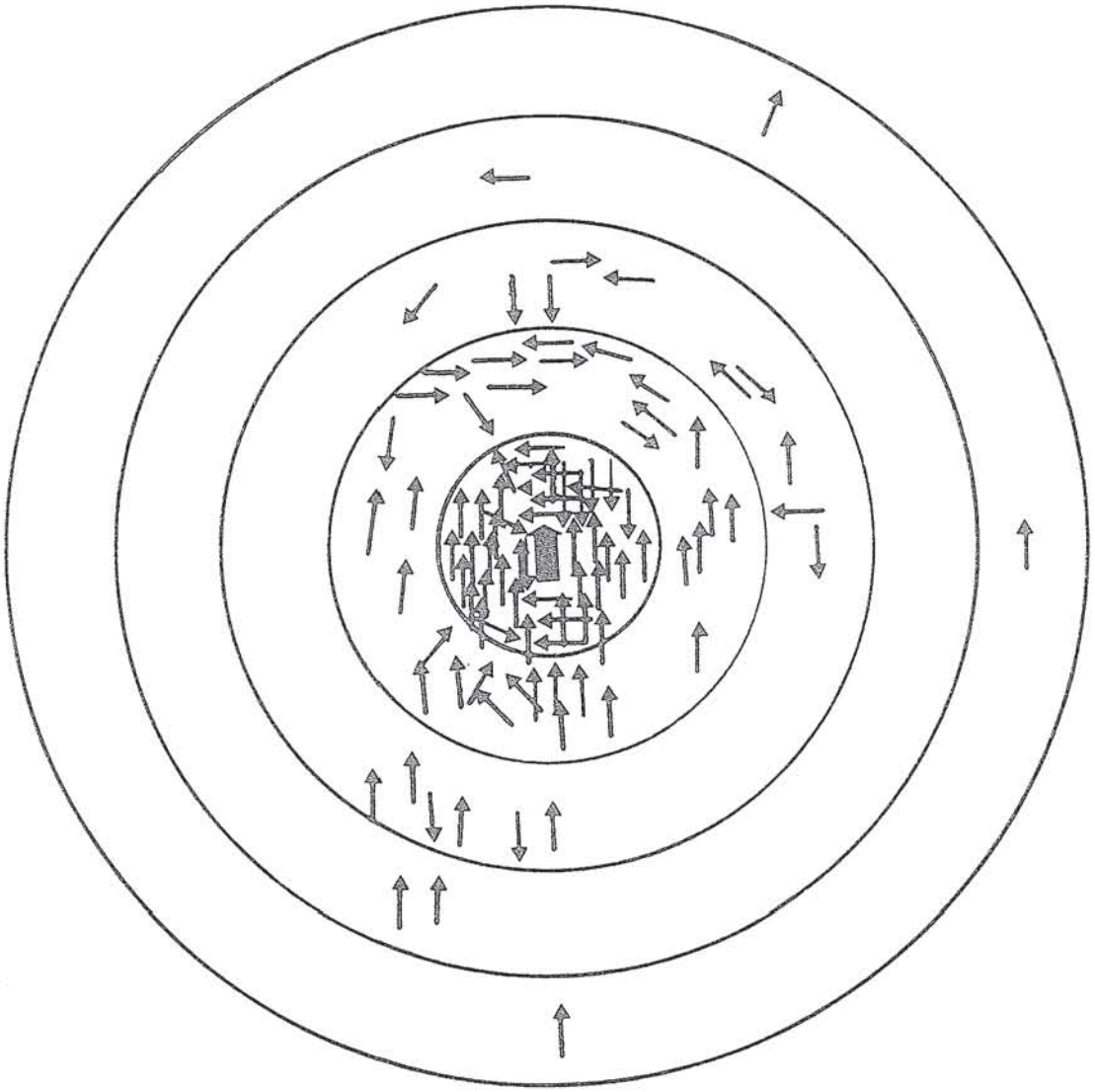
WU usually was given when the male was within 0.5 m of the female while side-on to her field of vision (Fig. 23). Thus, it likely also served to draw the female's attention. Occasionally this display was given as the male Faced (14 times) prior to swimming aggressively at other males nearby (Fig. 24). Often (17 times) WU was given concurrently by two males in a face-off (head to head or side to side) position. Other males in the group also frequently performed this display simultaneously (138 occasions). On at least six occasions bouts of WU performed by courting males were followed immediately by aggressive chases resulting in the female flushing into a courtship-pursuit-flight. On 21 February 1977 WU was given repeatedly by males courting on land prior to a courtship-pursuit-flight.

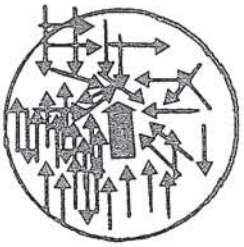
Wings-up was also seen commonly on the breeding grounds (19 times). Here it was performed quickly prior to a more aggressive action (i.e., chase or fight). Paired males performed WU prior to spacing out onto territories (three times in each of April 1976 and 1977). When two pairs swam or fed less than 2 m apart at this time, it usually led to Inciting and Chin-lifting by the females and brief WU displays by the males. Males followed this with an aggressive chase with head out and bill open, usually directed at the female of the other pair. This resulted four times in one pair swimming away (2-3 m) and twice flying a short distance (2-6 m).

Once territories were established, WU was given only briefly by paired males when they trespassed onto a territory and were threatened by the resident male prior to a pursuit flight. Later in the spring, territorial males also performed this display when lone males trespassed.

Fig. 23. Position of male wigeons performing Wings-up. Dark arrow in centre indicates female's position. Distance between adjacent circles is 0.3 m. Lower circles indicate additional observations within 0.3 m of the female.

Wings-up





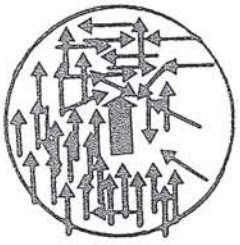
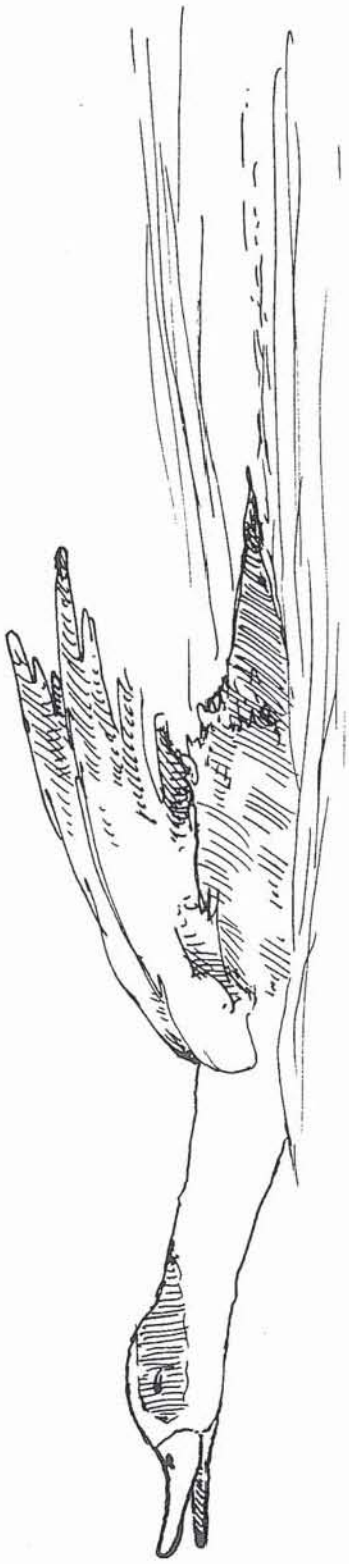


Fig. 24. Male wigeon swimming aggressively toward another male.



This was followed by a bout of Tandem-swimming (TS) and then usually by a pursuit flight between the two males (four in 1976 one in 1977). It should be noted, however, that most of the TS observations did not include WU (see below).

As in other aggressive displays, the male performing WU dramatically increased his apparent body size. This may have assisted in establishing dominance over other males (Chapter 5). Again, with the wings raised the white upper wing patch, indicative of age (Wishart 1981) was displayed. Tail-wagging also drew attention to the black and white rump bands again indicative of the stage of molt (see Chapters 3 and 5).

Aggression

Aggression was a common component of wigeon courtship. The most usual threatening posture was performed with body low and tail straight. The head and neck were stretched low, parallel to the water, and the bill opened (Fig. 24). While in this posture the bird swam rapidly with the intended recipient in retreat. This was recorded 51 times on film. As mentioned, this behavior often followed Wings-up displays. Eleven times this ended with the aggressor nipping the tail of the victim and once grabbing his dorsal feathers. As mentioned, paired males frequently performed this threat from the Face position. Six such aggressive streaks averaged 2.7±0.8 s with the male requiring 4.7±2.2 s (N=4) to rejoin his female after breaking off the pursuit. In these attacks the male chased an average of 1.7±0.7 m (N=8) before swimming back, travelling at approximately 2.4 km/h.

Vigorous fighting between courting males was recorded 13 times. This activity involved grabbing the opponent's feathers with the bill, pecking it and beating it with the wings. One male usually could be distinguished as the aggressor, often with the other attempting to escape and join the female. While two males fought, especially in an extended bout, the female and the other males watched alertly.

Often during courtship, males were aggressive toward the female. Five times males nipped at the female's rump forcing her to spurt ahead. At other times vigorous grabbing chases of the female occurred similar to the forced copulation attempts seen later during the breeding season (Chapter 6) (see also Soutiere et al. 1972).

On 8 January 1975 in a courtship party, two males briefly mounted a partially submerged female. In another group on 14 January 1975, one male vigorously attempted to move the female away from the others. She tried to avoid him but he succeeded in mounting her briefly several times. While on top he pecked and grabbed repeatedly at the back of her head as if attempting to copulate (see below). The female flushed eventually, but when she landed, a male (possibly the same one) again attempted several times to mount her. On one of these attempts he struggled over her completely submerged body. On 4 January 1977 a courting male tried unsuccessfully to mount a female forcefully. On 17 January 1977 during vigorous courtship, several males apparently tried to mount a female. She dived repeatedly (each time for less than 1 s) apparently in an attempt to escape. On 21 February 1977 a courtship party was observed in a wet potato field on Westham Island, British

Columbia. Several males fought vigorously and it appeared that two attempts were made to copulate forcefully with the female. In none of these sequences was cloacal contact observed before the male(s) dismounted or the female escaped.

Group Flights Associated with Social Display (GFASD)

Group Flights Associated with Social Display (GFASD) (Hochbaum 1944, Dzubin 1957), described for wigeon by Soutiere et al. (1972), occurred commonly (N=120) throughout the winter in British Columbia. Six GFASD were also seen during April at Moose Jaw (Chapter 6). First GFASD were observed on 11 December 1974 and 3 January 1977. During casual observations on 30 October 1982 at the Maplewood study area, a vigorous GFASD occurred consisting of one female and seven males. Courtship activity continued on the water afterward for at least 10 min.

These flights usually followed aggressive chases of a female on the water by courting males. These appeared to be attempts by the males to get closest to the female. At other times forced copulation of the female seemed to be the objective (see also Soutiere et al. 1972). Chases usually began if one male was unable to dominate the others, or if the female did not favor a particular male. Several times dominant males lunged aggressively at another male and, in his brief absence, the other males had an opening in which to press close to the female. The female's retreat led to more aggressive wing-flapping chases over the water until eventually a GFASD ensued.

GFASD averaged 6.8±2.6 males (Range=3-16 males) and 1 female (N=120), whereas courtship parties before flights averaged 7.2±3.0 males (Range=4-18 males) (N=30). GFASD were characterized by rapid, twisting, down-up flying, interspersed with periods of gliding. Females seemed to be trying to avoid males, and they uttered inciting calls and several times performed over-the-shoulder Inciting. Males repeatedly performed Fast Whistles and several times adjacent birds collided wings in an effort to manoeuver after the female.

Often flights ended after short dashes over the water but others lasted much longer (i.e., 50 s, 125 s, 270 s, 303 s, 476 s, +600 s, and +840 s). As flights continued, some males flew up to join in, whereas others dropped out. Usually over the course of the flight, the female set her wings as if to land but then resumed flight. This usually resulted in some of the males dropping down and landing. One GFASD that consisted of up to eight males and one female ended with only one male and the female continuing on together. Of 15 flights observed for at least 2 min, only two ended with more males than when the flight began. Overall, the average number of males decreased 1.8±2.4 (Table 21).

Female Displays

Chin-lifting and Inciting (CL and INC)

Chin-lifting (CL) and Inciting (INC) were the most common displays performed by the female during courtship. The threatening component (INC) consisted of a posture in which the head was lowered and the neck stretched forward as the bill was opened. The head was drawn back

Table 21. Changes in number of participants over the course of 15 extended Groups Flights Associated with Social Display (GFASD) observed in British Columbia during winter, 1977.

GFASD number	Date[1]	Sequential number of participants	Overall change[2]	Time[3] (s)
1	3/1	11-9	-2	125
2	15/1	9-10-8-7-6-7-6	-3	
3	20/1	17-11	-6	
4	21/2	9-8	-1	
5	23/2	6-5-6-5	-1	
6	24/2	6-7-9-10-13-15-6	0	
7	24/2	6-7-9-8-7-8-9-8	+2	
8	24/2	9-8-7-6-8-7-8	-1	270
9	24/2	10-9-7-6-7-6-5	-5	476
10	8/3	9-7	-2	
11	10/3	10-11-12-13-15-10-8	-2	303
12	10/3	8-9-2	-6	
13	12/3	7-6-7-6-5-6	-1	+600
14	12/3	7-9	+2	
15	12/3	8-6-7	-1	
$\bar{X} \pm$ SD			-1.8 ± 2.4	

[1]Day/month.

[2]Change from beginning of flight to end.

[3]Blanks indicate that a time was not measured.

repeatedly and up and then out again (Fig. 25). A low growling vocalization (Inciting Call) was repeated during this movement (see below). When a female was following a male who was Turning-back-of-head, she often stretched her head back with bill open as she threatened other courting males who were following. This over-the-shoulder INC was given also while Facing the preferred male. Three times it was given by a female as she was pursued in a GFASD and once by a female on land while she was following a male who was Turning-back-of-head.

The CL component seemed to be directed toward a favored male. Here the head was drawn back and upward repeatedly, often between bouts of threatening other males (Figs. 25 and 26). Several times in captive birds, CL occurred continuously with Bill-dipping. Thus, the bill was raised out of the water forcefully with each CL. As this was performed a stream of water droplets was repeatedly flicked toward the intended recipient of the display (Fig. 27). This was similar to the directed Grunt Whistle display of other Anas species (Johnsgard 1965). Intermittently between CL and INC, the female also performed Bill-dips, Head-Shakes, Preen and Tail-wags.

The intensity of these displays varied greatly from intermittent, barely perceptible CL, to very pronounced, rapid CL interspersed with fast swimming, loud vocalizations and exaggerated over-the-shoulder INC. The most vigorous displays were performed when the female was pursued closely by several males, particularly just before or after a GFASD.

Fig. 25. Female wigeon performing Chin-lifting and over the shoulder Inciting. Numbers of film frames are indicated at the bottom.

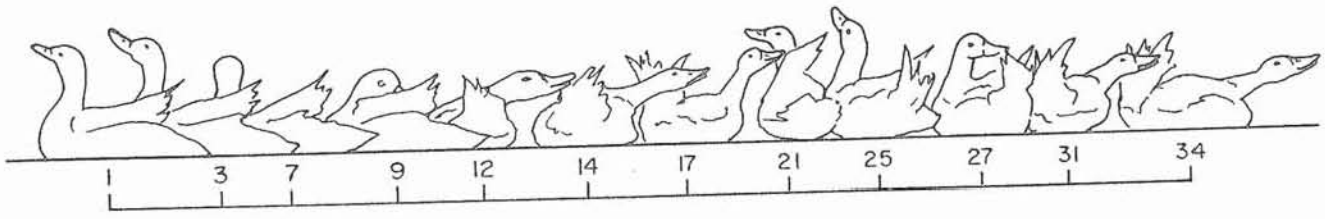

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34

Fig. 26. Female wigeon Chin-lifting. Numbers of film frames are indicated at the bottom.

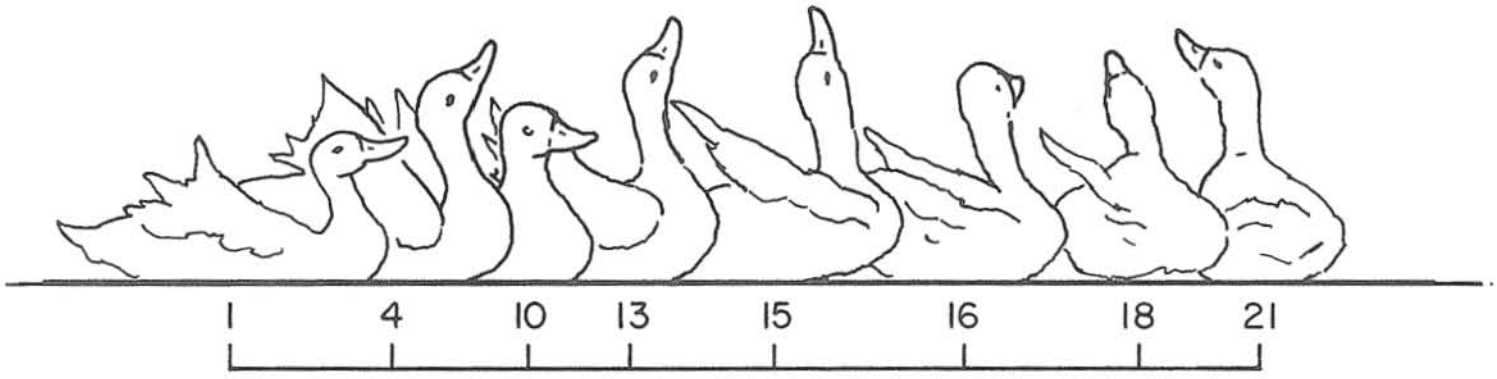
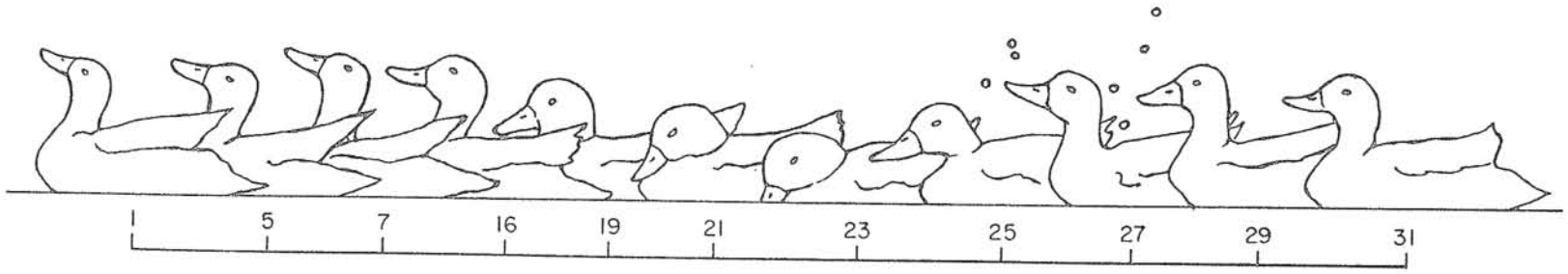

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21

Fig. 27. Female wigeon Chin-lifting. Note the bird Bill-dipping and flicking water droplets in frames 23 to 29. Numbers of film frames are indicated at the bottom.


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31

Inciting movements also were performed by females on the breeding grounds. Just after spring arrival, pairs remained in flocks. When two pairs moved within 1 m of one another, however, particularly when feeding, females reacted by CL and INC. This usually culminated in aggression between the males. In a captive flock, females INC and CL vigorously between bouts of threats and pecks at another female restrained in a cage within their territory. Such behavior also was performed by wild and captive females when harassed by unpaired males.

Inciting usually had a dramatic effect on males. For example, occasionally when following a male Turning-back-of-head, the female swam back among the other males while CL. When this occurred, male displays and aggression increased. Once on 20 January 1975, two males in a courtship party began fighting vigorously while the female was INC. Much pecking, feather pulling and wing beating occurred. Close to this fight the female, with Wings-up, and the other males, observed alertly. Several times during the fight the female swam into the melee while CL and INC, apparently indicating her choice of a mate. Eventually the fight ended with the female beside one of the fighting males and INC at the other.

During some interspecific aggressive encounters, females also performed INC movements. This occurred six times toward Mallards, five times toward Gadwalls, once toward an American Coot and once toward an American Crow. McKinney (1970) also observed interspecific INC in Blue-winged and Cinnamon Teals, which contradicts the assumption that this is exclusively a sexually related behavior.

Wings-up (WU)

During courtship, females also performed WU in an aggressive context. Usually it was less pronounced than that of males and I observed it only nine times. It usually was given during bouts of Chin-lifting and Inciting, and when other individuals were threatened. In most cases the wings were raised only slightly off the back and rarely were the primaries crossed (Fig. 26). Tail-wagging, characteristic of males, was observed only once.

On the breeding grounds I saw females perform WU only interspecifically; twice a paired female at another pair and a lone male Gadwall, respectively, and once a female with a brood at a lone male Gadwall.

Other Displays

Females infrequently performed other displays during courtship. Wing-flap was seen six times; five times following Wing-flap or Swimming-shake by males, and once when a female who was performing Chin-lifting swam back through a group of courting males. Females performed Swimming-shake six times. Five of these followed Swimming-shakes by courting males and once prior to threatening a male. Bathe was seen twice. Both times several courting males reacted by also Bathing. The Facing display has already been described for males. Females performed this display concurrently. Similar to males, females intermittently threatened other courting males nearby from this position.

Pair Maintenance

Once a pair bond formed, the individuals involved had to synchronize their activities. Otherwise, because they were congregated in large mobile flocks prior to breeding they easily could become separated.

The compatability of partners was constantly tested by the disruptive courtship intrusions of conspecifics (Chapter 5). Mates able to coexist, and resist these over the winter and early spring then were likely able to make a nesting attempt together.

Members of wigeon pairs displayed and vocalized in several ways to synchronize their activities, keep themselves together and strengthen their bond. It was apparently also a function of some of these displays to test the compatibility of potential mates (Chapter 5). Incompatibility probably would lead to a reduced or unsuccessful reproductive effort. A genotype having the ability to identify such individuals would be adaptive (Chapter 5).

Facing and Turn-back-of-head (FA and TBH)

These displays, described previously in relation to pair formation, were important also in pair maintenance. Mates concurrently performed the displays when conspecific courting males were present. On several occasions females did not cooperate with a displaying male. Several times females did not follow a male who was TBH but responded instead by Inciting. One male FA a female and attempted to direct her away from other males but was pushed aside by the female who succeeded in rejoining the other courters. In this situation a bond either did not form or was dissolved.

Preen-behind-wing (PBW)

Preen-behind-wing (PBW) also was associated regularly with courtship, but when performed concurrently by both sexes it probably signified that a pair bond existed (seen 14 times during winter). It often occurred while the pair was FA (Fig. 21) and occasionally while Turning-back-of-head. Eight times PBW was performed by only one of the mates.

Typically, an individual preened on the side facing his mate. While preening, the wing was partially opened, exposing the age-indicative wing coverts (Wishart 1981) (Fig. 28). Numerous other displays and displacement behaviors were associated with PBW (see Table 22).

Pre-flight-intention (PFI)

If birds were not suddenly threatened, flying usually was preceded by short or extended bouts of Pre-flight-intention movements (PFI). This behavior occurred both in paired and unpaired birds with the probable function of synchronizing take off, and maintaining either flock or pair bond integrity. When danger preceded flight, Slow Whistle vocalizations also were performed by males.

The primary display given by both sexes was a series of Head-jerks (HJ). This behavior differed from precopulatory Head-pumping in that the rapid head movement was up rather than down. In addition, only the head and bill were moved but not the neck, as in precopulatory displays.

Fig. 28. Female wigeon Preening-behind-wing while male Faces.

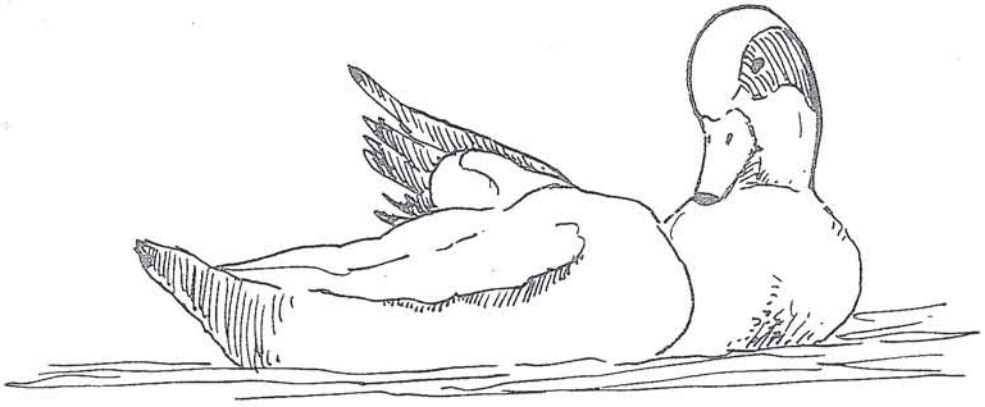


Table 22 . Frequency of behaviors occurring before and after Preen-behind-wing (PBW) by male and female wigeons during winter courtship in British Columbia.

Behavior	Before PBW			After PBW		
	Male	Female	Sig.[2]	Male	Female	Sig.[2]
Head-shake	21	7	**	10	5	NS
Bill-dip	3	0	NS	4	1	NS
Head-rub	2	0	NS	3	0	NS
Face	2	0	NS	0	0	NS
Tail-wag	0	2	NS	1	1	NS
Bathe	1	0	NS	1	0	NS
Head-flick	1	0	NS	3	0	NS
Turn-back-of-head	0	0	NS	0	4	NS
Chin-lift	0	5	NS	0	4	NS
Wing-flap	0	2	NS	0	3	NS
Swimming-shake	1	0	NS	0	1	NS
Retreat[1]	0	0	NS	1	0	NS

[1]Male performing Preen-behind-wing was chased by another male.

[2]NS=$P>0.05$, binomial test; **=$P<0.01$, $x^2=7.0$.

Typically the head and neck were held alertly while facing into the wind. The body was low and the tail was level with the water. The head was jerked rapidly up and backward which caused the forepart of the body to rock gently. As the head was jerked backward it was rotated down to the starting position and the movement repeated. By contrast, I noted that Mallards in a similar display tended to jerk the head up and forward.

Other displays and displacement activities associated with PFI included Head-shakes, Preen-behind-wing, Head-rub, Alert, Tail-wag, Preen-breast and Double-wing-stretch. The vigor of HJ was greater just prior to flushing.

Drink (D)

Drinking (D) was performed infrequently in the spring, either concurrently by pair members (four times) or by the male only (twice). This movement differed from functional drinking in that individuals performed exaggerated movements, occasionally in unison. After briefly touching the bill to the water the head and neck were extended up to a 45° angle and held briefly (N=2; 1.4 and 2.7 s). This movement was usually repeated several times (N=2; 2 and 5 times).

Once D occurred immediately after a pair landed on their territory and three times it was not preceded by any noticeable movements. Once a captive male performed D following copulation while his mate fed and once while the female (wild) was threatening another pair early in the spring.

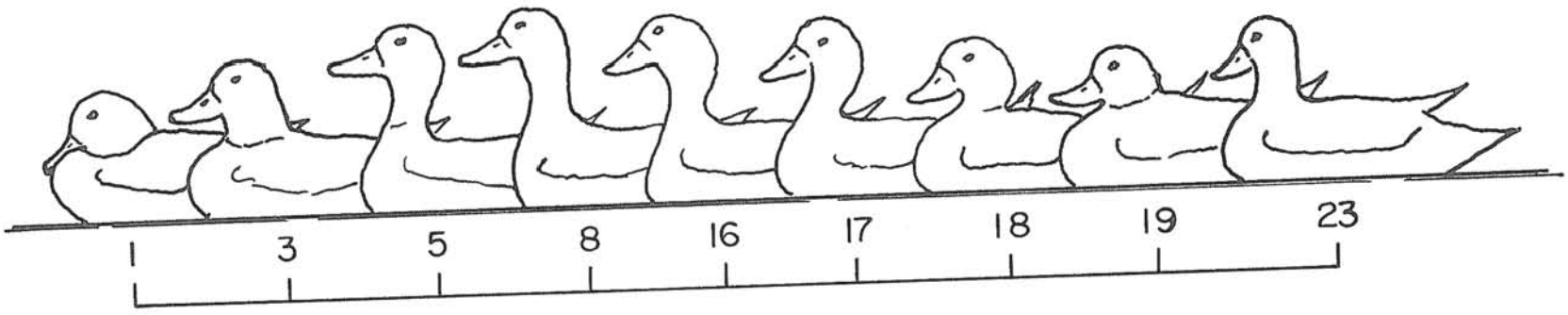
Copulatory Behavior

Wigeon copulation and associated displays have not been described fully, although there are several accounts (Hambleton 1949, Bartlett and Atwell 1955, Johnsgard 1965, Soutiere et al. 1972). In Chapter 6 I discuss wigeon copulation as it relates to the evolution of the mating system. Here I present a more detailed description of the behavioral sequences involved in copulation. As mentioned in Chapter 6, precopulatory Head-pumping (HP) did not always lead to copulation, whereas some copulations by paired birds were not preceded by HP (i.e., forced pair copulations).

Head-pumping was performed while the bird was either swimming or stationary on the water. The head held alertly, was elevated by stretching the neck up slowly, followed by a short pause and then a more rapid lowering by retracting the neck (Fig. 29). This pumping action was repeated several times before copulation occurred. The time between minimum and maximum head elevation averaged 0.83±0.15 s (N=4) for a male, whereas the downward motion occurred about twice as rapidly (0.39±0.18 s, N=4). Eight complete pumps took an average of 1.21±0.14 s each. The vigor (amount of neck extension) and speed of pumping all increased prior to the male mounting the female.

Occasionally Dash-and-dive (DD) rather than HP occurred prior to copulation. This behavior was similar to that occurring prior to forced pair copulation (Chapter 6). Four examples of this behavior which was observed only on the breeding grounds, are described below:

Fig. 29. Wigeon performing precopulatory Head-pumps. Numbers of film frame are indicated at the bottom.


1
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8
16
17
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19
23

1) (13 May 1976, 1020 h, male A3 and mate). The male swimming alertly dived beside the female and on surfacing Wing-flapped. Thirty seconds later the female initiated HP and the male, while swimming behind, reciprocated. Copulation did not occur. The male performed Bathe, Wing-flap, Tail-wag and Head-shake and the female concurrently Wing-flap and Head-shake and remained Alert. Thirty seconds later the pair flew to an adjacent stubble field.

2) (25 April 1977, 1600 h, pair A5/A4). The male swam toward the female. She, then he, dived with wings half open. As they surfaced both dashed across the water and dived again nine times in sequence. Between dives and dashes birds performed bouts of Preening, Scratching and Wing-flapping and several times the male grabbed unsuccessfully at the female as if attempting to mount her. Dives by the female averaged 6.0±3.5 s (N=3) and by the male 2.4±1.8 s (N=7). Intervals of dashing and displays between dives averaged 0.6±0.3 s (N=6).

3) (17 May 1977, 1004 h, female E3 and her mate). The male followed the female alertly. The male swam rapidly HP but the female did not reciprocate. The male Bill-dipped and both began HP. HP ceased and the male drifted away. The female resumed HP and the male rejoined her rapidly and HP. The male then chased the female and grabbed her tail. She dived as did he, they surfaced, dived again and resurfaced in unison. No copulation occurred and both birds performed a series of displays (male: Wing-flap, Bill-dip, Head-shake, Preen-behind-wing, Bathe, Wing-flap, Preen-behind-wing, Tail-wag and Head-shake; female: Bathe, Wing-flap, Bill-shake, Head-shake, Preen-behind-wing, Bill-dip and Preen-behind-wing).

4) (30 May 1977, 1342 h, pair 06/E3). The female dived with half open wings for 5 s, surfaced and preened. The male swam to join her and both dived for 5 s. When they surfaced the male was mounted holding the female's nape in his bill. He remained mounted for 4 s but I could not see if intromission occurred. Afterward the male Wing-flapped and the female Preened.

Usually before mounting, the female stopped HP and assumed a Prone (PR) position. The male mounted her from the side while grasping her nape in his bill and continued to perform HP movements. Seven upward movements recorded on film averaged 0.51±0.35 s and 6 downward 0.21±0.0 s. This action by the male forced the female's head up and down also. When down, the male pushed her until often she was completely submerged. Possibly this action was a means of forcing the female to elevate her tail, facilitating cloacal contact.

Once intromission occurred the male dismounted immediately and postcopulatory displays followed. Twenty-seven sequences were observed on the breeding grounds or in pens.

Male behavior differed markedly from that of females (Table 23). Males became Alert in 93% of cases compared to 37% for females. Conversely, females performed Wing-flap and Bathe 96% of the time and males just 59% and 26%, respectively. Preening and Scratching were primary activities of females, whereas the sexes performed about equally Swimming-shake, Bill-shake, Head-shake, Tail-wag and Dabbling. Males occasionally Vocalized (Slow Whistle) and Faced their mate following copulation but females did not perform these behaviors. On one occasion (23 April 1977, 1346 h, pair A5/A6) DD (male 6 dives and female 5 in 4.4 s) occurred following copulation. Cramp (1977) reports a similar DD sequence following copulation by a pair of Eurasian Wigeon.

Other descriptions of American Wigeon post-copulatory behavior are sparse. Johnsgard (1965) reports the male assuming an Alert posture while Facing the female. Soutiere et al. (1972) also observed males becoming Alert in two out of three post-copulatory sequences they observed in winter.

To summarize, a description of a complete copulation sequence filmed in a flight pen at the Delta Station is given below. This sequence was performed on 9 May 1978 by a pair of captive birds.

Table 23. Frequency of behaviors occurring after 26 observed wigeon copulations.

Behavior	Frequency		Statistic[1]	Significance[2]
	Male	Female		
Alert	25	10	20.8	***
Bill-dip	13	8	11.0	***
Swimming-shake	3	2		NS
Scratch	5	14	4.2	*
Bathe	7	26	11.0	***
Bill-shake	6	7	0.1	NS
Head-shake	13	18	0.8	NS
Preen-behind-wing	3	14	7.1	**
Tail-wag	25	25	0	NS
Face	2	0		NS
Dive	1	1		NS
Dabble	9	9	0	NS
Drink	3	1		NS
Vocalize	3	0		NS
Wing-flap	16	26	2.2	NS
Preen-body	14	21	1.5	NS
Head-rub	0	9		**

[1] x^2 value. Missing values indicate use of the binomial test.

[2] NS=$P>0.05$, *=$P<0.05$, **=$P<0.01$, ***=$P<0.001$.

Both birds performed 4 HP, the male behind the female. The female assumed the PR position and the male required 53.0 s to mount her from the right side. The male grasped the female's nape with his bill and performed 12 HP. The female's head was submerged 5 times, each for an average of 0.4±0.2 s. She did not struggle but attempted to maintain her PR position. Due to the rocking motion, the pair revolved 130° and then back again to almost the starting position. The male rotated his tail to his left, attained cloacal contact and flopped to his right off of the female after mounted for 33.8 s. When off, the male assumed an Alert posture and Tail-wagged for 1.5 s. The female with head alert but body still flattened and wings slightly opened, remained motionless for 3.9 s. She then performed ruffle Bathing for 2.5 s and Wing-flap for 2.7 s (11 wing flaps). This was terminated with a Tail-wag and Head-flick. After an interval of 1.6 s she performed Bill-dip, Preen-behind-wing in 2 sequences of 11.1 and 4.7 s each. This was followed by a 0.5 s interval, a Bill-dip, a 3.0 s interval and 20.9 s of drink and dunk Bathing (4 dunks). The male continued Alert and Faced 0.3 m away. The female then did a Wing-flap for 3.5 s (13 flaps), a Tail-wag, swam for 3.2 s and did a Head-flick. She then Preened-behind-wing for 1.7 s, Head-flicked, Bill-dipped, Head-flicked, swam, Dabbled, Head-flicked and swam. The male swam Alertly following her and performed Drink for 2.7 s. The pair then fed while swimming to shore.

Territorial Displays

Paired wigeon males did not tolerate conspecifics on their breeding territories. In Chapter 6 I describe the pursuit flights used to expel intruders. Pursuits of pairs were initiated rapidly. However, Tandem-swimming (TS) usually occurred prior to pursuit of single male trespassers.

Tandem-swimming was a common display seen only on the breeding grounds and usually late in the spring after females were nesting. It occurred when a lone male entered another male's territory, either when his female was present or absent (Chapter 6). The territorial male swam alertly towards the intruder who responded by swimming away, usually facing into the wind. The birds continued to swim alertly in single file with the territorial male eventually overtaking the intruder. Tandem-swimming early in the spring generally was shorter but overall averaged 103.4±158.7 s (N=34).

The most conspicuous component of this display was the rapid Chin-lifting (CL) performed simultaneously by both males as they swam. These movements seemed identical to those performed by Inciting females. Chin-lifting was performed with the bill pointed up. The bill was jerked up rapidly, dropped to the starting position more slowly and these movements were repeated many times in succession.

Other behaviors were interspersed frequently with sequences of CL. Both males regularly performed Head-shakes, Bill-dips, Preening and Dabbling movements as they swam. Scratch, Swimming-shake, and Tail-wag occurred with lower frequency. From Table 24 it is seen that territorial males performed significantly ($P<0.05$) more Bill-dips, Bill-shakes and Dabbles, whereas trespassers performed more Scratches, Preening, Swimming-shakes, and Tail-wags. Both groups of males performed Head-shakes at about the same frequency.

As the birds moved, the greatest acceleration and intensity of displays coincided with CL. The leading male usually proceeded with his head held sideways which undoubtedly allowed him to observe better the following male. The displays usually ended with the males drifting apart or flushing into a pursuit flight (Chapter 6).

Tandem-swimming has not been recorded before for wigeon. I have seen male Gadwalls perform similar movements (Wishart, unpubl. data), but Dwyer (1974) has imprecisely described this behavior. The function of this display seems similar to that of threatening hostile pumping, characteristic of blue-winged ducks (McKinney 1970). Aggressive Cl

Table 24. Frequency of behaviors occurring between sequences of Chin-lifting during Tandem-swimming by territorial and trespassing male wigeons at Moose Jaw.

Behavior	Frequency		Statistic[1]	Sig.[2]
	Territorial	Trespasser		
Bill-dip	36	17	6.8	**
Head-shake	45	36	1.0	NS
Scratch	9	30	11.3	***
Bill-shake	14	5	4.3	*
Preen	31	49	4.1	*
Dabble	44	6	28.9	***
Swimming-shake	1	8		*
Tail-wag	0	6		*

[1] x^2 value. Missing values indicate that the binomial test was used.

[2] NS=$P>0.05$, *=$P<0.05$, **=$P<0.01$, ***=$P<0.001$.

displays are widespread in waterfowl species (Johnsgard 1965). This movement and the associated displacement activities are similar to those given by wigeons prior to normal flights (Preflight-intention-movements). Indeed pursuit flights often followed TS. However, normal Pre-flight-intention movements served a social function to synchronize flight, whereas TS communicated hostility and potentially physical aggression.

Vocalizations

Males

Slow Whistle (SW)

The principle vocalization of the male American Wigeon was the Slow Whistle (SW), a trisyllabic, high pitched whistle. It has been denoted phonetically by Bent (1962) and Johnsgard (1971) as "Whew-whew-whew" and also as "fi-ew-whew" by Griscom (1922).

Bellrose (1976) pointed out that the second syllable was of highest pitch and sonographic analysis has indicated that the accent was given on this note (Johnsgard 1971). The fundamental frequencies of the other two syllables were of about equal maximum pitch, at about half that of the second (Fig. 30, Table 25).

Three of four males tape recorded also gave this call in a four syllable phrase interspersed with the usually more common three syllable pattern (Fig. 31, Table 25). Overall, the characteristics of the first three syllables seemed similar to those of the three-noted call (Table 25).

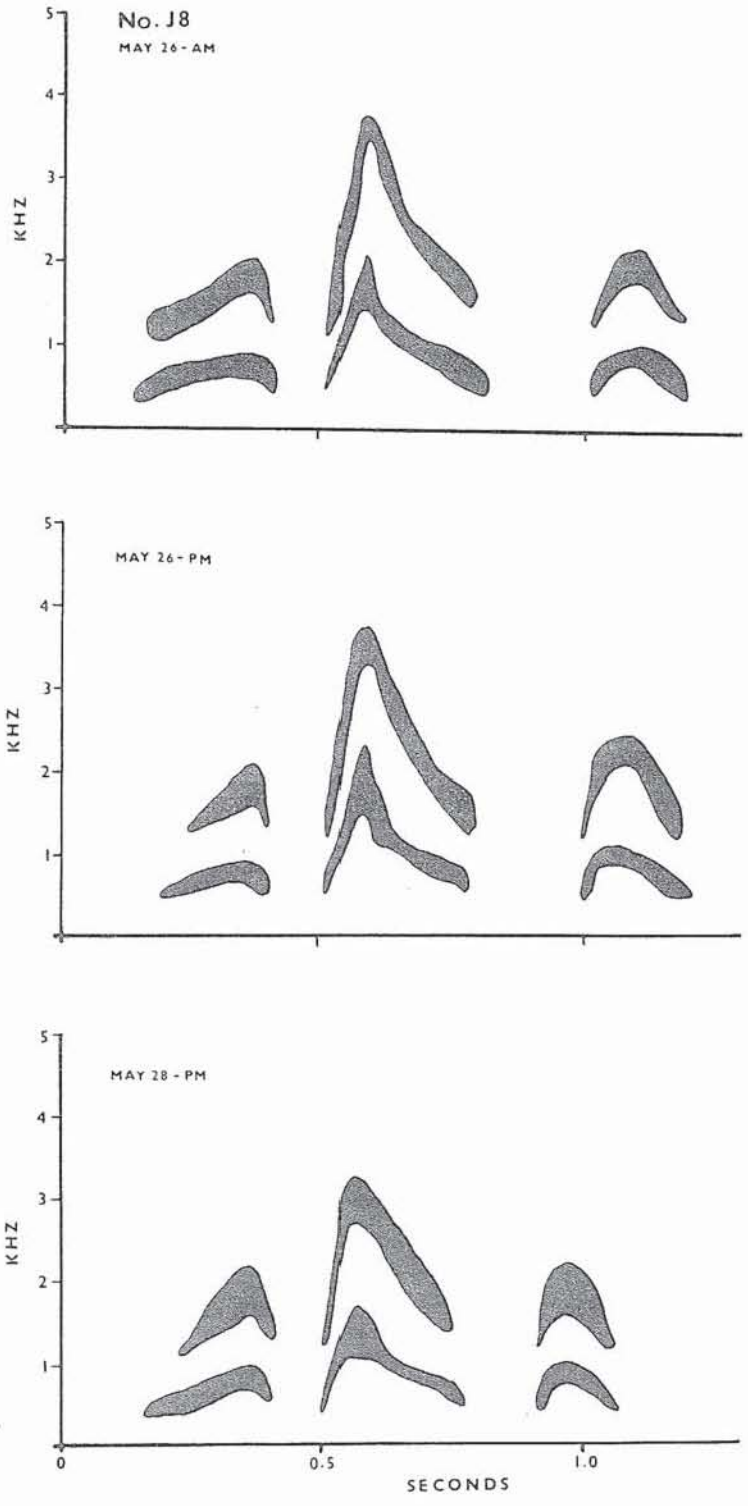

No. J8
MAY 26 - AM
MAY 26 - PM
MAY 28 - PM
KHZ
5
4
3
2
1
0
0.5
1.0
SECONDS

Table 25. Characteristics of Slow Whistles uttered by male wigeons. Measurements from sonograms (see Fig. 14).

Measurement[3]	Syllable	Three syllables[1] Mean	Three syllables[1] Range	Four syllables[2] Mean	Four syllables[2] Range
Peak frequency	1	973.0	864.9-1057.1	970.0	864.9-1009.1
	2	2306.4	1537.6-2642.8	2473.5	2354.5-2594.7
	3	1441.5	672.7-1777.9	1794.5	1633.7-2018.1
	4			921.5	768.8-1153.2
Harmonic frequency[4]	1	1189.2	1057.1-1393.5	1261.0	1105.2-1393.5
	2	2018.1	1393.5-2690-8	2231.0	2066.2-2642.8
	3	1407.9	961.0-1777.9	1600.5	1489.6-1777.9
	4			1455.0	816.9-2354.5
Total duration	1	0.17	0.08-0.28	0.15	0.08-0.26
	2	0.22	0.16-0.29	0.19	0.16-0.24
	3	0.14	0.08-0.19	0.16	0.15-0.18
	4			0.10	0.80-0.21
	1+2+3[5]	0.80	0.66-1.03	0.75	0.69-0.84
	1+2+3+4[5]			1.05	0.99-1.15
Syllable interlude duration	1-2	0.10	<0.01-0.13	0.11	0.07-0.12
	2-3	0.15	0.10-0.38	0.12	0.08-0.16
	3-4			0.21	0.13-0.27

Table 25. Cont'd

Measurement[3]	Syllable	Three syllables[1] Mean	Three syllables[1] Range	Four syllables[2] Mean	Four syllables[2] Range
Up slope	1	43.8	34.0-59.0	40.8	32.0-50.0
	2	83.3	79.0-85.0	83.0	81.0-85.0
	3	78.5	57.0-82.0	81.0	78.0-83.0
	4			63.0	35.0-80.0
Down slope-top	1	72.0	63.0-77.0	70.5	50.0-79.0
	2	76.0	56.0-82.0	80.0	78.0-83.0
	3	70.3	50.0-77.0	73.0	70.0-80.0
	4			64.0	50.0-70.0
Down slope-bottom	1	72.0	63.0-77.0	70.5	50.0-79.0
	2	62.3	50.0-72.0	67.0	60.0-72.0
	3	65.3	50.0-72.0	68.0	63.0-72.0
	4			68.0	63.0-72.0

[1]N=22 calls from 4 individuals.

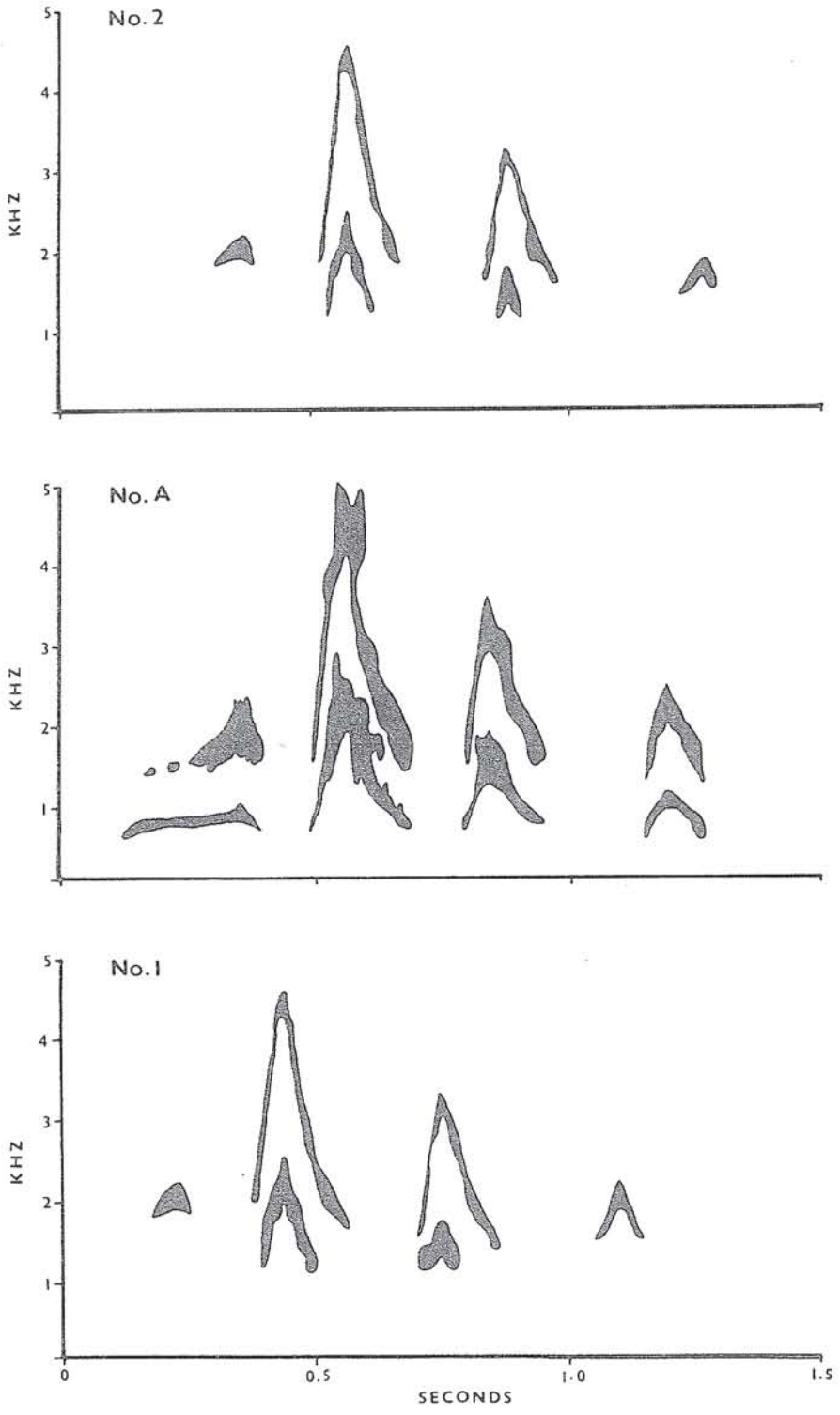
[2]N=12 calls from 3 individuals.

[3]Frequency=hz; duration=s; slope=degrees.

[4]Frequency range between peak of fundamental and peak of first harmonic.

[5]Includes syllable durations plus intervals between syllables.

Fig. 31. Sonograms of four syllable Slow Whistle given by three different male wigeons (A=captive, 1 and 2=wild). All calls given while the female was absent.


No. 2
No. A
No. 1
KHZ
5
4
3
2
1
0
0.5
1.0
1.5
SECONDS

Normally one to five evenly spaced harmonics of each syllable occurred above the fundamental, but occasionally the first and fourth syllables lacked these. The highest harmonic of the second syllable reached up to 15 khz.

The SW occurred at all times of the year in contexts similar to the Repeated Call of blue-winged ducks (McKinney 1970), Burp Call of Pintail (Derrickson 1977) and Green-winged Teal (McKinney 1975) and Slow Raehbs of the Mallard (Abraham 1974). However, sonograms were not available for this call in all of its social contexts and subtle differences in pitch and timing may exist.

The SW was given in response to distant disturbance or danger. It was noted most frequently when raptors or other potential predators approached wild wigeons slowly from afar, or when a human entered a pen of captive individuals. This was often followed by flight or Pre-flight-intention movements. Slow Whistles also were given frequently in the winter and spring during social courtship. The Burp display accompanied this call.

Once pairs were formed, SW was given when mates became separated. This often occurred in large mobile flocks of wintering or staging birds. After arrival on the breeding grounds wigeon pairs dispersed from flocks onto individually defended territories (Chapter 6). The SW was an important contact call given either while the female was at the nest or when the male returned to his female after being absent in pursuit of territorial trespassers (Chapter 6).

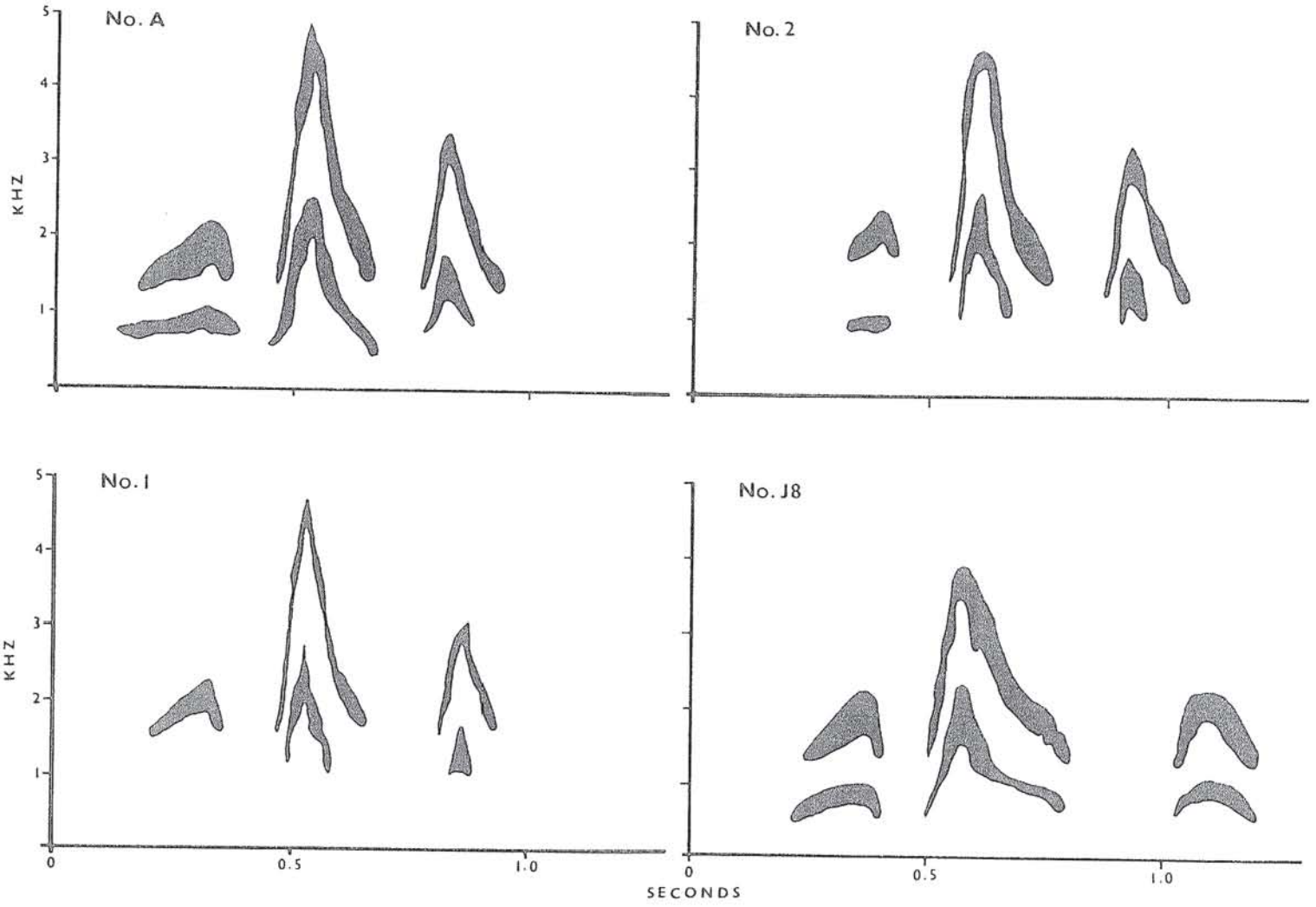
Lone males also performed SW as they searched emergent aquatic vegetation for females other than their own. The actions of these males seemed to be sexually motivated (see four examples of this behavior described in Chapter 6).

Sonograms indicate the similarity in pattern of three syllable SW given by the same male, even when recorded several days apart (Fig. 30) but the calls of different individuals varied greatly (Fig. 32). One-way analysis of variance of factor scores for each vocalization corroborated this ($P<0.01$, N=4 males, 22 vocalizations).

Stepwise discriminant analysis selected frequency (F3) and time to complete (T5) the third syllable, and the bottom part of the down slope of the second syllable (S5) (i.e., the speed and frequency range of termination) (Fig. 30) as the most useful discriminators of individual three syllable SW. These variables alone permitted 93.8% of the vocalizations to be correctly identified using the U-method of Lachenbruch and Mickey (1968).

There were too few four syllable SW to test if they too could be separated individually by discriminant analysis. However, the discriminant functions derived from three syllable calls were not useful in identifying an individual based on the characteristics of the first three notes of his four syllable call. A classification error rate of 50% occurred indicating some modifications of the first three syllables when a fourth was added. The difference seems to be mainly of tempo, the notes being compressed slightly in time (Table 25).

Fig. 32. Sonograms of three syllable Slow Whistle given by four different male wigeons (A and J8=captive, 1 and 2=wild). All calls given while the female was absent.


No. A
No. 2
No. 1
No. J8
KHZ
KHZ
5
4
3
2
1
0
0.5
1.0
SECONDS

Fast Whistle (FW)

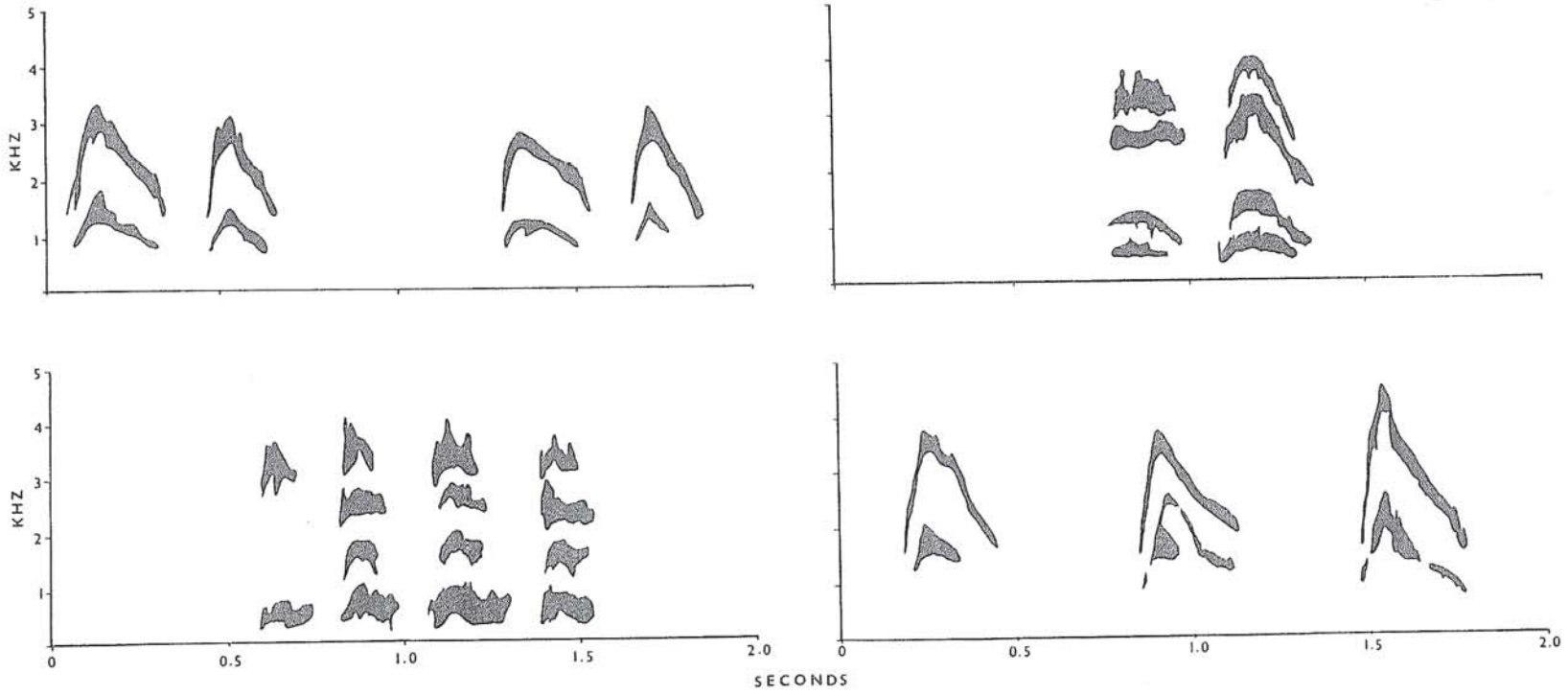
The Fast Whistle (FW) was usually a single or multiple syllabic "whew" call given by the male in times of anxiety (Fig. 33). Thus, it occurred in similar contexts to the Gee Call of Pintail (Derrickson 1977), Fast Call of blue-winged ducks (McKinney 1970) and Rabrab Call of Mallard (Abraham 1974).

The FW was given by captives when approached closely by a human. Thus, it occurred at times of greater danger than situations in which the SW was performed. The rate and intensity of the call and the range of frequencies emitted increased with the closeness of the danger.

The FW was given in the wild during aggressive encounters between courting males, or when pairs came into conflict during the prebreeding period and breeding seasons (see also Wetmore 1920, Palmer 1976a). During courtship, males uttered these calls while in aggressive chases and when displaying with Wings-up. It was heard frequently when the female Incited. It is possible that the FW was given also during Tandem-swimming and in male:male pursuit flights, but I did not hear it.

A possible variant of FW was given occasionally by males while they flew over the breeding territory accompanied by their mate. In this situation a low drawn out "pheeooo pheeooo" call was given. The function of this call is unknown.

Fig. 33. Sonograms of four patterns of Fast Whistles given by captive male wigeons during interpair territorial encounters.


KHZ
5
4
3
2
1
KHZ
5
4
3
2
1
0
0.5
1.0
1.5
2.0
0
0.5
1.0
1.5
2.0
SECONDS

Females

Inciting Call

The Inciting Call was performed concurrently with Chin-lifting and Inciting displays. It consisted of a series of repeated low gutteral growls and has been variously described as "kaow kaow" (Eaton in Bent 1962), "qua-auk qua-auk" (Wetmore 1920) and "errr errr" (Johnsgard 1965). It occurred commonly in social courtship on the water but also continuously during Courtship-pursuit-flights.

Alarm Calls

Low, slowly repeated "errr" calls were performed while in alert posture when individuals were mildly alarmed. One series of these calls was recorded from a captive female as she was approached by a human in a flight pen. The calls varied in duration from 0.5-0.8 s. with a fundamental frequency of 50-200 hz. Strong harmonics occurred up to 1 khz and lower amplitude harmonics to 5 khz (Fig. 34). The intensity of these calls increased as the disturbance came closer. On several occasions when I approached females with broods, they uttered "errr" calls while flying and performing Distraction displays. Munro (1949) gives a detailed account of this behavior.

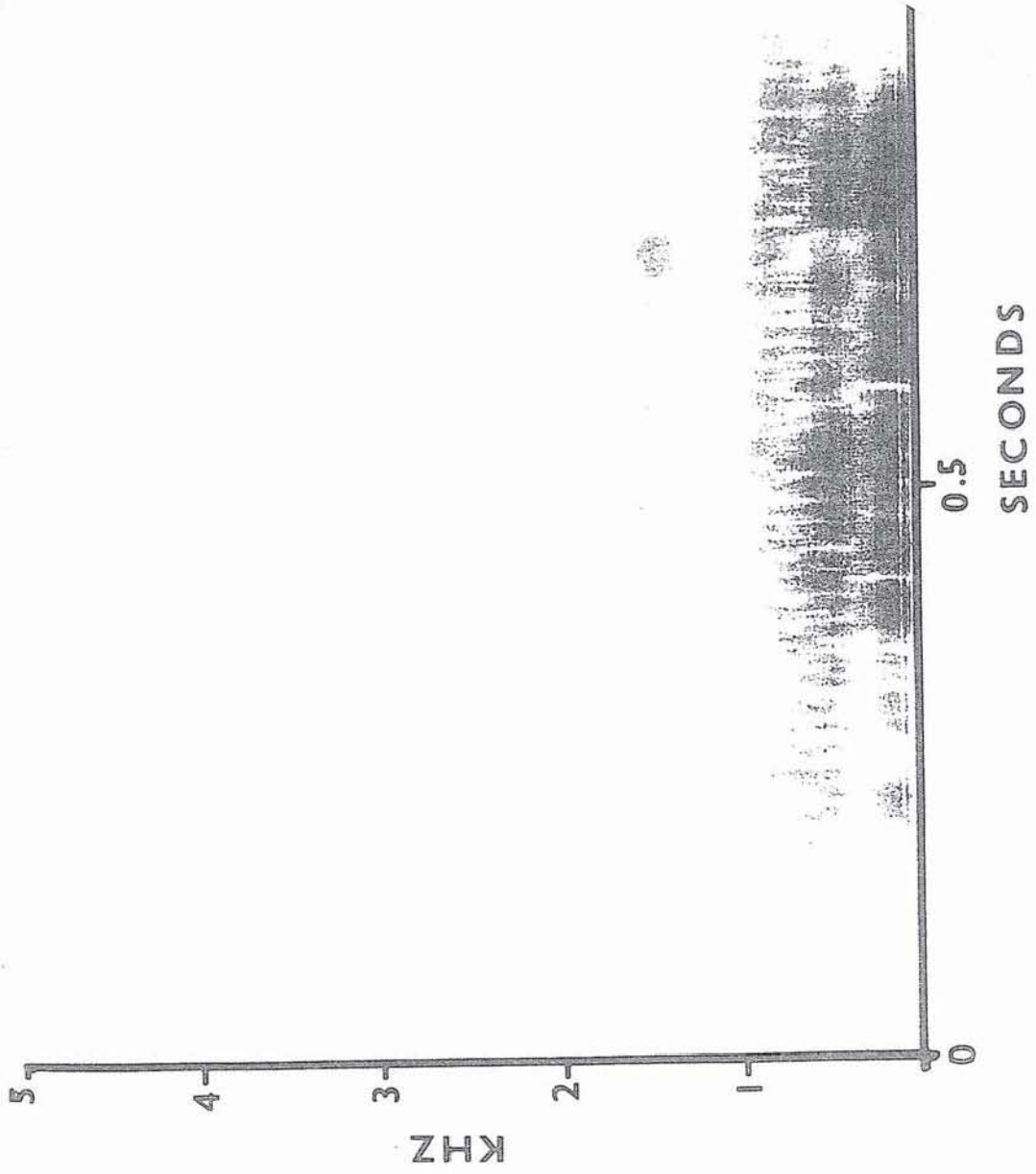
Females surprised suddenly gave single syllable, loud "squak" alarm calls. These were given frequently by females attending broods, particularly in response to the sudden appearance of avian predators (Swainson's Hawk three times, Ring-billed Gull once). Broods usually reacted, either by entering the water quickly if on shore (twice), or by diving if on the water (three times).

Fig. 34. Sonogram of the "errr" call of a female wigeon given in response to an approaching human.

ıg Call of

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Flying Call

The Flying Call may be homologous to the Persistent Quacking Call of other Anas species. (Dzubin 1957, McKinney 1970, 1975, Abraham 1974, Derrickson 1977). It was given by the female after she took wing while leading her mate in flight. The calls were low, evenly spaced "errr" syllables given as the pair flew, often while repeatedly circling the territory. This call was noted 17 times in the Prelaying period between 15 April and 12 May.

Decrescendo Call

Lorenz (1953) and Johnsgard (1965) reported hearing female wigeons produce a one to three syllable Decrescendo Call. I found this call rare in wigeon compared to its common occurrence in Mallard (Lockner and Phillips 1969, Abraham 1964), blue-winged ducks (McKinney 1970) and Northern Pintail (Derrickson 1977). Only three records of its occurrence, all in winter, were recorded as follows.

1) (14 February 1975, 1400 h). Decrescendo Calls heard from a flock of wigeons on the water. Five "gerrr" notes heard in succession in descending amplitude and with a gutteral ending.

2) (21 February 1975, 1030 h). On landing three females gave three-noted Decrescendo Calls ("eughhh eughhh eughhh"). Males in the flock were performing comfort movements and Slow Whistles.

3) (31 December 1976, 1030 h). In a flock of wigeons several females gave three to four syllable Decrescendo Calls.

Brood Call

Females vocalized in several different contexts while attending their broods. Occasionally they uttered low, "errr" calls that were repeated slowly while following or leading a brood that was dispersed over the water. Ducklings did not seem to respond to these calls but

this vocalization may have functioned to keep the brood together, by advertising the female's location.

During the prefledging period, the female regularly left her brood to feed in adjacent wetlands. Usually on her return (often after an absence of over 1 h), she uttered a series of two to three loud gutteral "errr" calls before she landed (heard five times). Once the female also gave one vocalization after landing. Her ducklings usually responded by emitting "peeping" calls and swimming to join her. At other times the individuals in her brood did not respond and the female swam to join them.

DISCUSSION

Woolfenden (1961) found that the wigeons differed slightly from other Anas species in the form of the tarsometatarsus, in the robustness of the humeral shaft and in the fusion of certain thoracic vertebrae. He agreed with Delacour and Mayr (1945), however, that these and other differences in external morphology did not warrant generic recognition. Further studies have shown that the wigeons are linked to the Anatini through similarities of behavior with the Falcated Duck and the Gadwall (Dwyer 1974, Johnsgard 1978). The downy young also resemble those of the Falcated Duck (Johnsgard 1978).

The present study of the behavior of the American Wigeon has supported this taxonomic arrangement. Several displays that apparently were evolutionarily conservative within the Anatini, including Decrescendo Calls, Inciting, Bathing, Turn-back-of-head, Swimming-shake

and Head-pumping, also occurred in wigeon. Other wigeon displays such as Jump-flight, Preen-behind wing, Wing-flap, Burp and Drink may be homologous with displays of other Anas species. However, other attention-getting displays which are important constituents of the courtship behavior in Mallard, Green-winged teal, Gadwall and Northern Pintail (i.e., Grunt-whistle and Head-up-tail-up) were lacking in wigeon, as they are also in the blue-winged ducks (McKinney 1970, Cramp 1977). The Down-up, another common display in the genus Anas, is also absent in both groups.

These similarities in displays suggest a close evolutionary link between wigeon and blue-winged ducks despite Johnsgard's (1961, 1962) alternate arrangement. Indeed, there are other similarities in displays (see below) and in aspects of the pair bond and territoriality (Chapter 6). It remains to be seen, however, whether these are simply artifacts of convergent evolution in response to occupying small economically defensible territories (Chapter 6).

Unlike blue-winged ducks, wigeon lack the ritualization of feeding movements in their courtship repertoire, although some dabbling and bill-dipping are interspersed between other displays. McKinney (1970) speculated that displays that originated from feeding movements probably evolved in tandem with the specialized plankton-straining mode of feeding in this group. Wigeon rely less on straining for food than do other Anas species (Chapter 1), but being grazers does not seem to have led directly to any unique displays. As in other species, courtship occurs on the water, although twice (once in winter, once in spring) I saw this activity taking place in agricultural fields where birds had been feeding.

The Dash-and-dive displays seen during wigeon pre-and post-copulatory behavior, however, may be related to feeding. In winter, wigeon dived strongly at sea when ebbing tides exposed new food resources (Chapter 1). On the other hand, McKinney et al. (1978) argued that Crash Diving in African Black Ducks and some sea ducks (Myres 1959, McKinney 1961), was more likely associated with predator avoidance (see also Lebret 1948). My evidence does not support this theory. On several occasions wigeons readily flushed when approached by a Northern Harrier. The same response occurred when a Bald Eagle flew over a wintering flock in an estuary. I have seen wigeons resort to diving only to escape danger when they were crippled or otherwise could not fly (i.e., pinioned, molting).

Lebret (1961) argued that social displays in Mallard functioned to reduce tension among birds in flocks. However, Weidmann and Darley (1971) supported the classical view (Heinroth 1910, Weidmann 1956, von de Wall 1965) that such social display promoted pair formation in ducks. McKinney (1975) concluded that signals evolved through individuals being selected by gaining advantages in their personal social relationships. Calls, breeding plumage and displays thus were selected for efficient signalling (McKinney 1970).

Displays such as Swimming-shake, Burp, Bathe, Wing-flap, Jump-flight, Bill-dip, Head-shake, Head-flick and Preen-behind-wing apparently functioned to attract females. In all these displays the health, vigor, plumage quality and often the age of the individual were revealed. All

these characteristics undoubtedly promote successful reproduction (Chapter 6). The adaptiveness of these displays probably has led to the evolution of the conspicuous plumage of male wigeon (Chapters 5 and 6).

During pair formation, the Burp, Head-shake, Turn-back-of-head and Face were attention-getting displays. The white crowns of the males were erected in each of these displays. The distinctive head markings probably also enhanced the maintainenance of pair bonds once they had been established. While the pair was together the male spent much of his time alert (Chapter 6). The conspicious male plumage may also have advertised to conspecifics that a territory was occupied and promote his female locating him. The white head markings were particularly noticeable to me against the dark background when birds were feeding in fields. In addition to allowing better visibility, lifting up the head during danger may be an important signal. This occurs also during pre-flight and precopulatory behaviors. Similar behavior occurs in other species of waterfowl, many of which also have colorful head and neck markings (often including patches of white).

The male performed the Slow Whistle vocalization during Burp. This call was given also in other social contexts after the pair bond was formed. Differences between calls of various males were readily apparent. Saunders (in Bent 1962) also noted that calls of different individuals often differed in pitch. With just three call variables, discriminant analysis distinguished four individuals by this call. Other unmeasured parameters may also be individual trademarks, such as ordering and tempo of three and four syllable phrases, and harmonic qualities.

Studies of other bird species have shown individuality of call characteristics (Borrer and Gunn 1965, Thompson 1970, Beightol and Samuel 1973, Martin 1979, Payne and Budde 1979). Several workers, using play-back experiments, have demonstrated that for some species, individuals recognize one another on the basis of call alone (Beer 1970, Moseley 1979).

Wigeons responded to and apparently recognized the calls of other birds. Some evidence of this was obtained with captives. Over the winter two adult males formed an atypical homosexual association. Each bird was placed with other wigeon in either half of a pen divided by a visual barrier. Both males performed sequences of Slow Whistles while moving back and forth in unison along either side of the partition. They did not use other parts of the pen but usually rested and fed between calling sequences within several metres of one another.

In normal heterosexual bonds, the early exposure of the female to the Slow Whistle during courtship may permit her to learn and distinguish the call of her eventual mate in comparison with those of other suitors. Once pair bonds have formed, calling of males prior to and during flight, and after landing probably promoted the integrity of the pair bond especially when birds were in large flocks.

Once on the breeding grounds, after establishing territories, males regularly performed bouts of Slow Whistle when pair members became separated (Chapters 5 and 6). This assisted in reuniting them and reduced the harrassment suffered by females from conspecific males

(Chapter 6). Because forced copulation was a potential threat to the female (Chapter 6), her ability to distinguish the voice of her mate from other males would be advantageous.

Other Anas species have similar pair contact calls. Heinroth (1911), Weidmann (1956), Lockner and Phillips (1969) and Klint (1980a) found the Slow Rahb of Mallards increased when mates were separated. Similar findings have been reported for the Northern Pintail (Smith 1968, Derrickson 1977), blue-winged ducks (McKinney 1970), Green-winged Teal (McKinney 1965b, 1975), Eurasian Wigeon (Cramp 1977), African Black Duck (McKinney et al. 1978) and Gadwall (Dwyer 1974).

The contact call (Slow Whistle) of wigeon differs from homologues of most other species in being composed of three to four syllables. In addition these are shrill musical tones that differ from the more nasal calls of Gadwall, Mallard and Northern Shoveler. However, the "geee" of Northern Pintail (Derrickson 1977) and "weeeps" of the African Black Duck (McKinney et al. 1978) structurally are similar to the wigeon call, and when analyzed, the "pew" of Blue-winged Teal may be also. The "wheee-oo" of Eurasian Wigeon and the "wibrurr" of the Chiloe Wigeon also structurally are similar (Johnsgard 1971) but are usually just one and two syllables, respectively.

Based on its complexity, the call of the male American Wigeon communicates a relatively high degree of individuality (e.g., multiple varying syllables, harmonics, wide range of frequencies, etc.). This underlines the importance of this call during courtship and eventually in the reproductive effort by the pair (Chapter 5 and 6).

Most female calls occurred in contexts similar to the apparently homologous calls of other Anas species (McKinney 1970, Abraham 1974, Derrickson 1977). However, it is noteworthy that the Decrescendo in wigeon was relatively rare. Lockner and Phillips (1969) and Abraham (1974) demonstrated experimentally that in the Mallard, this call communicated a female's location and identity to her mate and other conspecifics. Female wigeons were never heard uttering this call during the breeding season. In contrast, Derrickson (1977) found female Northern Pintails commonly gave these calls during the prenesting period when their mates rejoined them after separation. This indicates that it is primarily the role of male wigeons to re-unite the pair by calling.

The Brood Call of females was probably individually recognizable. To my knowledge, homologous calls of other Anas have not been described. This does not correspond to the Maternal Calls given during hatching described by Collias and Collias (1956), Gottlieb (1965) and Derrickson (1977). The structural characteristics of this call should be studied using spectrographs in order to determine what characteristics, if any, are used as signatures. The Alarm Call depicted in Fig. 34 has few apparent characteristics to denote individuality (e.g., no apparent harmonics, multiple syllables or pure tones). Play-back experiments and quantitative analysis are needed to test these hypotheses.

Female behavior influenced display frequency and orientation of males (see Weidmann and Darley 1971, Standen 1980) and Klint (1980b) has indicated the importance of female selection during pair formation (see Chapter 5). Facing functioned to indicate a bird's choice of mate.

Breast touching not only aided in cementing a new bond, but also kept other males away and held uncooperative females. Females regularly used Chin-lifting and Inciting to indicate positive and negative choices, respectively. One individual took an active role by intervening between two fighting males and selecting her mate.

Several authors have recognized the directional bias of some courtship displays (Smith 1968, McKinney 1965b, 1975, Simmons and Weidmann 1973). This has led to the conclusion that such action is important in indicating mate preferences (Simmons and Weidmann 1973, McKinney 1975) (see Chapter 5). Standen (1980) described display sequences of male Chilean Teal and concluded that "chaining tactics" functioned in gaining and monopolizing the attention of females. He found that aggression occurred among males when display orientations were confounded by other males (see also McKinney 1975). Similar behavior occurred during wigeon courtship.

Hostility was a conspicuous component of the wigeon social system. Wigeon were more dominant interspecifically than would be expected on the basis of body size (Chapter 6). Indeed, wigeons foraged opportunistically and depended significantly at times (particularly in fall and winter) on pirating food from other waterbirds (Munro 1949, Knapton and Knudsen 1978, see also Chapter 1). Pair bonds were strong and males aggressively defended their mate and territory from conspecifics (Chapter 6). This trait probably assures successful nesting (Chapter 5). As in African Black Ducks (McKinney et al. 1978), wigeon females used mate holding tactics (Head-pumping) to maintain their mate's attention (Chapter 6).

Cramp (1977) found that fighting and threats were common in courting Eurasian Wigeons. Johnsgard (1965:193) similarly described the American Wigeon pairing process as "ritualized aggression" with intense competition among males. I observed wigeons regularly fighting with and threatening other males while courting. The Wings-up display has probably evolved as a means of intimidating other males and, secondarily, to attract females. The contexts and characteristics of this display indicate its similarity to the Down-up of other Anas species (McKinney 1975:351).

Aggression was also often directed at females at the height of courtship activity. Frequently males rushed at and grabbed females in an apparent attempt at forced copulation. Soutiere et al. (1972) observed similar behavior. The significance of this behavior is difficult to interpret. Because testes are regressed (Chapter 5) and the nesting season is months away, successful forced copulation at this time would have no procreative benefits. This behavior may simply be an attempt by a male to enforce dominance over a prospective but uncooperative mate. McKinney et al. (1978) suggested that hostility in African Black Ducks may be a result of testing whether or not the female is willing to copulate. Male wigeons, through aggression directed at a potential mate, could have been testing her vigor as well as her ability to avoid forced copulation. A female able to avoid this intention on the breeding grounds would assure the paired male of a greater likelihood of siring all offspring (Chapter 5).

During courtship in waterfowl, a dominance hierarchy among the males is probably established (Weidmann and Darley 1971, see also Chapter 5). It is likely that the most dominant male gains the greatest advantage in display orientation. This ability then should be an important cue for the female in mate selection.

Periodically, males tested their advantage with the female by employing Turn-back-of-head. Cooperative females followed a male performing this display, whereas others reacted by Inciting or swimming back through the group of courting males. The success of a male in forming a pair bond was measured in his ability to lead the female away. The male often resorted to aggression if this tactic did not succeed. McKinney et al. (1978) rarely observed this display in the African Black Duck, a sedentary species that seldom indulges in social courtship.

Tandem-swim in wigeon was a distant to close-range threat display employed by territorial males against trespassers. This served a function similar to that of Rabrab calling of Mallard and the Bill-up of Green-winged Teal (McKinney 1965b, 1975). Blue-winged ducks have evolved the Hostile-pumping display used primarily as a long distance threat. McKinney (1970) contended that the development of such ritualized aggression is characteristic of strongly territorial species.

CHAPTER 5

PAIRING CHRONOLOGY AND MATE SELECTION IN THE AMERICAN WIGEON

INTRODUCTION

Several recent studies have examined mate selection in birds. Klint (1975, 1980b), Cheng et al. (1978, 1979) and Cooke et al. (1972) demonstrated that plumage color influenced mate choice in the Anatidae. Assortative mating based on male size occurs in Snow Geese (Ankney 1977b) and the Great Tit (Greenwood et al. 1979). Searcy (1979a,b) found correlations in some years of female harem size with male (harem master) experience, body condition and body size, in Red-winged Blackbirds. Territory quality is also known to affect avian mate choice (Garson 1980, Yasukawa 1981).

Work by Orians (1969) and Garson et al. (1981) has related mate and territory traits to characteristics of the mating system. Emlen and Oring (1977) discussed the evolution of mating systems in relation to economic defendability of resources (Brown 1964). An important link between winter resources and reproduction has also been drawn by Fretwell (1969, 1972).

Weller (1965) found a relationship in Aythya species among population pairing chronology, acquisition of alternate plumage and timing of nesting. In the Common Eider, younger individuals paired and nested later than older birds (Spurr and Milne 1976a,b). O'Donald (1972) also discussed selective forces affecting the timing of pair formation in birds.

American Wigeon males attained their alternate plumage almost completely before migration in fall (Chapter 3) and spent the winter in

large mixed-sex flocks. Ritualized courtship took place over winter (Chapter 4) and some birds formed pair bonds long before their return to the breeding grounds (Soutiere et al. 1972, see also Chapter 6).

In this chapter I discuss the adaptive significance of winter pairing by wigeon and test the hypothesis that paired birds are physically superior to those pairing late or not at all. Male characteristics predicted to be important in acquiring a mate were age, size, plumage color and body condition.

METHODS

Wintering American Wigeons were studied at the British Columbia study area between December and March in 1974-75 and 1976-77 (Chapter 1). While concealed in a blind or vehicle, I observed flocks of wigeons on the water or in fields with a 20-45 power spotting scope. The sex of each bird was noted on a tape recorder that ran continuously. At bi-weekly intervals, the sex ratio of the population was calculated and the significance of any departure from an equal ratio was tested by Chi-square. Some sequences of behavior were filmed with an 8 power Nizo super 8 mm movie camera (Chapter 4).

While scanning a flock, each female was observed for at least 4 s and her pairing status was assessed. Those accompanying a male closely and performing activities concurrently with him (see Afton and Sayler 1982), or engaged in courtship displays were classified as "paired" and the remainder, were considered to be "unpaired". The pairing chronology

of the population was plotted at bi-weekly intervals over the winter and the patterns for both years were compared. Pairing chronology for British Columbia was compared with that for Texas as reported by Soutiere et al. (1972).

In 1976-77 males in flocks were observed through a spotting scope to identify those not in alternate plumage (Chapter 3). The head, flanks and rump were examined carefully. The proportion of males that had not completed the prealternate molt was plotted over the winter.

Birds were live-trapped with rocket nets operated by Canadian Wildlife Service personnel. Prior to banding, the sex and age (adult=>1 year old, juvenile=≤1 year old) of each bird were determined using feather criteria prescribed by Carney (1964). These birds provided additional information on sex and age ratios. On 20 December 1976, I examined 53 of these birds and recorded more detailed descriptions of plumage (Wishart 1981, Chapter 3) before they were marked and released.

Between January and March 1977, wigeons were collected from tidal marsh and foreshore habitats in British Columbia. In April of 1976, 1977 and 1978 additional wigeons were collected just after they had returned to the breeding grounds on the Moose Jaw study area (Chapter 1). Birds were shot when attracted to decoys or by employing pass-and jump-shooting methods. When possible, the social status (paired, unpaired, courting) of each bird was determined prior to collecting it to see if there were physical differences between birds in different categories. In the laboratory birds were measured and aged as described

by Wishart (1979, 1981). The excised left breast muscle, left leg, ovary, oviduct, left testis and other organs were weighed wet as described in Chapter 2. Carcass water, skeletal mass, lipid and protein were estimated using techniques described by Wishart (1979).

Weights of protein and lipid reserves were estimated for each carcass by subtracting total measured levels in the body from mean starvation values of each, respectively (Wishart 1979). The total energy reserve (TE) in kcal was estimated by:

$$TE = 9.0\ LR + 4.3\ PR$$

Where LR=lipid reserve (g) and PR=protein reserve (g). The constants of 9.0 kcal/g oxidized lipid and 4.3 kcal/g oxidized protein were used (Ricklefs 1974).

Morphological variables did not meet the assumption of normality and so were subjected to $\log_{10}$ transformation. Data were grouped by stage-month as follows: Early Winter=January and February, Late Winter=March, and Early Arrival=April. Carcass constituents were compared among sex-social status groups by analysis of covariance. The structural index (wing length+body length) (see Wishart 1979) was used as a covariate to take account of size differences among individuals.

A captive flock of individually marked wild stock wigeons was studied over the winter and spring of 1977-78 at the Delta Waterfowl Research Station. These birds had been kept together in pens for between four months and several years. On 13 October 1977, prior to their pairing,

seven males and seven females were segregated by sex into separate pens. On 18 November these birds were weighed, measured, aged and reunited with other waterfowl in an indoor enclosure for the winter. Every two weeks until 4 May, they were observed for 1-2 h from a blind installed inside the enclosure. Intraspecific interactions among individuals were noted (see Chapter 4), as were mate selection and pairing chronology. On 4 May the birds were wing-clipped and released onto a fenced, open air pond at the station. Weekly observations were continued from a tower blind until 1 June.

Captive females were ranked based on their weight, age and date of first observed pair formation. Males were ranked on these characteristics as well as their plumage quality. Ages were recorded as either juvenile (<1 year old) or adult(>1 year old), and male plumage subjectively as "full alternate", "medium" (grey feathers in white wing patch), "poor" (mid-way between basic and alternate) and "very poor" (mostly basic plumage) (see Chapter 3). Tied ranks were treated as prescribed by Seigel (1956) and a mean rank for each bird was calculated. Kendall coefficient of concordance and Spearman rank correlation tests were used to elucidate the relationships among male and female characteristics and their pairing dates (Siegel 1956).

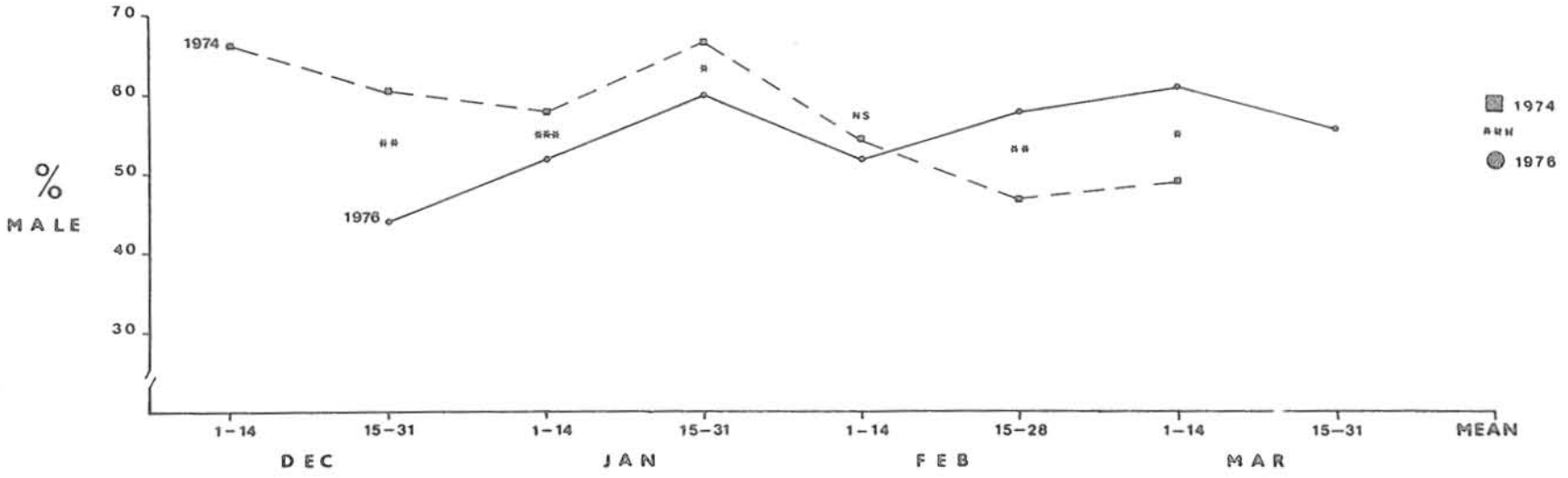
RESULTS

Sex and Age Ratios

During the winters of 1974-75 and 1976-77, 3,360 and 14,806 wigeons, respectively, were observed. The sex ratio varied widely over both winters and between years (Fig. 35). In 1974-75 ratios ranged from over

Fig. 35. Change in sex ratio of wigeon at British Columbia over the winters of 1974-75 and 1976-77. Chi-square comparisons at top test the bi-weekly difference each year from equality of males:females. Chi-square comparisons on the graph test the difference of ratios between years. NS=$\underline{P}>0.05$, *=$\underline{P}<0.05$, **=$\underline{P}<0.01$, ***=$\underline{P}<0.001$.

YEAR	SAMPLE	SIZE (SIG. IS DIFF. FROM 50:50 RATIO)							TOTAL
1974	944 ***	76 NS	1279 ***	207 ***	483 *	175 NS	196 NS	—	3,360 ***
1976	—	2,548 ***	5,513 NS	1,492 ***	1,872 *	2,567 ***	244 ***	573 **	14,806 ***



66% males in late Janaury to 47% a month later. In 1976-77 a similar range occurred except that in December females were more abundant. Overall, the sex ratio was skewed significantly in 1974-75 (59.6% males) ($P<0.001$, $x^2=124.2$) and in 1976-77 (52.4% males) ($P<0.001$, $x^2=34.0$) (Fig. 35). Initial counts after spring arrival at Moose Jaw indicated a sex ratio ranging between 55.5-62.6% males (Chapter 6).

Banding operations by the Canadian Wildilfe Service in British Columbia yielded 857 captures between 22 October and 20 December in 1975 and 1976. In contrast, these samples from the late fall had fewer males (43.4% in 1975 and 41.2% in 1976) and this differed significantly ($P<0.001$, $x^2=20.6$) from an even ratio (Table 26). Juveniles averaged 54.5% over both years.

Male Plumage

Adult males generally completed the prealternate molt by late December (Chapter 3). However, the timing of the prealternate I molt in juvenile males varied considerably. Some completed it by October, whereas in others it was postponed until March (Chapter 3).

Of six juvenile males banded on 20 December 1976, none had completed this molt. All had orange flanks and mottled rump patches and two lacked the white head patch. Two juvenile males of unknown pairing status collected on 10 and 12 March 1977, respectively, were in the

Table 26. Sex and age ratios of wigeons live-trapped in British Columbia between 22 October and 20 December, 1975 and 1976.[1]

		Juvenile		Adult		Percent juveniles			Percent males		
Year	N	Male	Female	Male	Female	Male	Female	Total[2]	Juvenile	Adult	Total[3]
1975	396	67	146	105	78	39.0	65.2	53.8	31.5	57.4	43.4
1976	461	89	165	101	106	46.8	60.9	55.1	35.0	48.8	41.2

[1]Data provided by G. Kaiser (Canadian Wildlife Service).

[2]Males and females combined.

[3]Juveniles and adults combined.

latter stages of this molt, whereas 11 others collected in April were in full alternate I plumage. All of these birds retained a grey wash through the otherwise white median secondary coverts (Wishart 1981).

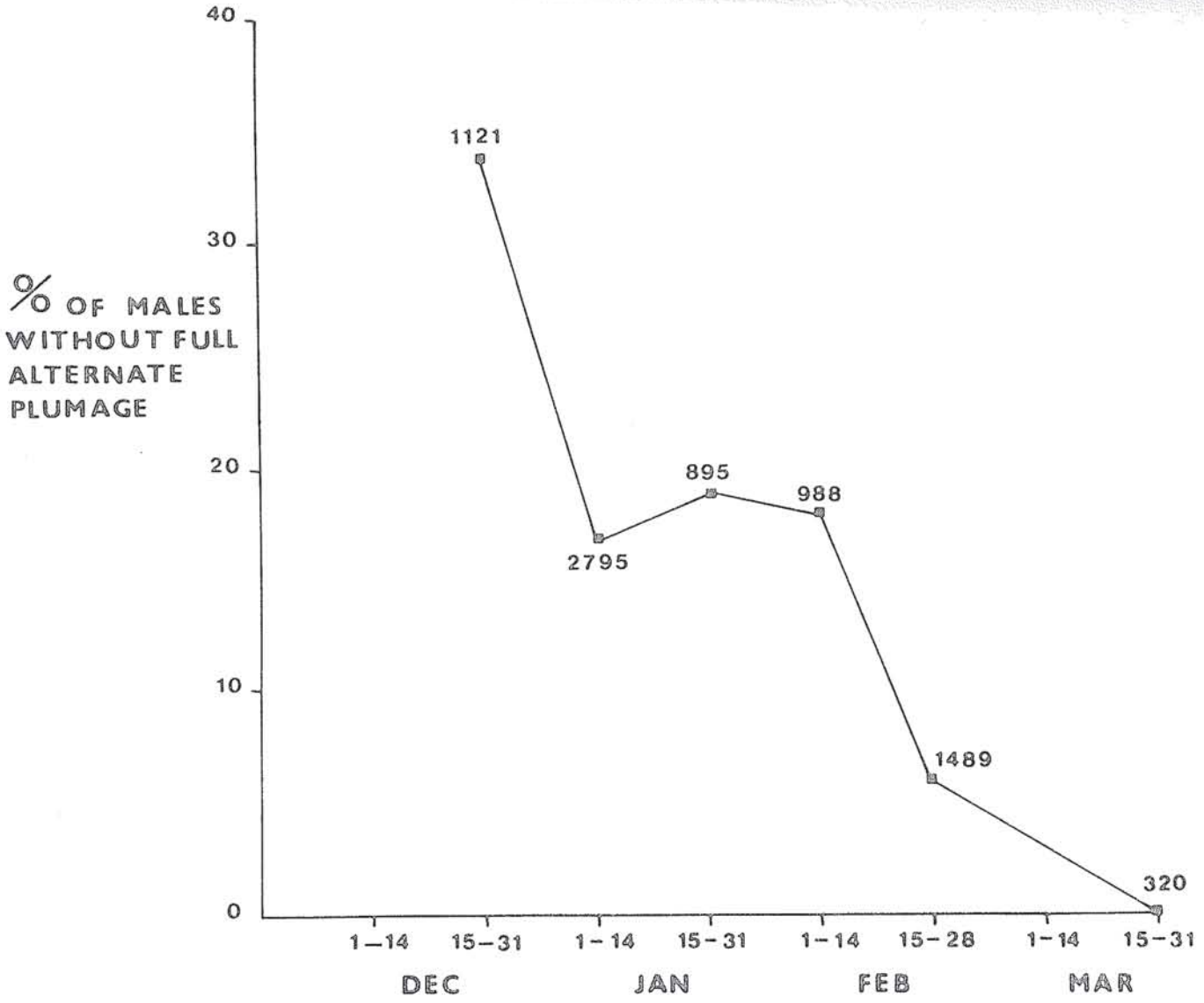
Figure 36 illustrates the reduction over the winter in the proportion of males without full alternate plumage. This declined from a high of 34% in December to zero by late March.

Pairing Chronology

Males competed for females through overt aggression and ritualized displays (Chapter 4). Displays highlighted plumage patterns and served to attract the female's attention and/or intimidate other males. Vigorous Courtship-pursuit-flights (see Chapter 4 for a description of displays) were a part of this process and resulted in some males dropping out (Chapter 4). Many unpaired males and females did not join or show any apparent interest in nearby courtship parties.

Although birds in winter were not marked, some pair bonds were apparently ephemeral. On five occasions (filmed) all males closely attending or courting one female, abandoned her abruptly to accompany another unattached female nearby. On 15 January 1977, one male abandoned his presumed mate to follow another female but quickly returned when his original partner was courted by an unpaired male. They swam off together but the male continued to lag behind and showed interest in other courtship parties. In another incident on 20 January 1975, a female began Inciting toward a male, who until that point seemed

Fig. 36. The decrease over the winter of the percent of wigeon males, identified through a spotting scope, that were without their full alternate plumage in British Columbia in 1976-77. Numbers on graph indicate sample sizes.


40
30
20
10
0
% OF MALES WITHOUT FULL ALTERNATE PLUMAGE
1121
2795
895
988
1489
320
1–14
15–31
1–14
15–31
1–14
15–28
1–14
15–31
DEC
JAN
FEB
MAR

to be her mate. The male responded by chasing her while others in the courtship party followed. This led to a vigorous fight between the original mate and another male. Eventually the female swam away with one of these birds but because they were not marked I could not determine the "winner".

The proportion of paired females in the population increased steadily from 10-15% in December up to 81% by March (Fig. 37). Although courtship was observed also on the breeding grounds, all females were paired by April (Chapter 6).

The pairing chronology in British Columbia differed between the two years of study. In 1974, 50% of females were paired by early January, whereas in 1976 it was only 20% by this date ($P<0.001$, $x^2=168.7$). By mid-February proportions were both about 60% ($P>0.05$, $x^2=2.8$) (Fig. 37). Wigeon pairing chronology in Texas documented in 1970 by Soutiere et al. (1972), was similar to that for British Columbia over both years (Fig. 37).

Correlates of Morphology With Age and Social Status

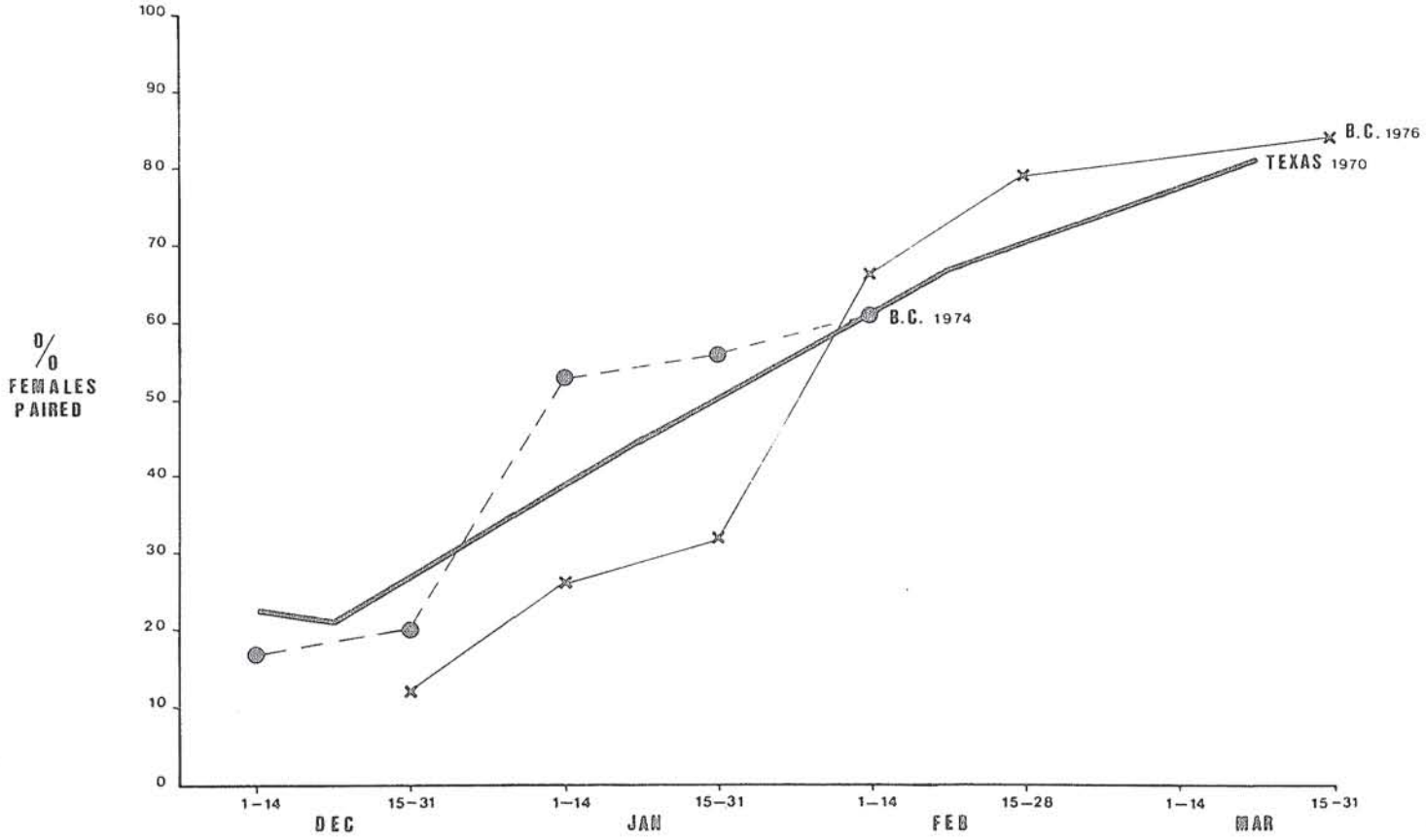
Plumage

Rarely did males with noticeably incomplete alternate plumage court or accompany females. On 14 January 1977 a "juvenile-like" male was filmed in a courtship party with five adults (alternate plumage). This bird appeared smaller than the others but except for having orange flanks, he otherwise seemed to be in alternate plumage. He performed the Wings-up display 0.3 m behind the female as she swam ahead but I

Fig. 37. Pairing chronology of female wigeons in British Columbia over the winters of 1974-75 and 1976-77. Data for Texas are from Soutiere et al. (1972) for 1970. Chi-square comparisons are NS=$P>0.05$, *=$P<0.05$, **=$P<0.01$, ***=$P<0.001$.

SAMPLE SIZES	DEC	JAN	FEB	MAR	TOTAL
B.C. 1974	343	602	219	—	1164
B.C. 1976	1428	3315	1962	250	6955
TEXAS	98	452	785	432	1767

COMPARISONS				
TEXAS vs B.C. 1974	x	x	NS	—
TEXAS vs B.C. 1976	x	xx	xxx	NS
B.C. 1974 vs B.C. 1976	NS	xxx	xxx	—



could not determine if he had a juvenal wing patch. Another male in full alternate plumage (adult?) performed Wings-up parallel to him and with an aggressive lunge, forced him away from the female.

On 17 January 1977 a male with almost no white head patch swam behind an unattended female and performed a series of precopulatory Head-pumps. The female swam away without reciprocating.

All males of known social status that I collected during the winter were adults. This included 11 unpaired, 8 paired and 5 courting individuals. Overall, there were no noticeable differences in the plumage of these birds and all appeared to be in full alternate plumage. Some males in each category were undergoing a limited body molt (Chapter 3).

All females I collected during winter were either paired (N=10) or involved in courtship flights (N=2) (the status of 2 others could not be determined before collecting). One paired bird was classified as a juvenile as was one female of unknown status. All the rest were adults. The plumage of these birds was indistinguishable among the groups except for subtle wing characteristics useful in aging individuals (Wishart 1981). Females of both age groups were undergoing limited to heavy prealternate body molt, particularly on the capital, cervical, ventral, upper spinal and humeral pterylae (Chapter 3). Two birds, including one juvenile, also were molting their rectrices.

Of 56 male wigeons of known pairing status, trapped or collected throughout the winter and breeding season, 8 juvenile males were

unpaired and 4 were paired. This compared to 36 paired and 8 unpaired adults (Table 27). The age ratio in each of the groups was significantly different ($P<0.01$, $x^2=8.3$) (Table 27). For paired females (no unpaired females were collected), 12 were juveniles and 28 were adults. The age structure of paired males compared to paired females was different ($P<0.05$, $x^2=3.8$) but when unpaired males were included in the analyses, age structures for both sexes were similar ($P>0.05$, $x^2=0.5$) (Table 27).

Of 40 pairs I handled over the winter and spring, 26 were comprised of adults, 2 of juveniles, 2 of an adult female with a juvenile male and 10 of a juvenile female with an adult male (Table 28). One pair, comprised of an adult female and a juvenile male, changed to an adult-adult association after a mate switch that occurred in late May (Chapter 6).

Anatomy

In December, a sample of live-trapped wigeons of known age but of unknown pairing status was obtained. Body weights and structural indices were greater for adults than juveniles of both sexes (Table 29).

In Early Winter I collected three paired and seven unpaired adult males. Although the paired males were structurally larger ($P<0.05$, $F=4.0$) and heavier ($P<0.05$, $F=4.0$), unpaired males had greater lipid ($P<0.001$, $F=50.1$) and total energy ($P<0.01$, $F=27.2$) reserves. Protein reserves and other characteristics were not different (Table 30, Fig. 38).

Table 27. Age ratios of paired females, paired males and lone males live-trapped and collected during winter in British Columbia and the breeding season at Moose Jaw.

	Juveniles		Adults		Comparisons	
Status	N	%	N	%	X^2	Significance[1]
Lone males	8	50.0	8	50.0		
					8.3	*
Paired males	4	10.0	36	90.0		
					3.8	*
Paired females	12	30.0	28	70.0		
Total males	12	21.4	44	78.6		
					0.5	NS
Total females	12	30.0	28	70.0		

[1]Comparisons are between ratios of juveniles to adults in adjacent rows.

NS=$\underline{P}$>0.05, *=$\underline{P}$<0.05.

Table 28. Observed distribution of the age composition of 40 wigeon pairs.

Members of pairs		
Male	Female	Observed pairs
Adult	Adult	26
Adult	Juvenile	10
Juvenile	Adult	2
Juvenile	Juvenile	2

Table 29. Mean body weights and structural indices of juvenile and adult wigeons of either sex that were live-trapped on 20 December, 1976, in British Columbia.

Variable	Female			Male		
	Juvenile (11)[1]	Adult (18)	Sig.[4]	Juvenile (7)	Adult (19)	Sig.[4]
Weight (g)	600.2 (575.3-626.3)[2]	629.5 (608.0-651.8)	NS[5]	646.4 (608.8-686.1)	689.4 (660.7-719.3)	NS
Structural index (mm)[3]	691.7 (677.3-706.3)	697.1 (689.1-705.2)	NS	743.2 (722.3-764.5)	760.3 (751.8-769.0)	*

[1]Sample size in parenthesis.

[2]95% C.I. in parenthesis.

[3]Structural index=(body length+wing length).

[4]NS=$P>0.05$, *=$P<0.05$, analysis of variance.

[5]$P<0.1$.

Table 30. Anatomical characteristics of paired and unpaired adult male wigeons in Early Winter, 1977, in British Columbia.

Variable[2]	Unpaired (7)[1] $\bar{X}$	Unpaired (7)[1] 95% C.I.	Paired (3) $\bar{X}$	Paired (3) 95% C.I.	Sig.[3]
Breast	74.1	70.0 - 78.5	80.2	63.8 - 100.0	NS
Leg	24.9	22.4 - 27.7	25.1	19.6 - 32.1	NS
Testis	0.12	0.08 - 0.17	0.09	0.06 - 0.14	NS
Carcass	588.8	562.0 - 615.2	609.5	502.3 - 739.6	NS[4]
Structural index	763.6	754.2 - 773.0	789.3	739.8 - 841.8	NS[4]
Lipid reserve	42.7	30.8 - 59.2	18.9	4.4 - 81.7	***
Protein reserve	59.4	49.3 - 71.6	58.7	43.0 - 80.5	NS
Energy reserve	647.1	515.2 - 811.0	430.5	194.1 - 952.4	**

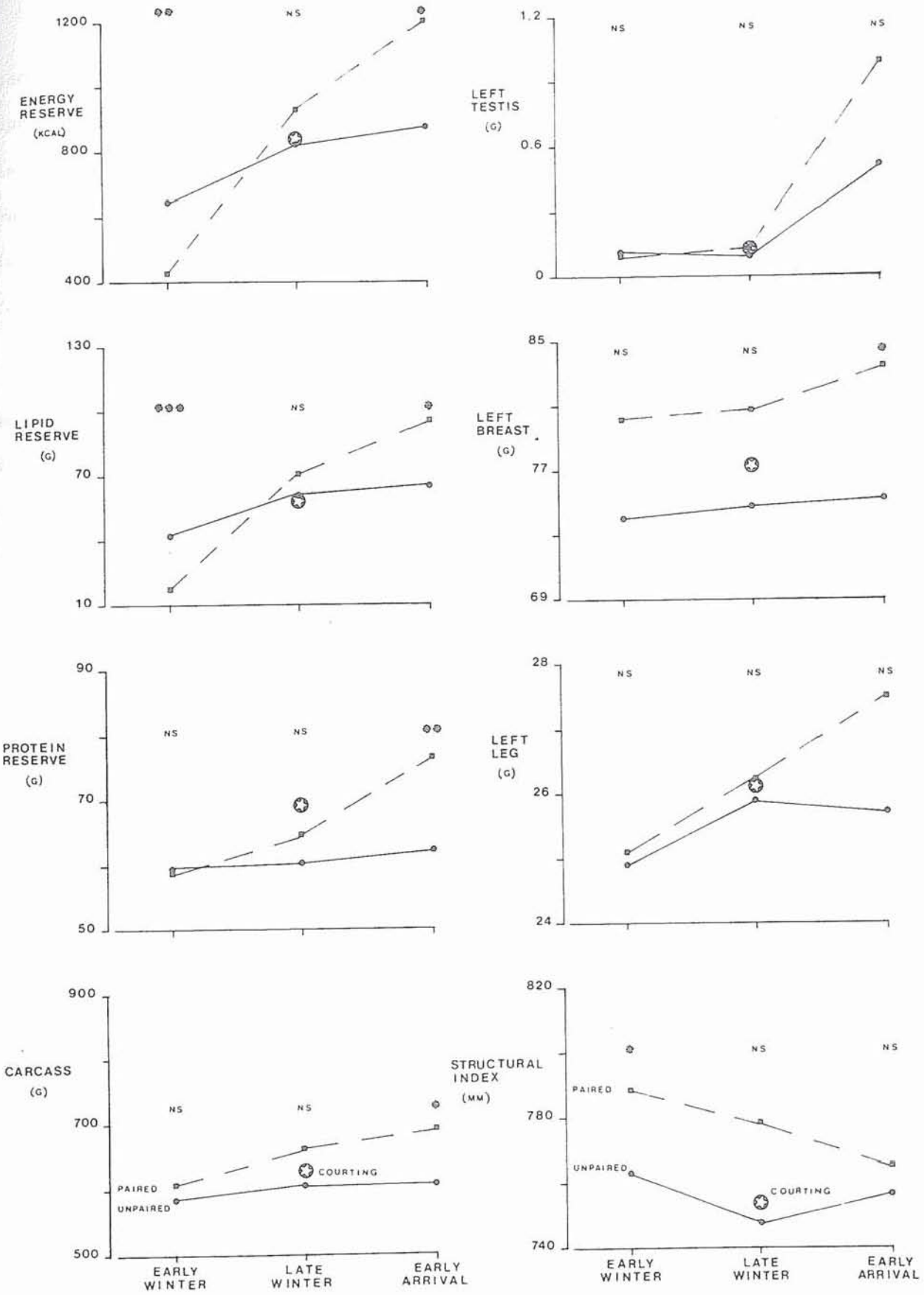
[1]Sample size in parenthesis.

[2]Wet weights in g, structural index in mm, energy reserve in kcal.

[3]NS=$P>0.05$, **=$P<0.01$, ***=$P<0.001$, analysis of covariance.

[4]$P<0.1$.

Fig. 38. Comparison (ANCOVAR) of carcass weight, protein reserve, lipid reserve, total energy reserve, structural index, left breast muscle weight, left leg weight and left testis weight between paired (dashed line), unpaired (solid line) and courting (star) male wigeons. Birds collected in British Columbia during Early Winter (January-February) and Late Winter (March) in 1977, and Moose Jaw during Early Arrival (April) in 1976 and 1977. NS=$P>0.05$, *=$P<0.05$, ** =$P<0.01$, ***=$P<0.001$.


ENERGY RESERVE (KCAL)
1200
800
400
NS
LEFT TESTIS (G)
1.2
0.6
0
NS
LIPID RESERVE (G)
130
70
10
NS
LEFT BREAST (G)
85
77
69
NS
PROTEIN RESERVE (G)
90
70
50
NS
LEFT LEG (G)
28
26
24
NS
CARCASS (G)
900
700
500
NS
COURTING
PAIRED
UNPAIRED
STRUCTURAL INDEX (MM)
820
780
740
NS
PAIRED
UNPAIRED
COURTING
EARLY WINTER
LATE WINTER
EARLY ARRIVAL

Although there were no significant differences among variables by social status for males in Late Winter, nevertheless a trend in data was apparent (Table 31, Fig. 38). In most cases, paired birds averaged largest, courting birds were intermediate in size and unpaired were the smallest. A different trend occurred for females, with courting birds largest (Table 32). In comparisons by age, adults of both sexes tended to be larger (Tables 33 and 34).

During Early Arrival, paired males again were larger than unpaired males. Breast muscle ($P<0.05$, $F=4.9$) and carcass ($P<0.01$, $F=14.1$) weights were larger in paired males, as were lipid ($P<0.05$, $F=4.4$), protein ($P<0.01$, $F=8.3$) and total energy ($P<0.05$, $F=5.6$) reserves (Table 35, Fig. 38). Adults again tended to be larger than juveniles (Table 36). The 10 females collected at this stage were paired adults, thus no comparisons could be made.

An analysis was performed to test the null hypothesis (Ho) that adult males paired to adult females (group 1) were not structurally larger than those paired to juvenile females (group 2). The structural index for group 1 males averaged 764.4 ± 19.9 mm (N=24) and for group 2 it was 757.4 ± 15.3 mm (N=9). However, this difference was not significant ($P>0.05$, $Z=0.84$) and Ho was accepted.

Captive Birds

Process of Pair Formation

Pairing behavior spanned the winter in captives and wild populations. Male NN and female K5 were paired on the first day of

Table 31. Anatomical characteristics of paired, unpaired and courting adult male wigeons, Late Winter, 1977, in British Columbia.

Variable[2]	Unpaired (4)[1]		Courting (5)		Paired (3)		Sig.[3]
	$\bar{X}$	95% C.I.	$\bar{X}$	95% C.I.	$\bar{X}$	95% C.I.	
Breast	74.8	67.9 - 82.4	77.3	69.8 - 85.5	80.7	78.3 - 83.0	NS
Leg	25.9	23.3 - 28.8	26.1	23.7 - 28.8	26.2	23.0 - 29.9	NS
Testis	0.09	0.07 - 0.12	0.12	0.07 - 0.18	0.12	0.10 - 0.14	NS
Carcass	609.5	566.2 - 657.7	629.5	533.4 - 716.1	662.2	638.3 - 685.5	NS
Structural index	748.3	697.4 - 801.7	754.4	727.3 - 782.0	777.8	757.0 - 798.9	NS[4]
Lipid reserve	62.1	44.3 - 87.1	60.0	47.0 - 76.6	71.3	46.9 - 108.4	NS
Protein reserve	60.2	52.6 - 68.9	69.2	55.7 - 87.3	64.6	54.2 - 76.7	NS
Energy reserve	822.2	642.5 - 1054.4	843.3	688.7 - 1030.4	933.3	717.8 - 1210.6	NS

[1]Sample size in parenthesis.

[2]Wet weights in g, structural index in mm, energy reserve in kcal.

[3]NS=$P>0.05$, analysis of covariance.

[4]$P<0.1$.

Table 32. Anatomical characteristics of paired and courting female wigeons, Late Winter, 1977, in British Columbia.

Variable[2]	Paired (6)[1] $\bar{X}$	Paired (6)[1] 95% C.I.	Courting (2)[3] $\bar{X}$	Sig.[4]
Breast	69.7	64.1 - 75.5	70.3	NS
Leg	26.4	21.4 - 32.5	22.9	NS
Ovary	0.19	0.16 - 0.23	0.30	**
Oviduct	0.38	0.32 - 0.46	0.50	**
Carcass	576.8	529.7 - 628.1	619.4	NS
Structural index	706.5	693.6 - 719.4	704.0	NS
Lipid reserve	54.7	32.6 - 91.6	110.9	NS[5]
Protein reserve	59.7	51.7 - 69.0	57.4	NS
Energy reserve	767.4	562.3 - 1047.1	1244.5	NS[5]

[1]Sample size in parenthesis.

[2]Wet weights in g, structural index in mm, energy reserve in kcal.

[3]95% C.I. not calculated for N<3.

[4]NS=$P>0.05$, **=$P<0.01$, analysis of covariance.

[5]$P<0.1$.

Table 33. Anatomical characteristics of adult and juvenile male wigeons, Late Winter, 1977 in British Columbia.

Variable[2]	Adult (15)[1] $\bar{X}$	95% C.I.	Juvenile (2)[3] $\bar{X}$	Sig.[4]
Breast	77.5	74.6 - 80.6	73.5	NS
Leg	26.1	24.9 - 27.3	24.3	NS
Testis	0.11	0.09 - 0.12	0.08	NS
Carcass	633.6	607.9 - 660.2	588.7	NS
Structural index	760.5	745.8 - 775.7	721.9	*
Lipid reserve	64.3	55.4 - 74.4	61.6	NS
Protein reserve	64.7	59.6 - 70.2	66.6	NS
Energy reserve	864.6	779.8 - 958.3	840.6	NS

[1]Sample size in parenthesis.

[2]Wet weights in g, structural index in mm, energy reserve in kcal.

[3]95% C.I. not calculated for N<3.

[4]NS=$\underline{P}>0.05$, *=$\underline{P}<0.05$, analysis of covariance.

Table 34. Anatomical characteristics of adult and juvenile female wigeons, Late Winter, 1977, in British Columbia.

Variable[2]	Adult (7)[1] $\bar{X}$	95% C.I.	Juvenile (2)[3] $\bar{X}$	Sig.[4]
Breast	69.5	64.0 - 75.5	66.7	NS
Leg	25.5	21.3 - 30.6	23.7	NS
Ovary	0.21	0.16 - 0.26	0.24	NS
Oviduct	0.42	0.34 - 0.53	0.37	NS
Carcass	591.3	547.5 - 638.3	549.4	NS
Structural index	705.2	694.9 - 715.6	696.3	NS
Lipid reserve	64.6	38.0 - 109.6	60.7	NS
Protein reserve	59.6	52.0 - 68.1	53.4	NS
Energy reserve	865.0	616.6 - 1213.4	776.6	NS

[1]Sample size in parenthesis.

[2]Wet weights in g, structural index in mm, energy reserve in kcal.

[3]95% C.I. not calculated for N<3.

[4]NS=$\underline{P}$>0.05, analysis of covariance.

Table 35. Anatomical characteristics of paired and unpaired male wigeons, Early Arrival, 1976-78, at Moose Jaw.

Variable[2]	Unpaired (9)[1] $\bar{X}$	Unpaired (9)[1] 95% C.I.	Paired (9) $\bar{X}$	Paired (9) 95% C.I.	Sig.[3]
Breast	75.2	69.3 - 81.5	83.4	80.4 - 86.5	*
Leg	25.7	23.3 - 27.7	27.5	26.2 - 28.9	NS
Testis	0.53	0.24 - 1.16	0.99	0.57 - 1.71	NS
Carcass	608.1	578.1 - 639.7	690.2	654.6 - 727.8	**
Structural index	756.8	747.0 - 766.3	765.3	751.6 - 778.8	NS
Lipid reserve	65.6	48.1 - 89.5	96.2	72.4 - 127.4	*
Protein reserve	62.2	55.8 - 69.3	76.7	66.8 - 88.3	**
Energy reserve	870.6	698.2 -1083.9	1202.3	944.1 -1527.6	*

[1]Sample size in parenthesis.

[2]Wet weights in g, structural index in mm, energy reserve in kcal.

[3]NS=$P>0.05$, *=$P<0.05$, **=$P<0.01$, analysis of covariance.

Table 36. Anatomical characteristics of adult and juvenile male wigeons, Early Arrival, 1976-78, at Moose Jaw.

Variable[2]	Adult (13)[1] $\bar{X}$	Adult (13)[1] 95% C.I.	Juvenile (6) $\bar{X}$	Juvenile (6) 95% C.I.	Sig.[3]
Breast	81.0	76.4 - 85.9	73.7	69.2 - 78.5	NS[4]
Leg	26.9	25.6 - 28.2	24.9	21.7 - 28.5	NS
Testis	0.90	0.57 - 1.42	0.38	0.13 - 1.12	NS[4]
Carcass	664.4	631.7 - 698.7	597.0	543.3 - 655.4	*
Structural index	762.1	753.0 - 771.1	756.9	738.8 - 774.6	NS
Lipid reserve	86.5	69.0 - 108.4	55.3	30.3 - 100.8	NS[4]
Protein reserve	70.8	63.4 - 79.0	63.9	51.7 - 79.1	NS
Energy reserve	1086.9	896.8 -1317.3	793.4	525.7 -1197.8	NS[4]

[1]Sample size in parenthesis.

[2]Wet weights in g, structural index in mm, energy reserve in kcal.

[3]NS=$P>0.05$, *=$P<0.05$, analysis of covariance.

[4]$P<0.1$.

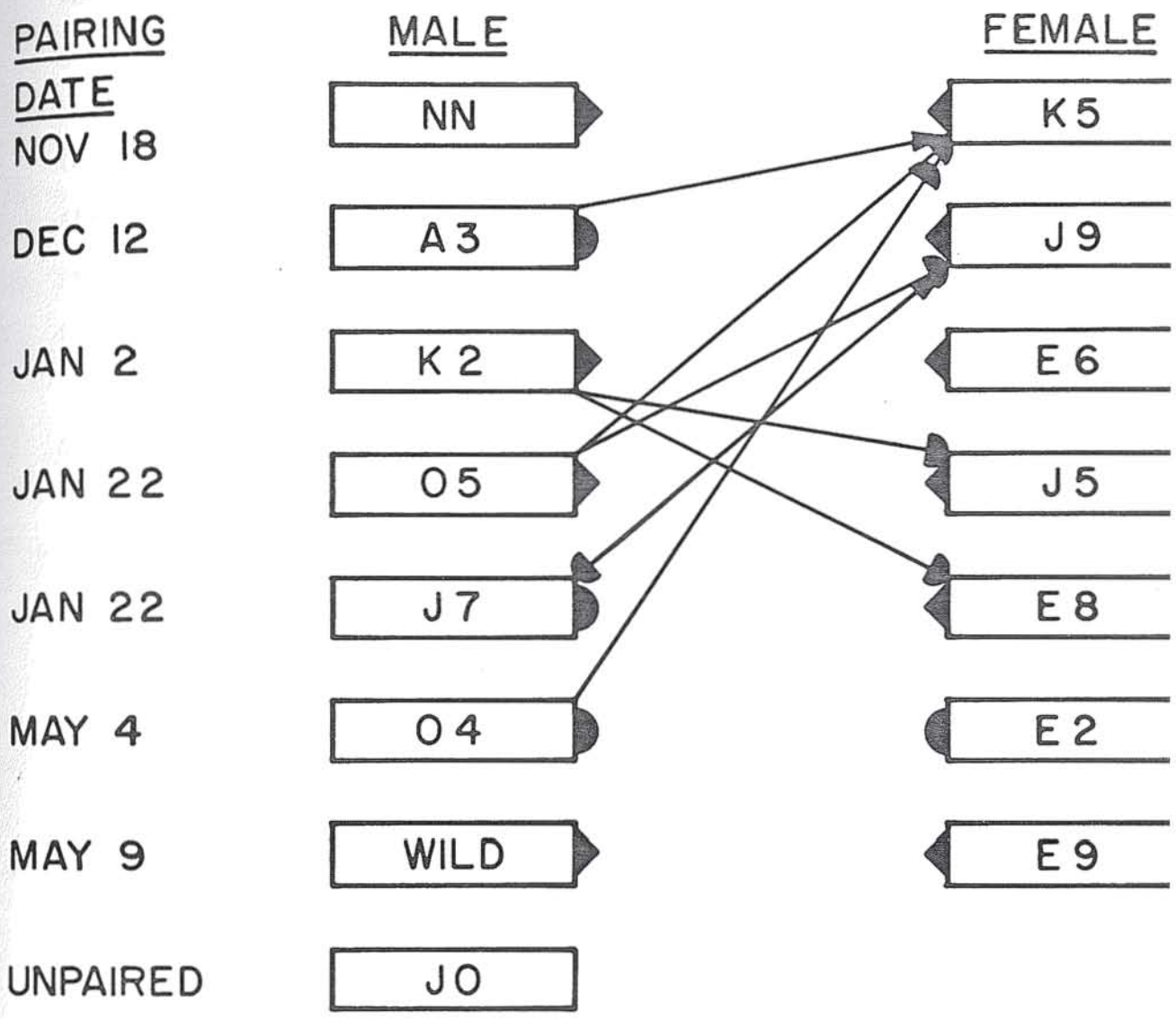
observation (18 November). Their bond remained firm throughout the winter despite regular interactions with other males. On 12 December, male A3 associated occasionally with female J9 (Fig. 39). However, on 2 January A3 attempted to associate with female K5 and while he was absent, male 05 attended his female (J9). Male NN stayed between A3 and K5, although no overt aggression was seen. Also on 2 January, male K2 occasionally associated with female E6.

On 22 January, males A3, 04 and 05 attempted to accompany K5 and her mate (NN). Female J5 followed 05 but he did not reciprocate. Male J7 was paired with female E8 on this date. Although J7 was a juvenile, he was by then almost fully in alternate I plumage. When male 05 was absent, J7 associated with his female (J9). She tolerated this attention but when A3 returned to her, J7 returned to his original mate (E8).

On 9 February, male J7 again frequently associated with female J9 when A3 was absent. J9 attempted to follow A3 on several occasions. When female E8 was unattended by her mate (J7), male K2 frequently accompanied her. When J7 returned, K2 reassociated with his original partner (E6). This chain of association continued during observations made on 6 March.

On 22 March, several bonds had strengthened and some females were more aggressive. Males 04 and 05 continued to associate with K5/NN. Male K2 was strongly attached to E6 but still occasionally associated with female J5 when her mate (05) was absent. Female E6 followed K2 and

Fig. 39. Pairing chronology of captive wigeons at Delta over winter, 1977-78. Birds opposite one another were mated. Lines joining birds indicate liaisons that occurred regularly.


PAIRING DATE
MALE
FEMALE
NOV 18
NN
K5
DEC 12
A3
J9
JAN 2
K2
E6
JAN 22
05
J5
JAN 22
J7
E8
MAY 4
04
E2
MAY 9
WILD
E9
UNPAIRED
JO
= STRONG BOND
= WEAK BOND

Incited at female J5. The birds, A3/J9 were more strongly associated than before and when male J7 came near, J9 Incited and pecked at him aggressively. In turn, J7's mate (E8), Incited at J9.

On 4 May all previous pair bonds appeared firm and a new one (04/E2) had formed. Both male J0 and female E9 were still unpaired. After their release outdoors, the pairs remained together despite the presence of full-winged, unpaired wild male wigeons. On 9 May, unpaired female E9 formed a bond with one of these wild birds.

Correlation of Pairing Date With Individual Characteristics

A significant correlation resulted ($P<0.05$, $w=0.64$, $s=250.2$, $K=4$, $N=7$) among the four criteria used to rank males (Table 37). This analysis performed for females yielded a similar result ($P<0.05$, $w=0.69$, $s=159.0$, $K=3$, $N=7$). When the ranks of pair members were combined, the correlation again was significant ($P<0.05$, $w=0.42$, $s=296.1$, $K=5$, $N=7$).

The only significant correlations between individual ranks for paired males and females occurred between male plumage and pairing date and male age and female weight (Table 38). Mean rank for males correlated highly with pairing date but that for females was not significant (Table 37). Overall, however, there was a significant correlation ($P<0.05$, $r_s=0.71$) of mean male rank with that of the female partner (Table 38).

Table 37. Mates and relative ranks for weight, plumage, age and pairing date for captive male and female wigeons in 1977-78, at Delta.

Sex	Bird[1]	Weight[2]		Plumage[3]		Age[4]		Mean Rank[5]	Pairing date[6]		Mate[1]
		Mass	Rank	Condition	Rank	Age	Rank		Date	Rank	
Male	NN	985	3.0	Full	2.5	A	3.0	2.8	18/11	1.0	K5
	A3	1025	1.5	Full	2.5	A	3.0	2.3	21/12	2.0	J9
	K2	935	5.0	Full	2.5	A	3.0	3.5	2/1	3.0	E6
	05	965	4.0	Full	2.5	A	3.0	3.2	22/1	4.5	J5
	J7	1025	1.5	Medium	5.0	J	6.5	4.3	22/1	4.5	E8
	04	735	7.0	Poor	6.0	A	3.0	5.3	4/5	6.0	E2
	J0	860	6.0	Very poor	7.0	J	6.5	6.5	Unpaired	7.0	
Female	K5	895	1.0			A	2.0	1.5	18/11	1.0	NN
	J9	795	4.0			J	5.5	4.8	21/12	2.0	A3
	E6	725	5.0			A	2.0	3.5	2/1	3.0	K2

Table 37. (Cont'd)

Sex	Bird[1]	Weight[2]		Plumage[3]		Age[4]		Mean Rank[5]	Pairing date[6]		Mate[1]
		Mass	Rank	Condition	Rank	Age	Rank		Date	Rank	
Female (cont'd)	J5	820	2.0			A	2.0	2.0	22/1	4.5	05
	E8	560	7.0			J	5.5	6.3	22/1	4.5	J7
	E2	800	3.0			J	5.5	4.3	4/5	6.0	04
	E9	660	6.0			J	5.5	5.8	9/5	7.0	Wild

[1]Nasal saddle number.

[2]Weighed on 18 November.

[3]See text for description of plumages. Female plumage not ranked.

[4]A=adult, J=juvenile.

[5]Mean of ranks for weight, age and (for males only) plumage.

[6]Day/month.

Table 38. Rank correlations for weight, age, plumage and pairing date for captive wigeons of either sex in 1977-78, at Delta.

Comparisons	r_s	Significance[1]
Male weight vs pairing date	0.65	NS
Male plumage vs pairing date	0.86	*
Male age vs pairing date	0.56	NS
Male weight vs female weight	0.08	NS
Male plumage vs female weight	0.55	NS
Male age vs female weight	0.74	*
Male weight vs female age	0.52	NS
Male plumage vs female age	0.66	NS
Male age vs female age	0.65	NS
Male mean rank vs pairing date	0.90	**
Female mean rank vs pairing date	0.68	NS
Male mean rank vs female mean rank	0.71	*

[1]NS=P>0.05, *=P<0.05, **=P<0.01, Spearman rank correlation test.

DISCUSSION

Sex Ratios

The wintering and breeding populations of wigeon had higher proportions of males than females, as do those of most other waterfowl species (Bellrose et al. 1961, Aldrich 1973). Olson (1965) indicated that this might be attributed artificially to the greater vulnerability of female ducks to hunting.

However, females also suffer higher natural mortality as a direct or indirect result of the greater energetic demands they experience, relative to males. Korschgen (1977) found incubating Common Eider females suffered critically low energy reserves, and Ankney and MacInnes (1978) reported several female Lesser Snow Geese that starved to death. Wigeon females also declined closer to starvation during the spring than did paired males (Chapter 6).

Female waterfowl are vulnerable to predators while they attend their nests (Lack 1968a). Johnson and Sargeant (1977) concluded that natural predation alone was sufficient to account for the skewed sex ratio of waterfowl species. There is evidence also that populations that are unexploited by hunting have more males (Batt 1975). Therefore, the disparate sex ratio seems to be a natural phenomenon.

Sexual Selection

A disparate sex ratio and a monagomous mating system (Chapter 6) means that some males are unable to obtain mates. If females discriminate during pairing (Darwin 1871, Fisher 1930), then it follows that males that pair must be more fit than those that are not selected. Thus, characteristics upon which mate selection is based must be genetically linked to fitness (Fisher 1930).

Traits that are effective in acquiring mates are favored only to the point where they are limited by natural selection (Davis and O'Donald 1976, Murton and Westwood 1977). Possession of full alternate plumage was important in mate acquisition by male wigeons. Displays highlighting colorful plumage patterns drew the attention of females and advertised the age and vigor of the courter (Chapter 4). Male wigeons do not incubate and their bright plumage would, therefore, not seem to be a handicap (see Zahavi 1975).

Wigeon are sexually dimorphic, that is the males are larger than the females. I would expect the opposite (reversed sexual dimorphism) to be true. Males provide no direct parental investment and a female with a larger frame would be better adapted to carry nutrient reserves for use during egg production and incubation (Kolata 1977, Afton 1980, Ralls 1976). This suggests that larger male size is a function of strong sexual selection. Thus, larger males are more successful in acquiring mates, and/or pairs with larger males produce more offspring (see below).

However, larger birds would be at an energetic disadvantage (require more food) and be less manouverable in flight (Selander 1972). Efficient flight by wigeon males is necessary to escape predators, acquire and protect mates and territories, and to steal copulations opportunistically (Chapter 6). Thus, an upper limit to male size must be established by a combination of natural and sexual selection pressures. Displays and feather erection used during courtship (Chapter 4) are tactics used to increase an individual's apparent size without incurring these disadvantages.

Pairing Chronology

Many holarctic bird species undergo a late winter prealternate molt and pair on the breeding grounds after males have acquired territories (Pettingill 1970). The success of males in pairing may be contingent on the quality of their territory (e.g., nest sites, food, etc.) (see review by Brown 1975). In contrast, wigeon males and those of most other North American duck species undergo the prealternate molt in late summer and early fall and substantially are in full alternate plumage when they arrive on their wintering grounds (Chapter 3). Wigeon courtship and pairing began in fall, continued over winter and most females were paired before they reached the breeding grounds (see also Lack 1940, Sowls 1955). Thus, mate selection occurred prior to reproductive fertility and was not based on territory quality.

Weller (1965) discussed the timing of winter pair formation by several duck species but speculated little on the adaptiveness of its early occurrence. The cost of courtship and maintaining a pair bond is

high in terms of an individual's time and energy (Daly 1978). The longer the duration of the bond, the greater the cost. However, strong competition for mates increases the pressure (i.e. the benefits) to pair early (Parker 1974, O'Donald 1972). As more birds in the population pair, the availability of unmated individuals declines and birds pairing later might then be faced with the more difficult task of breaking an already existing bond. Birds pairing early also have a greater opportunity to "test" the quality of their chosen mate and if necessary seek other mates prior to breeding. Paulus (1980) found that paired Gadwalls were dominant and had priority to feeding areas (see also McLandress and Raveling 1981). Ashcroft (1976) also reported that paired female Common Eiders spent a high proportion of their time feeding. Females attended by a vigilant male probably would be less vulnerable to predation and receive greater protection from the sexual attentions of other males (Paulus 1980). Spurr and Milne (1976a,b) found that eiders that paired late tended to nest late or not at all.

One of the proximate factors regulating timing of sexual behavior is photoperiod (Murton and Kear 1973, Crews and Williams 1977). Gorman (1974) found strong correlations among photoperiod, androgen production and pair formation. He showed that shorter day length in winter was necessary to stimulate development of testicular leydig cells, whereas longer light regimes stimulated spermatogenisis (see also Lofts 1975).

Wigeon pairing chronology in British Columbia differed between the two years of this study. On the other hand, birds wintering in Texas and British Columbia, areas separated by 1700 km of latitude, overall

had similar pairing chronologies. Thus, reproductive behavior was not strictly controlled by photoperiod and possibly weather played an important role.

There is considerable evidence that other less predictable proximate factors are also important reproductive regulators. Several studies have documented a waning of courtship activity during inclement weather (Lebret 1961, Raitasuo 1964). Perrins (1970) has found that the timing of breeding may be governed by food availability and Huxley (1976), studying captive Common Moorhens, showed that hormonal development was affected by food supply.

Habitat quality and food availability, both on wintering and fall staging areas, would be factors regulating overall condition of populations, whereas experience and competitive abilities would affect individual condition within these constraints. This combination of factors may be responsible for the wide variation among individuals in their timing of pair formation and in the overall difference in chronology I saw from year to year. It is noteworthy that wigeons wintering further south did not seem to have any reproductive advantage by pairing earlier than birds in northern populations.

Adaptive Significance of Mate Selection

Trivers (1972) predicted that the sex making the relatively smaller parental investment will be forced to compete for mates. In wigeon it is energetically more costly or even impossible for the female to obtain

a new mate and renest should the first attempt fail (Chapter 6). Therefore, because they have more at stake if an incorrect choice in mates is made (Dawkins and Carlisle 1976, Maynard Smith 1977), female wigeons should be selective when pairing.

During courtship it was evident that both sexes had mate preferences. Some apparently paired males courted other females and females did not respond positively to all males. Captive birds showed an intricate pattern of mate preference and association. Some males and females had several alternate choices. In the wild where the number of potential mates is much greater, the system would be even more complex. Dominance played a role in determining which males obtained mates. Thus, dominant individuals with priority would be genetically favored (Wilson 1975, Ralls 1976). In wild Mallards, Lebret (1961) also documented mate preferences by both sexes and recorded changes in partners over the winter. Similar behavior has been recorded for other waterfowl species by Weidmann (1956), McKinney (1975) and Armbruster (1982).

Many studies have considered dominance systems in birds. In general, adults are dominant to juveniles (Rippen and Boag 1974, Paulus 1980), heavier individuals to lighter (Noble 1939, Fretwell 1969), larger individuals to smaller (Burger et al. 1979, Searcy 1979a,b) and individuals with colorful plumage to those with drab plumage (Rohwer 1977, Parsons and Baptista 1980). All of these patterns prevailed in wigeon. In both wild and captive birds, age, size and condition were correlated with an individual's success in acquiring a mate.

Although juvenile males were numerous in wintering flocks, I saw none that was paired. It was not until early spring that I observed some paired juveniles and only twice did this occur with adult females. Even in captivity where competition was limited, juvenile males with incomplete alternate plumage did not pair. One unpaired captive female did not pair with a juvenile male even though he was the last unattached male available. However, when a wild male in full breeding plumage was introduced she paired with him quickly.

Klint (1975) discovered that female Mallards preferred males in full alternate plumage and other workers have found that these males are the most active courters (Weller 1965, McKinney 1970, Armbruster 1982). Paulus (1980) saw only four male Gadwalls without full plumage paired on the wintering grounds. Blohm (1982) for the same species on the breeding grounds, found juvenile males forming an inordinately high proportion of the unpaired group.

Adult male wigeons were heavier than juveniles and usually completed the molt and paired ahead of them. Work by Stotts (1958), Lebret (1961) and Spurr and Milne (1976a,b) also has shown that older birds pair more successfully. Korschgen and Fredrickson (1976) pointed out that juvenile Wood Ducks displayed less effectively than adults, and females probably are able to detect this difference. Afton and Sayler (1982) also found subadult male Common Goldeneyes less proficient in courtship and did not observe any of them paired over winter. Dominant, older birds are likely able to gain a more favorable position closer to the female during courtship and perform displays with greater effect (Standen 1980, Chapter 4).

Similar results have arisen from studies of other species. In grouse, dominant males acquired more females (Evans 1969, Rippin and Boag 1974), and Ankney (1977b) found female Snow Geese selecting larger males. Patterson (1977) studying captive Shelducks reported that dominant birds paired first.

Paired male wigeons in Early Winter were structurally larger than unpaired males and had equal protein reserves. However, they also had lower lipid levels and overall energy reserves. Conversely, during Late Winter and Early Arrival paired males had larger reserves. It is difficult to understand why females would pair with seemingly less fit males early in winter. It is possible that the time and energy used by a male to initate and maintain a pair bond at this time was responsible for depleting reserves. Paulus (1980) and McLandress and Raveling (1981) found that once waterfowl were paired, the individuals spent less time moving about and more time feeding. This may explain why paired male wigeons were in better condition relative to lone males later in the year.

In Late Winter, both paired and courting males were relatively larger and in better condition than unpaired males. This suggests that birds reach some threshold level of condition before investing time and energy in acquiring a mate. It would be adaptive for an individual to balance the benefits of pairing early against the costs (e.g., energetic and risk) of courtship and bond maintenance. Before courtship is initiated the odds of success should be high. Otherwise time and energy would be wasted and the chances of pairing later would be reduced. The

individuals in the best condition seem to pair first, but forming a bond late would still be more advantageous than not pairing at all.

Unlike males, two courting females had larger nutrient reserves than those that were already paired. Courting females also had larger reproductive organs indicating they had higher blood-hormone levels (Gorman 1974). Although these females were collected from courtship flights, it is conceivable that they were already paired to one of the males in the group. Females with greater hormone levels might be more sexually active and thus "desirable" to males. It would be advantageous for females, particularly those with large energy reserves, to invest more heavily in "testing" the "quality" of potential mates before a final choice was made. A larger sample of females is needed to test this hypothesis.

Dominant male wigeons paired more successfully (Chapter 4). Thus, qualities associated with dominance should be measures of individual reproductive fitness. The main role of the male during the breeding season was to defend the territory from conspecifics and to guard the female from harassment by other males (Chapter 6). This provided the female with a food source, and undisturbed feeding time (see also Stewart and Titman 1980), and allowed her to conserve energy. Females invested nutrient reserves in egg production, incubation and brood attendance (Chapter 6).

In order for a male to perform his reproductive role successfully he had to be attentive and aggressive. Vigor was necessary to win

aggressive encounters. During the spring, a high percentage of the time budget of paired male wigeons was devoted to alert behavior and territorial defence, and this resulted in their negative energy balance (Chapter 6). Males with larger nutrient reserves would be able to invest more heavily in guarding the female and make a greater parental investment indirectly through her. Females without an attentive, aggressive mate might have to spend a considerable portion of their time and energy escaping and hiding from other males (Chapter 6). Females with depleted reserves could be less productive (see Ankney and MacInnes 1978).

Therefore, male qualities required for successful defence of breeding territories (Chapter 6) were those tested earlier during winter courtship (i.e. persistence, aggressiveness and flying abilities). Dextrous flight and aggression also were required for males to be successful in obtaining forced copulations (Chapter 6). Females paired to an accomplished rapist and producing offspring with this genotype might be more fit.

Concurrently, during courtship flights and attempts at copulation during courtship (Chapter 4), the female's ability to avoid aggressive males was tested. A male paired to an elusive female would have a greater chance of ensuring that all her offspring would be sired by him.

Once pair bonds formed, both individuals synchonized their activities so as to remain together until the breeding season (see also Erickson 1977). Male vocalizations were important in maintaining pair

integrity and were also a conspicuous part of courtship (Chapters 4 and 6). A female selecting a mate who was a proficient caller might assure herself of an attentive partner.

CHAPTER 6

REPRODUCTIVE BIOLOGY, BEHAVIOR AND MATING SYSTEM OF THE AMERICAN WIGEON

INTRODUCTION

As many as eight species of Anas ducks nest sympatrically in North America (Bellrose 1976). Although the niches they occupy in freshwater ecosystems are similar, adaptive radiation in morphology (Goodman and Fisher 1962), food habits (Bellrose 1976) and habitat use (Nudds 1980) has occurred. McKinney (1965c, 1973) proposed that the variation among these species in resource defendability (see Brown 1964) has led to the evolution of a variety of reproductive strategies.

A general refinement of this model has been proposed by Titman and Seymour (1981). Using territoriality as their criterion they have identified a continuum of strategies within the genus Anas. These authors ordered the species with "strong" to "weak" territorial systems as follows: Northern Shoveler, Blue-winged Teal, Gadwall, American Black Duck, Mallard and Northern Pintail. In addition, McKinney's work (1970, 1975) indicates that the Green-winged Teal has a Pintail-like system, whereas the Cinnamon Teal should be grouped with the Blue-winged Teal.

The American Wigeon is a member of Anas about which little has been reported. In this chapter I present a quantitative description of its breeding biology and social behavior. In some aspects of its behavior, the wigeon resembles most closely the Gadwall (Johnsgard 1965, 1978), although similarities with the blue-winged ducks have also been identified (Chapter 4). In Chapters 1 and 2, I characterized the wigeon as a grazing specialist. Aquatic vegetation is a patchy and predictable food source (Anderson 1978). In this light I examine the hypothesis

that breeding wigeon exhibit strong pair bonds relative to other species of Anas. In addition I discuss the wigeon's position in the Titman-Seymour model and discuss the differing reproductive strategies of males and females.

METHODS

Data were collected on the Moose Jaw study area (Chapter 1) between 18 April and 25 August 1976, 13 April and 18 August 1977, 19-25 April 1978, and 9 June and 21 July 1978. Incidental observations were made between 6-7 June 1975.

Twenty-five males and two females were captured in decoy traps (Blohm and Ward 1979) and seven males and six females with rocket nets projected over shoreline loafing sites. Fifteen females were captured while on their nests; 5 with a long-handled (2.5 m) dip net and 10 with automatic nest traps (Weller 1957a). Between 7-14 July, 1 adult male and 11 adult females were captured with decoy traps baited with grain.

Each captured bird was leg-banded (Canadian Wildlife Service leg bands), marked individually with a colored, numbered plastic nasal saddle (Sugden and Poston 1968) and measured to determine its age (Wishart 1981). Some birds were also marked individually with airplane dope paint applied to their dorsal lesser secondary coverts. This permitted identification of flying birds.

Marked wigeons were observed with a 20-45 power spotting scope from blinds or a stationary vehicle. Intra- and interspecific social interactions were described into a tape recorder or filmed with an 8 power super 8 mm movie camera. Behavioral sequences were timed with a stopwatch. The distance and height of bird movements were estimated in relation to the known heights of reference objects (i.e., trees, fence posts, etc.). At 15 s intervals (Wiens et al. 1970), the activity of each individual was recorded (see Chapter 1). Activities were assigned to six main categories as follows: alert, comfort, social interaction, locomotion, feeding, and resting (see Table 39). Data were grouped into four equal time blocks (0500-0900 h, 0900-1300 h, 1300-1700 h, 1700-2100 h CST). Females that were laying and incubating eggs were monitored with a thermistor implanted in one egg and an electric eye at the nest connected to a remote event recorder (Cooper and Afton 1981).

Within each time block for each sex and stage of the reproductive cycle (Early Arrival, Prelaying, Laying and Incubation) a time budget was calculated. To stabilize the variance (Kleinbaum and Kupper 1978), percent data were transformed to their arcsin. Data were compared among time blocks for each sex-stage using one-way analysis of variance to test the null hypothesis (Ho) that time budgets were similar throughout the day. This Ho was rejected in most cases ($P<0.05$) (see Chapter 1) and thus, data over the day could not be combined. In subsequent analyses, data for each time block were weighted proportional to sample size and analyzed by two-way analysis of variance with time blocks and sex or stage as main effects. There was no significant interaction ($P>0.05$) between main effects.

Table 39. Wigeon behaviors included in time budget categories.[1]

Comfort	Social	Locomotion	Rest	Feed	Alert
preen	preflight	walk	inactive	tip up	swim alert
bathe	copulation	swim	sleep	feed below surface	walk alert
shake	forced copulation	fly	time on nest	dabble	alert not moving
wing-flap	vocalize	pursuit flight		graze	
stretch	aggression	walk alert			
scratch	pursuit flight	swim alert			
tail-wag	display				

[1]Some behaviors may be included in more than one category.

Wigeon were collected at all stages of their annual cycle and dissected (see Chapters 1, 2 and 5). Carcass water, lipid and protein were measured as described by Wishart (1979) and the total energy reserves of each individual estimated (Chapter 5). To induce normality, carcass variables were submitted to $\log_{10}$ transformation and compared for each sex by stage of the annual cycle with analysis of covariance. The structural index (wing length+body length) (see Chapter 5 and Wishart 1979) was used as a covariate to correct for differences among individuals in structural size and age.

From 12 June through mid-July the study area was searched systematically for wigeon nests. The rope drag technique (Labisky 1957) was employed using two observers, either walking or riding horses. Each nest was marked with a lath set 3 m away and the eggs were counted and candled (Weller 1956) to determine their stage of incubation. This information was used to assign a breeding stage to birds observed for time budget. An analysis was done to test the Ho that adult and yearling females produced equal numbers of eggs per clutch. After eggs had hatched or been abandoned by the female, the occurrence of vegetation species within 1 m (quadrat) of each nest was recorded.

In 1976 and 1977, a weekly (between 0800-1200 h CST) survey of waterbirds on the study area helped to locate marked individuals and document population changes. An effort was made to observe each wetland secretly from a vantage point so as not to flush birds. Roadside transects bordering the study area were driven at least weekly to locate marked individuals.

Locations of marked birds were plotted on maps. Outer sighting locations for each bird or pair were joined with straight lines to estimate the size of their home ranges (or territories) at various stages of the breeding cycle.

All potholes on the study area were classified (Stewart and Kantrud 1971). Types were grouped into two permanence classes; persistent (Stewart and Kantrud's Classes IV and V) and unpersistent (Classes I, II, III). Regular use of wetlands by wigeon was defined as those on which individuals were seen on at least five surveys in 1976 and 1977 combined (for surveys done between 28 April-16 June). A Chi-square analysis was used to test the Ho that wigeon used persistent and nonpersistent wetlands equally.

RESULTS

Spring Populations, Movement and Territories

Wigeons first arrived on the study area on 11 April in 1977 and 1978 and were already present in small numbers when observations began on 19 April 1976. Birds remained in small groups of 2 to 15 pairs and lone (unpaired) males upon initial arrival. All females were paired, however, Group Flights Associated with Social Display (GFASD) similar to those occurring in winter (Chapter 4) were seen six times. Initial surveys in 1976-78 indicated an average sex ratio of 55.5% males (N=236 birds) (Table 40).

Table 40. Sex ratios of wigeons during first spring surveys at Moose Jaw, 1976-78.

Year	Survey date	Pairs	Unpaired males	Percent males
1976	1 May	32	7	54.9
1977	14 April	32	4	52.9
1978	20 April	41	15	57.7
Total		105	26	55.5

Pair members remained closely associated while in flocks and other conspecifics generally were not tolerated closer than 2-3 m without aggression. Females performed Chin-lifting and Inciting (see Chapter 4 for a description of displays) and their males responded with threats and rushes. These interactions resulted in birds swimming away (N=17) or engaging in a short retreat flight of 2-9 m (N=9).

During early spring, pairs moved widely over the area. In 1977, one pair (FE3/MO6) (F=female, M=male, other letters and numerals indicate nasal saddle markings) was observed using four different wetlands in a home range of 25.3 ha during April (Table 41).

Not all wigeons were in small groups at this time. On 18 April 1977, a flock of about 1,500 was present on a shallow wetland 12 km east of the study area. These birds loafed on the water and fed on waste wheat in stubble fields surrounding the pond. This flock, consisting of 62.6% males (N=489 birds), remained until 30 April and then the birds either dispersed onto adjacent wetlands or migrated.

In 1977 drought occurred. Correlated with this was a delay in dispersal and nesting. In 1976, 100% of the pairs were disassociated from conspecifics by the third week of May, whereas this did not occur in 1977 until the second week of June (Table 42). Similarly in 1976 the first wigeon nests were initiated in the third week of May but not until a week later in 1977 (Fig. 40).

Table 41. Sizes of areas and numbers of wetlands used by wigeons at various stages of their reproductive cycle at Moose Jaw, 1976-77.

Stage	Birds[1]	Year	Sightings[2]	Ponds used	Area used (ha)[3]
Early arrival[4]	MO6/FE3	1977	63	4	25.3
Territorial prior to incubation	MA8/FE3	1976	121	2	4.0
	MA6/FA5	1976	63	3	16.9
	MEO/FA9	1976	14	2	8.5
	MO6/FE3	1977	63	3	4.3
	MT1/FJ1	1977	23	1	5.5
	MY4/FY5	1977	37	1	7.8
Males while mates incubating	MA8	1976	33	4	14.9
	MA6	1976	23	4	33.5
	MO6	1977	22	4	11.4
Unpaired males	MA1	1976	8	5	56.5
	MA2	1976	12	7	67.1

[1]M=male, F=female. Other letters and digits indicate nasal saddle markings.

[2]Number of observations.

[3]Area bounded by outer limits of where birds observed for each stage.

[4]Prior to defending territories in April.

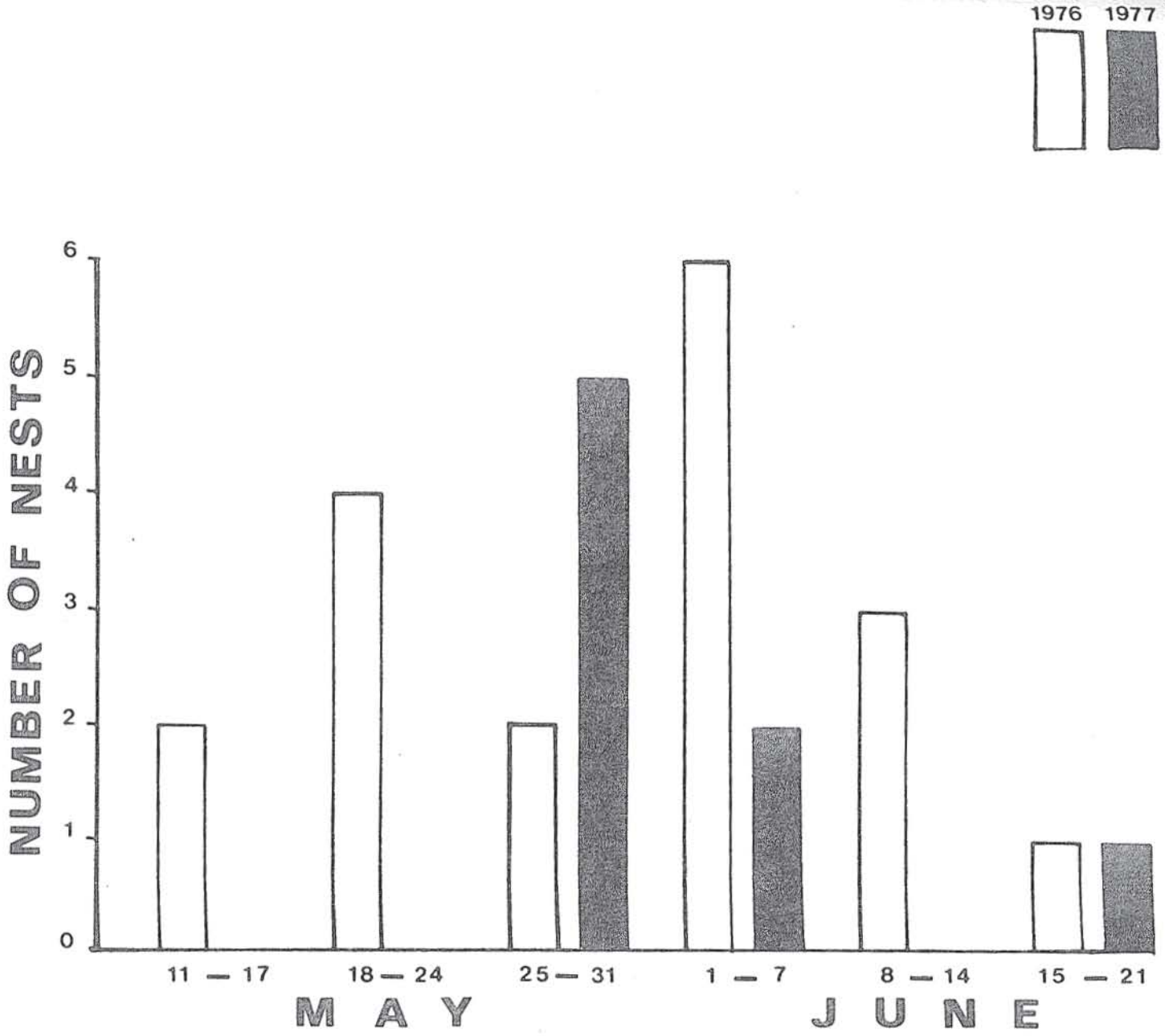
Table 42. Weekly surveys of wigeons on the Moose Jaw study area, in 1976 and 1977, showing percent of total pairs that were not associated with other wigeons[1].

	Week[2]									
Year	1	2	3	4	5	6	7	8	9	10
1976			76.9	81.3	85.7	100	100	100	87.5	86.7
			(53)	(33)	(29)	(22)	(23)	(34)	(26)	(28)
1977	0	8.1	33.3	29.6	46.2	65.2	80.0	75.0	100	100
	(27)	(80)	(38)	(57)	(59)	(50)	(40)	(34)	(26)	(28)

[1]Number of wigeons observed in parenthesis. At 100%, all pairs disassociated from conspecifics and defending territories.

[2]Weeks 1 and 2 in last half of April, 3 to 7 in May, and 8 to 10 in June.

Fig. 40. Clutch initiation of wigeon nests at Moose Jaw, 1976-77.


1976
1977
NUMBER OF NESTS
0
1
2
3
4
5
6
11 — 17
18 — 24
25 — 31
1 — 7
8 — 14
15 — 21
MAY
JUNE

Territories during the Prelaying stage consisted of 1-3 potholes ($\bar{X}$=2.0, N=6 pairs). Areas, including uplands surrounding wetlands, were defended from conspecifics and averaged 7.8±4.8 ha (N=6 pairs) (Table 41).

Pothole Use

Most wetlands and adjacent uplands (see Chapter 1) were used exclusively by only one pair of wigeons. However, five potholes supported at least two pairs simultaneously. Four of these were greater than 3 ha (3.3-6.2 ha) and three had natural barriers (peninsulae, trees, emergent cover, etc.) which acted as a visual screen between pairs. One pothole used by two pairs in 1977 was only 0.5 ha and had rectilinear shorelines. Each pair restricted its use to, and defended just half of the water surface of this pond, but both pairs also used other adjacent wetlands.

Another small pothole (0.7 ha) also was used in 1976 by at least two pairs. However, these birds were at different reproductive stages. One pair used the pothole exclusively until 3 June by which time the female (FE3) had just begun to incubate (day seven). The second pair then also began to use the pothole but the female (FJ2) did not start egg-laying until 7 June. By this time the male of the original pair (MA8) was frequently absent from the pond and the second pair was able to become established. They eventually became dominant over the first pair. While MA8 was frequently evicted, FE3 was forced to hide or go elsewhere during her incubation recesses. Thus, sequential use of this habitat occurred over the breeding season.

Of 78 potholes on the study area, 54 were classified as unpersistent and 24 as persistent. In 17 surveys in 1976 and 1977, wigeon were observed at least once on 73.1% of all wetlands. Regular use occurred 65.4% of the time on persistent potholes and irregular use (i.e., $\leq$4 observations) 13.5% there. Thus, wigeons more consistently used the persistent wetlands in both years ($P<0.001$, $x^2=19.6$).

Pair Bond Stability

Most wigeon pairs exhibited characteristics of a strong pair bond. Males accompanied their females closely and actively defended them when approached or harassed by other males, either on or off the territory.

While moving about the water, females usually swam ahead with the male following within 0.2-1.5 m in alert posture. The male followed also when walking through nesting cover or while in stubble fields. Although males normally initiated Pre-flight-intention movements, the female usually (79.7%, N=64) flushed first and led in flight (98.5%, N=65) to fields or other wetlands. When the male swam ahead, the female frequently did not follow. If the male flushed first and the female did not react (N=12) he would circle back and land beside her. This action was usually followed by more Pre-flight displays and then flight, with the female leading.

When returning to the nest from an incubation recess, the female either flushed first and flew directly to the nest (5 times), landed

nearby and then flew to the nest (once), or landed near the nest and then walked to it (once). The male followed her in flight but when the female landed he continued on and circled back to land alone on the pothole.

When the female was at the nest the paired male spent a large proportion of his time on the water alone and often even slept there (Chapter 1). He spent little time in stubble or on shore. Thus, he was usually easily located by the female when she returned from an incubation recess.

As incubation proceeded the stability of the pair bond weakened. The male spent less time on his territory and moved about more widely. At this time, males (N=3) used home ranges averaging 19.9±11.9 ha (R= 11.4-33.5 ha) that encompassed 4.0 potholes (Table 41). When the female returned on recess, the male often was not present to join her. When together on the water the male frequently did not attend the female closely and swam 90-150 m apart. The female made no apparent attempt to follow her mate. Twice (23 and 24 June), just 2-3 days before the eventual termination of the bond, when the female flew back to her nest at the end of a recess, the male did not follow.

The duration of wigeon pair bonds was variable. One male abandoned on day six of incubation, whereas three others were still associated on the day of hatch (Table 43). Although one male abandoned on day nine of incubation, his female was renesting and this added 10 days to the original nest initiation date. The calendar date rather than the stage

Table 43. Stage of incubation at which the pair bond was broken for seven pairs of wigeons at Moose Jaw.

Pair[1]	Year	Date pair broken	Days of incubation[3]	Days since first egg laid
ME0/FA9	1976	27 June	11	19
MA8/FE3	1976	20 June	25	34
M?/FE5	1976	25 June	25	35
MA6/FA5	1976	17 June	6	15
M?/FE7	1976	17 June	25	27
M06/FE3[2]	1976	23 June	9	27
MY4/FY5	1977	26 June	22	29
Mean		22 June	19.0[4]	26.6

[1]M=male, F=female; other letters and digits indicate nasal saddle markings.

[2]Pair was renesting.

[3]Days since last egg of clutch laid. Normal incubation is 25 days (Wishart, unpubl. data).

[4]Does not include value for the renest attempt.

of incubation seemed to be more important in affecting the timing of bond termination. Males on average abandoned on 25 June (R=17-27 June, N=7 pairs) after spending an average of at least 26.6 days (R=15-35) with the female from when the first egg was laid (Table 43).

On 21 June 1978, a male was observed attending a female and brood of four newly hatched young. The male alternately followed and led the female but the young only followed the female. At one point, the male swam aggressively toward another pair of wigeons nearby before swimming back to the brood. The following day the male was still attending the brood. On my approach to collect these birds at 1915 h, the female gave Alarm vocalizations (Chapter 4) but neither she nor the male abandoned the brood.

Time and Energy Budgets

Time budgets were based on 197 (318.4 h) and 137 observation periods (227.0 h) for males and females, respectively, from Early Arrival through Incubation (Table 44). Except for differences due to attendance at the nest by females during Laying and Incubation, the frequency of most behaviors (comfort, social, locomotion and rest) changed little for either sex over the spring (Table 45). When females were on the water during Laying and Incubation, time budgets were similar to those at other stages (Table 46).

Table 44. Number of observation periods and hours of observation of paired wigeons during the breeding season, 1976-77 at Moose Jaw.

	Male		Female	
Stage	N[1]	Hours	N[1]	Hours
Early arrival	26	41.3	26	42.1
Prelaying	67	114.3	64	112.1
Laying	37	61.6	31	53.2
Incubation	67	101.2	16	19.6
Total	197	318.4	137	227.0

[1]Number of observation periods.

Table 45. Time budgets (percent of time) of male and female wigeons during the spring at Moose Jaw, 1976-77.[1]

Behavior	Stage	Male $\bar{X}$	Male SD	Female $\bar{X}$	Female SD	Sig.[3]
Comfort	Early arrival	10.1	8.1	12.9	11.1	NS
	Prelaying	9.3	5.5	11.6	7.6	NS
	Laying	9.7	4.4	7.1	5.1	***
	Incubation	10.2	8.5	2.0	0.9	***
Locomotion	Early arrival	21.8	16.8	21.2	17.1	NS
	Prelaying	28.3	18.2	26.1	17.9	***
	Laying	22.0	12.2	28.4	16.7	***
	Incubation	12.3	8.8	2.1	1.3	***
Alert	Early arrival	5.9	6.0	2.7	3.4	**
	Prelaying	17.6	15.6	7.0	7.0	***
	Laying	32.1	12.6	6.5	6.9	***
	Incubation	29.6	18.1	1.2	1.1	***
Social	Early arrival	2.8	3.6	1.9	2.6	NS
	Prelaying	3.1	3.6	0.8	1.6	***
	Laying	3.3	4.6	0.5	0.8	NS
	Incubation	3.2	5.3	0.6	1.1	*

Table 45. (Cont'd)

Behavior	Stage	Male $\bar{X}$	Male SD	Female $\bar{X}$	Female SD	Sig.[3]
Rest	Early arrival	17.3	21.0	17.5	20.6	NS
	Prelaying	24.2	21.9	24.6	24.1	NS
	Laying	19.6	14.8	34.7	19.4	***
	Incubation	31.0	26.7	90.3	2.2	***
Feeding	Early arrival	42.1	20.2	42.7	22.1	NS
	Prelaying	17.6	16.5	29.1	18.0	***
	Laying	13.4	8.6	23.7	15.7	***
	Incubation	13.5	12.1	3.5	2.3	***

[1]Lines joining adjacent values indicate a significant difference ($P<0.05$), analysis of variance.

[2]Female time budgets during Laying and Incubation include the time spent on the nest (see text).

[3]Differences between adjacent male and female mean values; NS=$P>0.05$ *=$P<0.05$, **=$P<0.01$, ***=$P<0.001$, analysis of variance.

Table 46. Time budgets (percent of time) of female wigeons attending their mates away from the nests during Laying and Incubation at Moose Jaw, 1976-77.

	Laying (31-53.2 h) [1]		Incubation (13-16.7 h)	
Behavior	$\bar{X}$	SD	$\bar{X}$	SD
Alert	8.8	11.7	10.1	9.8
Feed	29.7	17.8	26.9	16.7
Comfort	8.6	5.5	15.4	6.5
Rest	16.6	18.0	22.8	18.6
Locomotion	35.1	20.2	17.7	12.0
Social	1.0	2.8	4.3	6.8

[1]Observation Periods - hours of observation.

Major changes occurred in the proportion of alert and feeding behaviors (Table 45). Feeding took up a similar proportion of time for both sexes during Early Arrival (42%) but declined significantly ($P<0.001$, $F=7.8$ for females, 30.2 for males) by Prelaying (Table 45). In contrast, alert behavior increased for both sexes ($P<0.001$, $F=11.8$ for females, 15.6 for males), but to a much greater extent for males than females (Table 45). This trend continued for males through Laying ($P<0.001$, $F=26.2$) and held steady during Incubation ($P>0.05$, $F=1.1$).

A comparison of time budgets was made for males between those times when the female was present and absent (at the nest) for both the Laying and Incubation stages, respectively. During Laying, behaviors changed little, except that social activities increased ($P<0.05$, $F=6.6$) when the female was absent (Table 47). Social behaviors accounting for much of this increase were vocalization (Slow Whistles), Tandem-swimming and attempts at forced copulation with other females (Table 48) (see Chapter 4 for an explanation of terms).

During Incubation males performed series of Slow Whistles when the female was absent, repeating the call from two to hundreds of times in each sequence. One series of 27 calls was emitted over 9.5 min, or 1 call every 21.1 s on average. The longest almost continuous sequence I measured was 237 calls in 2.5 h, or a call every 38 s on average. These calls also were performed by the male in the air and on the water when he returned to the pothole after defending his territory. If the female was present, the male continued calling until he observed her, and then swam to rejoin her.

Table 47. Time budgets (percent of time) of paired male wigeons during Laying and Incubation with the female and while alone (female at nest) at Moose Jaw, 1976-77.

	Laying					Incubation				
	Paired[1]		Alone[2]			Paired[1]		Alone[2]		
Behavior	$\bar{X}$	SD	$\bar{X}$	SD	Sig.[3]	$\bar{X}$	SD	$\bar{X}$	SD	Sig.[3]
Alert	32.4	13.4	32.6	9.0	NS	41.9	18.7	23.6	13.7	***
Feed	14.1	8.8	8.8	7.0	NS	11.3	9.6	13.3	12.7	NS
Comfort	9.5	4.7	11.0	2.8	NS	10.4	7.7	9.7	8.3	NS
Rest	19.4	15.8	17.8	10.0	NS	21.8	22.0	37.2	27.3	***
Locomotion	22.7	13.3	20.2	4.4	NS	9.5	5.1	12.6	9.6	NS
Social	1.9	3.2	9.9	4.0	*	4.9	9.2	3.4	5.7	NS

[1]Female is present with male.

[2]Female is absent at the nest.

[3]NS=$P>0.05$, *=$P<0.05$, ***=$P<0.001$, analysis of variance.

Table 48. Percent of time spent in social behaviors by male wigeons during Laying and Incubation when either attending the female or when alone (female at the nest) at Moose Jaw, 1976-77.

	Laying					Incubation				
	Paired[2]		Alone[3]			Paired[2]		Alone[3]		
Behavior[1]	$\bar{X}$	SD	$\bar{X}$	SD	Sig.[4]	$\bar{X}$	SD	$\bar{X}$	SD	Sig.[4]
Vocalization	0.03	0.1	4.1	3.0	*	0.2	0.5	1.5	5.4	NS
Tandem-Swim	0.2	1.2	2.1	4.3	*	1.0	2.9	1.2	2.0	NS
Forced copulation	0		0.9	2.5	*	0.1	0.5	0.1	0.4	NS

[1]Vocalization=Slow Whistle. Behaviors described in Chapter 4.

[2]Female with the male.

[3]Female at the nest, male alone.

[4]NS=$P>0.05$, *=$P<0.05$, analysis of variance.

During Incubation, male alert behavior declined significantly ($P<0.001$, $F=26.4$) when the female was absent, whereas rest increased ($P<0.001$, $F=8.6$). Other activities including feeding did not change significantly ($P>0.05$, $F=0.2$) (Table 47). Individual social behaviors also did not change appreciably (Table 48).

Energy reserves changed over the spring in accordance with the time budgets (Tables 49 and 50). Between Early Arrival and Prelaying, male lipid reserves stabilized ($P>0.05$, $F=0.05$), whereas those of females showed a downward trend ($P<0.1$, $F=3.4$). By Late Prelaying (one pair was collected about two days prior to laying) female energy reserves increased dramatically (Table 50). By contrast, male reserves dropped during this stage (Table 49).

Reserves of both sexes decreased through Laying and Incubation (Tables 49 and 50). Female reserves underwent a further reduction to just 206.7 kcal above starvation by the time that broods hatched. Male reserves on the other hand began to rise after broods hatched, from their low of 425.3 kcal above starvation during Incubation.

Sexual Activity

Thirty-one copulations were observed in the spring (5 in 1976, 26 in 1977). The last observed copulation of the breeding season was recorded on 2 June 1976 and 11 June 1977. Of 27 copulations observed for birds of known reproductive status, 17 occurred in Prelaying, 8 in Laying and 2 in Incubating birds. One pair was observed copulating twice on each of

Table 49. Lipid, protein and energy reserves of male wigeons over spring at Moose Jaw.[1]

		Lipid reserve (g)		Protein reserve (g)		Energy reserve (kcal)	
Stage[2]	N	$\bar{X}$	95% C.I.	$\bar{X}$	95% C.I.	$\bar{X}$	95% C.I.
Early arrival	19	75.0	59.6 - 94.5	68.5	62.6 - 75.1	969.6	825.7 - 1173.3
Prelaying	3	80.2	51.7 - 124.4	73.7	40.8 - 113.0	1038.7	705.0 - 1543.5
Late prelaying[3]	1	38.8		49.6		562.5	
Laying	12	23.8	12.4 - 52.6	59.4	46.6 - 83.2	469.6	341.8 - 742.1
Incubation	2	16.3		64.8		425.3	
Brood rearing[4]	1	36.3		58.2		577.0	

[1]No means in adjacent stages were significantly different ($P>0.05$, analysis of covariance).

[2]Stages defined in Chapter 1.

[3]Approximately two days prior to egg laying.

[4]An adult attending a brood <two weeks old.

Table 50. Lipid, protein and energy reserves of female wigeons over the spring at Moose Jaw.[1]

Stage[2]	N	Lipid reserve (g) $\bar{X}$	Lipid reserve (g) 95% C.I.	Protein reserve (g) $\bar{X}$	Protein reserve (g) 95% C.I.	Energy reserve (kcal) $\bar{X}$	Energy reserve (kcal) 95% C.I.
Early arrival	10	91.9	74.8 - 112.9	72.5	62.0 - 84.7	1138.9	976.3 - 1355.5
Prelaying	3	46.2	7.7 - 278.4	52.5	17.1 - 161.8	641.6	138.2 - 3020.6
Late prelaying[3]	1	77.5		67.1		986.0	
Laying	16	58.7	42.6 - 81.5	72.5	63.3 - 82.6	840.1	670.1 - 1078.9
Incubation	6	23.1	12.8 - 41.7	50.4	32.9 - 77.4	424.6	296.7 - 658.3
Broodrearing 1[4]	6	3.9	1.1 - 13.2	39.9	28.3 - 62.1	206.7	153.0 - 382.9
Broodrearing 2[5]	3	6.9	2.5 - 19.2	40.8	15.2 - 99.4	237.5	89.8 - 587.6
Broodrearing 3[6]	4	17.6	7.9 - 39.4	52.3	42.1 - 65.0	383.3	287.5 - 539.4

[1]Vertical lines join means that are significantly different ($P<0.05$, analysis of covariance).

[2]Stages defined in Chapter 1.

[3]Approximately two days prior to egg laying.

[4]Adults attending broods one and two weeks old.

[5]Adults attending broods three and four weeks old.

[6]Adults attending broods five and six weeks old.

three days. Although these were not on days of continuous observation and other copulations may also have occurred, double copulations were spaced 2.7, 4.0 and 9.4 h apart. Copulations occurred at all times of the day with no apparent pattern (0500-0900 h = 7, 0900-1300 h = 13, 1300-1700 h = 5, 1700-2200 h = 9).

Precopulatory Head-pumping was of short duration ($\bar{X}$=4.7±3.2 s, N=9) (Chapter 4). This was usually given by both members of the pair but in three cases only the female pumped before being mounted by the male. The female initiated Head-pumping eight times and the male only once. Nine times either a few or no Head-pumps were given before copulation. In these latter instances, the male usually rushed at the female who tried to escape. He then seized her by the back of the head with his bill and mounted her in an apparent forced pair copulation (FPC) (Burns et al. 1980). Two rushes involved vigorous Diving-and-dashing before the male could mount the female. In copulations preceeded by Head-pumping, the female assumed the Prone position prior to a deliberate but slow mount from the side by the male. Once mounted, males spent an average of 23.4±12.4 s (N=22) on top of the female in copulation in which intromission presumably was achieved. Two other birds dismounted after just 3 and 7 s on top of the female, respectively.

After post-copulatory behavior had ended (see Chapter 4) the female began to swim with the male following alertly. In 66.7% of the cases (N=27), the pair then moved up onto shore or a log. They did this by swimming 16 times and flying twice. The interval from dismounting to reaching shore averaged 144.2±81.7 s, (N=10). Here a bout of preening and then usually sleep occurred.

Precopulatory Head-pumping often did not lead to copulation (Chapter 5). Eleven times this was initiated by the male and 10 times by the female. Those begun by the male occurred significantly earlier in the spring (2 April-10 June) than those by the female (25 May-10 June) ($P<0.01$; $U=18$; Mann Whitney U test). Six times the male initiating precopulatory displays was aggressive toward the female and appeared to be attempting FPC. Five times he lunged at her, three times he grabbed her tail and three times the female followed by the male dived during pursuit (see Chapter 4). Of six unsuccessful FPC, one occurred a month prior to laying, one two days before laying and one during laying (status of three pairs unknown). Of seven successful FPC, four occurred during laying and one on the sixth day of incubation (status of two pairs unknown).

Nesting

Between 1976 and 1978, 30 wigeon nests were located (19 in 1976, 9 in 1977, 2 in 1978). The first clutch was initiated in 1976 on 11 May and in 1977 on 26 May. Nest starts in 1976 were relatively evenly spaced over the season with a slight peak between 3-10 June (Fig. 40). In 1977 six of nine starts occurred between 26 May and 2 June. In both years the last nest was initiated about mid-June (1976=18 June, 1977=17 June). One adult female (E3) whose first egg was laid on 3 June 1977, initiated a new clutch of eight eggs on 7 June at another nest 307 m away.

Nests were located an average of 42.5 ± 42.9 m (R=1.2-205.1 m) from the nearest wetland (N=26 nests). Most were situated in dense upland cover

associated primarily with shrubs (nine in pure stands of snowberry, six in snowberry and rose, seven in snowberry and Wolf-willow and two in a mixture of all three shrubs) (Table 51). Most of those not in shrubs were in thick stands of herbaceous cover (one in Alfalfa, three in Yellow Sweet Clover and one in mixed native herbs). Only one nest was found in relatively open mixed native herbs at the edge of a fallow field.

Wigeon females laid an average of 8.6±1.2 eggs (N=29) per clutch, one egg per day (Table 52). The proportion of these that were renests is not known but it is assumed that most initiated before 4 June were first attempts (i.e., one known renest began on 7 June). Of 13 nests initiated before this date, adults ($\bar{X}$=9.8±0.4 eggs, N=6) laid an average of 1.4 more eggs per clutch then juveniles ($\bar{X}$=8.4±1.0 eggs, N=7) ($P<0.05$, $U=4.5$) (Table 52).

Intraspecific Interactions

Group Flights Associated with Territorial Defence (GFATD)

Flights Involving Males and Females

Paired males defended their territories principally by GFATD. In 1976, the first flight was observed on 27 April and in 1977, 20 April. Most flights involved one male chasing one female or pair (79.5%, N=200) (Table 53). In a few cases (1.5%) a male chased a single female. Thirty-eight times, 2-8 chasing males were involved. In April, these flights appeared to be GFASD (six seen) similar to those observed on the wintering grounds

Table 51. Frequency of vegetation species found within 1 m of 30 wigeon nests at Moose Jaw, 1976-78.

Common name	Frequency (%)
Snowberry	80.0
Grass	66.7
Wolf-willow	30.0
Sow Thistle	30.0
Low Prairie Rose	26.7
Goldenrod	16.7
Canada Thistle	13.3
Dandelion	10.0
Yellow Sweet Clover	10.0
Fireweed	6.7
Canada Anemone	6.7
Gooseberry	3.3
Heart-leaved Alexanders	3.3
Alfalfa	3.3
Wooly Yarrow	3.3

Table 52. Laying chronology and clutch size of adult and juvenile female wigeons at Moose Jaw, 1976-78.

Year	Date initiated[1]	Female[2]	Age[3]	Clutch size
1976	11 May	E4	A	10
	14	E3		9
	21	E8	A	10
	22	E7	J	9
	22	E5	J	10
	23	E6	J	9
	30			6
	31			8
	1 June			10
	2	E9	J	7
	2	A5	A	10
	4			9
	7			8
	7	J5	J	8
	8			9
	8	A9	A	8
	11	J6	A	8
	14	J2	J	7
	18	J0	A	9

Table 52. (Cont'd)

Year	Date initiated[1]	Female[2]	Age[3]	Clutch size
1977	26 May	E4	A	9
	27	M6	J	8
	29	Y5	J	8
	30	M7	A	10
	31	M8	J	8
	6 June	Y8	A	5
	7	E3	A	8[4]
	17			9
1978	22 May	J2	A	10
	11 June			9

[1]Estimated by candling and back dating (Weller 1956).

[2]Nasal saddle number.

[3]A=adult, J=juvenile, missing values indicate that the female was not trapped and/or aged.

[4]A known renest.

Table 53. Number and percent of Group Flights involving various numbers of wigeons (all include at least one male and only one female) at Moose Jaw.

Number of wigeons involved	Number of flights	Percent of flights
2	3	1.5
3	159	79.5
4	23	11.5
5	10	5.0
7	3	2.5
10	2	1.0
Total	200	100.0

(Chapter 4). Later in May and June, most were probably Group Flights Associated with Forced Copulation (GFAFC) as described by McKinney (1965c). Flights involving a female and more than two males were most common between 15-29 April and 21 May-17 June (Table 54).

During Prelaying, Laying and Incubation, paired males spent much of their time alert (see above) and they usually were the first to observe trespassers entering their territory. Although unpaired males occasionally were involved in GFATD, most were initiated by paired males (93.2%, N=74).

Most flights (63.3%, N=109) were initiated by a male chasing an intruding pair from the water within their territory. The male flew at the pair and either landed beside them before chasing or the chased birds flushed directly into flight. In the remaining cases (36.7%), the male flew up to engage a pair flying overhead or attempting to land on the water.

In 31 cases, I observed a pronounced attempt by the male to direct his chase at the intruding female. In seven cases he grabbed her tail feathers in an apparent attempt to pull her down. In 32 cases the male of the chased pair acted aggressively toward the chasing male. This involved actual contact in the air at least 11 times (wing beating=6, tail pulling and pecking=5). In nine of the flights seen from beginning to end, I noted that no male:male conflict occurred. Twice the paired male lagged behind as the chasing male pursued his female vigorously.

Table 54. Number and percent of Group Flights involving more than two male wigeons over the spring at Moose Jaw (each also involves one female).

Week[1]	Total flights observed	Number with > 2 males	Percent with > 2 males
A1	4	2	50.0
B	13	3	23.1
C	24	3	12.5
D	36	4	11.1
D	35	5	14.3
F	39	8	20.5
G	29	7	24.1
H	30	8	26.7
I	6	1	16.7
J			
Total	216	41	19.0

[1] A=15-22 April, B=23-39 April, C=30 April-6 May, D=7-13 May, E=14-20 May, F=21-27 May, G=28 May-3 June, H=4-10 June, I=11-17 June, J=18-24 June.

GFATD generally were fast and vigorous reaching maximum heights of 100 m and lasting an average of 38.0±40.7 s (N=95). Usually the female led the flight, with her male attempting to stay between her and the chasing male. Males vocalized (Fast Whistle) continuously and females occasionally Incited over the shoulder while in flight. In 90.1% of GFATD, the chasing male returned immediately to his territory. In 84.1%, the chased pair did not return, but if they did (i.e. 15.9% of the time), a subsequent GFATD ensued and the pair eventually was expelled.

In 68.1% of cases (N=73), the mate of the chasing male had been present previously with him on the water and in the remainder she was absent (i.e., at the nest either laying or incubating eggs). In 65.0% of cases, she remained on the pothole while her mate was away, however, 17.5% of the time the female swam directly into emergent cover and 7.5% of the time up onto shore. Four GFATD were initiated while the pair was feeding in upland fields. On one of these occasions, the chasing male returned to his pothole following the flight and his female, who had remained in the field, flew immediately to join him on the water.

In 1976 and 1977 GFATD occurred most frequently between 7-13 May at a rate of 1.03 and 1.48 flights/h of observation, respectively (Table 55). The final flight involving females was observed on 15 June 1976 and 17 June 1977.

Table 55. Number and frequency of wigeon Group Flights over the spring at Moose Jaw.

	1976						1977					
		Male/Female[3]		Male/Male[4]		Total		Male/Female[3]		Male/Male[4]		Total
Week[1]	Obs.[2]	N	Freq.	N	Freq.	Freq.[5]	Obs.[2]	N	Freq.	N	Freq.	Freq.[5]
A							19.5	4	0.21			0.21
B	11.7	6	0.51			0.51	17.1	7	0.41			0.41
C	22.9	14	0.61			0.61	26.5	10	0.38			0.38
D	12.6	13	1.03	1	0.09	1.11	15.5	23	1.48			1.48
E	12.9	5	0.39			0.39	37.8	30	0.79	4	0.11	0.90
F	37.6	22	0.59	29	0.77	1.36	20.9	17	0.81			0.81
G	49.4	18	0.36	18	0.36	0.73	40.0	11	0.28	24	0.60	0.88
H	27.7	15	0.54	18	0.65	1.19	56.3	15	0.27	27	0.48	0.75
I	35.0	4	0.11	14	0.40	0.51	19.3	2	0.10	4	0.21	0.31
J	17.0			1	0.06	0.06	13.6					
Total	226.8	97	0.44	81	0.36	0.78	266.5	119	0.45	59	0.22	0.67

[1]See Table 54 for dates. [2]Hours of observation. [3]Group Flights involving male(s) and female(s), and frequency per hour. [4]Group Flights involving only males and frequency per hour. [5]Total frequency of male/female and/or male/male Group Flights per hour.

GRTE=Green-winged Teal, BUFF-Buffle[illegible]

Group Flights Involving Only Males

Other GFATD involving only males also occurred commonly. The first of these was observed on 13 May 1976 and 15 May 1977, and the last on 23 June 1976 and 25 June 1977. In 1976, they occurred most frequently between 21 May-10 June and in 1977 between 28 May-10 June (Table 55).

Flights usually were initiated when another male wigeon landed on the same pothole. The resident male then swam or flew to the trespasser and in 87 cases the 2 birds flushed immediately into a GFATD. On eight occasions the male flew up to engage a trespasser(s) flying over or attempting to land on the pothole. Although 95.7% of these flights involved just 2 males, 2.1% had 3, and 1.4% had 4 males.

In 37.9% of flights (45 cases) the trespassing male did not immediately flush but rather the two males engaged in bouts of ritualized Tandem-swimming (see Chapter 4). Both males swam rapidly with head erect, the aggressor closely behind the trespasser. Occasionally the aggressor pecked at the tail of the trespasser or lunged at him (14 times) and 6 times a wing-beating fight occurred. Bouts of Tandem-swimming early in the season generally were short but overall averaged 103.4±158.7 s (N=34). In 57.0% of cases Tandem-swimming was followed by the males flushing into a GFATD. In the remainder (N=40), males broke off their displays, associated with one another without aggression, swam apart, and/or continued one or several bouts of Tandem-swimming.

These flights were slower and less aggressive than GFATD that involved females, and contact in the air was noted only twice. Although most flights were characterized by short periods of rapid chasing, most of each flight was spent in slow wing-flapping and gliding; at times the birds were separated by 2-10 m. On average these flights lasted 38.8±40.1 s (N=95) and I did not hear males vocalizing during them.

In GFATD involving only males, 61.9% (N=113) occurred while the resident female was present on the pothole and 38.1% when she was absent (i.e., at her nest). In 26.7% of cases, when present, the female remained on the water but 55.0% of the time she moved into emergent cover and 18.3% of the time she went up onto shore to hide. Thus, females hid more frequently when male wigeons trespassed than when pairs or females did so ($P<0.001$, $x^2=17.1$).

On 90.9% of occasions the aggressor returned to his pothole and frequently (44.9%) the chased bird(s) was evicted. Often (55.1%), however, the trespasser(s) also circled back and either landed on the water or attempted to do so. When this happened, multiple GFATD occurred averaging 3.3±1.8 consecutive flights (N=18). Each time the trespasser(s) was expelled eventually.

Forced Copulation

McKinney (1965c) described the Group Flights Associated with Forced Copulation (GFAFC) characteristic of many *Anas* species. These flights occurred also in wigeon but covered long distances, and so the outcome of most was not observed. However, on 21 May 1976 at 1830 h a group

consisting of one female and three males landed on a pothole in front of me. Without any precopulatory behavior (Chapter 4), two of the males simultaneously mounted the female in an attempted copulation. One male succeeded at intromission, dismounted and flew off. The other remained on the female for almost 3 min before dismounting. He performed a Wing-flap before departing. The third male, during this activity, swam alertly but did not attempt to mount the female or defend her from the other males (see Wishart and Knapton 1978). When released, the female swam directly into cover surrounding the pothole and did not reappear. The third male remained for a further 10 min before flushing from the pothole.

Six other forced copulations and/or attempted forced copulations also were witnessed. All of those successful were inflicted on the same female (FE3) in 1976:

On 24 May at 1701 h, MA8 (mate of FE3) was involved in Tandem-swimming and two GFATD with a lone unmarked male. Following the second flight MA8 did not return to the pothole but the second male (or another one) did. The female was inactive on the shore. The male swam toward her and pursued her up onto the shore where presumably she was attempting to hide. The male forced her to fly back to the water and landed beside her. The female dived but the male grabbed and mounted her for 10 s in what appeared to be a successful copulation. Following this the female broke free and swam into emergent cover to hide. The male preened and then flew from the pothole. Eight minutes later the female reappeared alone, and bathed.

On 29 May at 1912 h, a lone unmarked male observed FE3 alone on the shore. As he swam toward her she swam away and then flushed. The male flushed in pursuit and MA8 (who was present but out of view) flew up to join in the flight. The chase lasted for 65 s and landed back on the same pothole. FE3 flew into the bordering emergents pursued by the male. The female was forced back out onto the water with the male on her back grabbing at her head in an attempted forced copulation. MA8 charged and dislodged the male and FE3 swam back into cover. The male attempted to follow but MA8 drove him away and stayed on the water between his female and the male. The male swam alertly, vocalizing (Slow Whistle) occasionally and did a Wing-flap. MA8 then flew across the pothole to rejoin FE3 on shore and no further interactions occurred.

On 3 June at 1910 h, an unmarked male pursued MA8 and FE3 from the stubble field in which they were feeding. A Group Flight lasting 25 s ensued and ended on the pair's territorial pothole. The unmarked male grabbed the female in an attempt to mount her but he was dislodged by MA8 and driven off the pothole. FE3 immediately swam into emergent cover and hid.

On 5 June at 1914 h, FE3 landed on the pothole alone. Another unmarked pair was present. The male flew directly at FE3. She crouched low and then flew to the south side of the pothole. On landing on the water the male also landed and mounted her successfully. On dismounting, FE3 swam into emergent cover and did not reappear until 2012 h. Following copulation the male performed Bathing and a Wing-flap before rejoining his female.

On 6 June at 1300 h, I captured FE3 on her nest and after I weighed her she was released onto her territorial pothole. Her mate was not present, however, an unmarked pair was. The male chased FE3 into the vegetation and mounted her for 30 s. After copulation he rejoined his mate and FE3 swam into cover and hid.

On 7 June 1975 at 1830 h, an unmarked pair and two males were observed on a pothole. Two of the males were fighting and when they broke apart the pair swam away into emergent cover. The other two males participated in six consecutive GFATD. Following the last flight the males swam to join the pair. While the paired male fought with one of the males, the other chased the female and attempted to mount her. The paired male returned immediately, pulled the other male off the female by the back of the head and wing-beat him. The male escaped and briefly mounted the female again. The female broke free and skittered into emergent cover followed by the two males (one the paired male). Eventually the paired male succeeded in chasing the other male to the far side of the pond and returned to his female on shore. The lone male swam alertly and vocalized (Slow Whistle) occasionally. At 1843 he swam toward the pair and the paired male swam at him with Wings-up and bill open. The lone male flushed with the paired male in pursuit. The paired male returned to his female and the lone male did not reappear. At 1848 the pair flew to another pothole 150 m to the east.

Several similar encounters were observed in 1976 but without my seeing a forced copulation attempt:

On 13 May at 1800 h, I observed two males (one marked unpaired male MA1) on a pothole. Males continually entered and left the pothole until by 1817 h there were five present. These males moved about the perimeter of the pothole apparently searching and vocalized (Slow Whistle) continuously. Brief periods of aggression and fighting occurred among

some of the males. Although no females were observed on the pond an unmarked pair was seen walking while crouched low in the grass. The pair moved about 45 m until they reached the opposite slope of a small hill rising from the pothole shore. They then flushed and flew low directly away from the pothole. Due to the topography, the lone males could not see them and continued to interact on the pothole until 1917 h when observations ceased.

On 22 May at 2000 h, a Group Flight involving an unmarked pair and a lone male landed on a pothole. The paired male showed aggression at the other male and the female swam directly into a belt of willows encircling the pond. The males followed but the paired male chased the other out onto the water while wing-beating him. A series of five male:male GFATD followed over the next 25 min; the lone male returning to the pond after each and attempting to search for the female in the vegetation while vocalizing (Slow Whistle). Finally the lone male was evicted and observations ceased at 2035 h with the female still hiding and the paired male on the water alert.

On 22 May at 1630 h, the female of a pair was hiding in emergent cover bordering a pothole and her mate (MA3) was out on the water. There were three unmarked lone males on the pond and MA3 chased one in a GFATD. Four more flights followed and on his final return MA3 joined his female up on shore. Another male entered the pothole at 1700 h and the pair walked low from the shore up into the hay field bordering the pothole. At 1705 h, one of the males left the pothole but 2 min later three more entered (one unmarked, MA8 a paired male from the neighboring territory, and MA1 an unpaired male). At 1710 h, MA8 (whose mate was mid-way through laying her clutch) returned to his territory. At 1715 h, MA1 also flew to MA8's territory and at 1826 h observations ceased without the return of the resident pair and with one lone male still present on the water.

One 3 July at 1352 h, a pair (MA3) moved quickly into the vegetation bordering a pothole when a male wigeon flew overhead. Three times, at 1400 h, 1420 h, and 1433 h, an unmarked male landed on the pothole and was chased off by MA3 while his female continued to hide on shore. At 1435 h a lone male landed, observed the female on shore and forced her into flight. The flight was rapid and as it progressed four other males flew up singly to join in until the seven birds in flight were lost to view.

Of these forced copulations and attempts made on FE3 (the only female known to be of breeding status), one occurred on the third last day of egg-laying and the remainder (four) while she was incubating.

In these observations, the common response of females to the presence of a male other than their own, was to move into cover and hide. The first response of the paired male often also was to crouch and hide when he observed a potential trespasser. One male herded (breast to breast and then followed closely on her tail) his female to shore when she did not respond to a lone male landing on the territory. This behavior was similar to Facing during courtship (Chapter 4).

These initial avoidance reactions by paired males were observed eight times when wigeons flew overhead. Twice males reacted this way briefly when a male Northern Pintail landed and once when a male Blue-winged Teal landed on the pothole. All of these observations occurred between 22 May and 10 June. Of nine responses by a pair of known breeding status, one occurred seven days prior to egg-laying and the rest during various stages of egg-laying.

Unpaired Males

Two unpaired males (i.e. I never observed them paired with a female) (MA1 and MA2) remained at the study area from at least 27 and 28 April 1976 (when first banded), respectively, until they were last observed on 27 May. These birds moved widely over the study area using a home range averaging 61.8 ha (R=56.5-67.1 ha) encompassing 6 wetlands (R=5-7). Although MA1 was observed in a group apparently attempting to enforce copulation on 13 May (see above) the strategy of unpaired males usually seemed to be to attempt to pair with females. Evidence of this is given below:

A pair (FE3/MA8) was resident on a pothole. On 26 May 1976, MA2 was observed on this pothole for the first time. On this date FE3 had laid her eighth egg of an eventual clutch of nine eggs in a nest 38 m west of the pothole. Continuous observations were maintained at the pothole between 0540-2115 h (15.6 h). At 0652 h, MA2 landed on the pothole and the female went up onto shore. MA8 chased the trespasser in a GFATD and evicted him. At 0801 h, for no apparent reason, MA8 flew from the pothole leaving FE3 alone on the water. At 0843 h, MA2 landed with FE3 alone up on shore. MA2 observed the female and flew to her causing FE3 to flush in two short flights over the water. MA2 made no attempt to mount her but vocalized (Slow Whistle) occasionally and swam alertly behind the female. He intermittently Bathed, Preened and did Swimming-shakes. The female's only response was to swim away, Incite and perform bill open aggression movements towards MA2. MA2 followed the female even when she went up onto shore. This behavior continued until 1005 h when MA8 returned. MA8 approached MA2 who performed Wings-up and a 23 s wing-beating fight ensued. Following this the males separated with MA2 the apparent victor. MA2 flew toward FE3 who ran up onto shore with Wings-up. MA8 swam toward them vocalizing (Slow Whistle). FE3 tried to avoid MA2, Inciting at him and at 1011 h she finally succeeded in rejoining MA8. No further interactions occurred. MA2 flushed at 1232 h but returned 10 min later. At 1243 h MA2 and another lone unmarked male flew after the pair in a GFATD. The lone males returned to the pothole alone at 1246 h. The pair returned only at 1336 h when the males were absent but they departed 9 min later. At 1415 h, MA2 entered and at 1453 h, MA8 returned alone. MA8 responded aggressively toward MA2 who was forced off the pothole in 14 GFATD over the next 6.4 h. During all of this time FE3 was absent.

I observed only one incidence of an unpaired male successfully breaking an existing pair bond, presumably employing this kind of persistence.

An adult female (FE4), nest-trapped on 15 June 1976 was sighted on the study area on 1 May 1977 paired to an unmarked male. She was observed again on 24 May again accompanying an unmarked male (the same one?). On 25 May juvenile male MM3 was captured in a decoy trap around which FE4 was swimming. MM3 and FE4 were observed paired twice on 27 May and again the next day. On 17 May adult male MO2 was captured in a decoy trap. MO2 was not seen with a female and was observed alone on 21, 27, 28 and 29 May on four different potholes on the study area. On 31 May at 0930 h MM3 was again captured in a decoy trap in the same pothole where he was trapped originally. At this time FE4 was not present and MM3 was released immediately. He flew normally and appeared healthy. On the morning of 1 June, FE4 was observed at this pothole but now paired with MO2. The new pair was observed here almost daily until 10 June. MM3 was observed alone on a neighbouring pothole on the evening of 1 June. He appeared healthy and was chased in several GFATD by the resident male there. After this date MM3 was not observed again on the study area.

Although not confirmed, by process of elimination, a nest belonging probably to FE4 was discovered on 15 June 1977, 80 m from where she was known to nest in 1976. By egg-candling it was estimated that this 1977 nest was begun on 26 May and completed (nine eggs) on 3 June. If this was in fact FE4's nest her pair bond with MM3 would have been broken during the latter part of egg-laying and MO2 would have fertilized potentially about three of her eggs.

No interactions between MO2 and the original pair were seen prior to the mate shift, however, MO2 was observed frequenting potholes also used by MM3/FE4. It is not known if the break took place during the time MM3 was restrained in the trap on 1 June and, therefore, would not have been available to defend his mate. It is possible also that he entered the trap to interact with the decoy female after having lost his own mate. In any event, MM3 apparently was healthy but despite this was unable to successfully retain his mate and territory.

Interspecific Interactions

Of 666 interspecific interactions I observed among waterbirds, 561 of them involved wigeons. Wigeons won 60.2% of their encounters and males were responsible for 71.3% of these. Males also were involved in 54.3% of lost encounters. Females were involved in fewer encounters ($P<0.001$; $x^2=47.4$) and lost a greater proportion of them than males ($P<0.001$; $x^2=16.1$).

Wigeon were subdominant to Mallards, Canvasbacks, American Coots, Horned Grebes and Pied-billed Grebes, losing 78.3%, 100%, 98.7%, 95.7% and 90.9%, respectively, of their interactions with these species. Coots and grebes also dominated all other duck species. Therefore, among the Anatidae, wigeon were dominated by only two species, both of which outweighed them (Tables 56, 57 and 58). Wigeon dominated all smaller species of ducks winning 88.9% of encounters with Northern Shovelers, 98.7% with Blue-winged Teals and 100% with Green-winged Teals. They also dominated Northern Pintail, Gadwall and Lesser Scaup, all of which are heavier than wigeon (Tables 56, 57 and 58), winning 84.4%, 67.1% and 94.1%, respectively, of their encounters with these species.

Wigeons interacted aggressively most often with Gadwalls and Blue-winged Teals with 28.7% and 26.6%, respectively, of interactions occurring with these two species. Waterfowl surveys for May were used to estimate relative abundance of each species in the area and this was compared with the proportions of interactions wigeons had with each using Ivlev's formula (1961) (see Chapter 1). Data indicated that wigeons interacted with Mallards, scaups, and shovelers less than expected according to their abundance, Blue-winged Teals, Gadwalls and coots more than expected, and with Northern Pintails at about the expected level (Table 59, Appendices 3 and 4).

Wigeons dominated Blue-winged Teals with little effort using aggressive postures and short chases. Just three longer chases involving flight and two fights occurred (3.4% of encounters). With Gadwalls, however, 36 chases involving flight and four fights occurred (24.8% of encounters).

Table 56. Mean weights of adult male ducks that were involved in dominance hierarchies at Moose Jaw.

Species	Weight (g)[1]	N
Canvasback	1251.9	191
Mallard	1247.4	1809
Northern Pintail	1025.1	390
Gadwall	966.1	37
Lesser Scaup	825.5	177
American Wigeon	821.0	84
Northern Shoveler	680.4	21
Bufflehead	517.1	9
Blue-winged Teal	462.7	35
Green-winged Teal	322.0	113

[1]From Bellrose (1976).

Table 57. *Interspecific encounters lost and won among waterbird species at Moose Jaw. Species arranged in approximate order of decreasing dominance as determined by lost:won ratios.*

	Winners[1]													
Losers[1]	PIGR	HOGR	AMCO	CANV	MALL	AMWI	GADW	NOPI	NOSH	LESC	BLTE	GRTE	BUFF	Total lost
PIGR						1								1
HOGR	1					1								2
AMCO		1			1	1								3
CANV														0
MALL	2	1	6	2		10								21
AMWI	10	22	78	14	36		53	5	1	2	2			223
GADW	3	2	7		2	108								122
NOPI			2			27	4							33
NOSH		1	1			8								10
LESC		29	2		1	32	1							65
BLTE	1	1	18	2	2	147	2		8					181
GRTE						3					1			4
BUFF										1				1
Total won	17	57	114	18	42	338	60	5	9	3	3	0	0	666

[1]PIGR=Pied-billed Grebe, HOGR=Horned Grebe, AMCO=American Coot, CANV=Canvasback, MALL=Mallard, AMWI=American Wigeon, GADW=Gadwall, NOPI=Northern Pintail, NOSH=Northern Shoveler, LESC=Lesser Scaup, BLTE=Blue-winged Teal, GRTE=Green-winged Teal, BUFF=Bufflehead.

Table 58. Percent of interspecific encounters that wigeons won with other waterbirds at Moose Jaw. Chi-square values indicate the significance of differences from a 50:50, won:lost ratio.

Relationship with wigeon	Species[2]	Encounters won by wigeon (%)	Chi-square value	Sig[3]
Dominant	CANV		14.0	***
	AMCO	1.3	75.0	***
	HOGR	3.6	19.2	***
	PIGR	9.1	7.3	**
	MALL	21.7	14.7	***
Subdominant	GADW	67.1	18.8	***
	NOPI	84.4	15.1	***
	NOSH	88.9	5.4	*
	LESC	94.1	26.5	***
	BLTE	98.7	141.1	***
	GRTE	100.0	3.0	NS
	BUFF			NS

[1]Based on percent of encounters won and lost each species is deemed either dominant or subdominant to wigeon (see Table 57).

[2]See Table 57 for species names.

[3]NS=$P>0.05$, *=$P<0.05$, **=$P<0.01$, ***=$P<0.001$.

Table 59. Number and proportion of each waterbird species in the community compared with number and proportion of encounters each had with wigeon at Moose Jaw.

	Population		Interactions		Index[3]
Species[1]	Number[2]	Proportions (p)	Number	Proportion (r)	(r-p)/(r+p)
MALL	850	26.9	46	8.2	-0.53
LESC	721	22.8	34	6.1	-0.58
BLTE	597	18.9	149	26.6	+0.17
GADW	376	11.9	161	28.7	+0.41
AMCO	203	6.5	79	14.1	+0.38
NOPI	140	4.4	32	5.7	+0.13
NOSH	101	3.3	9	1.6	-0.33
REDH	52	1.6			-1.00
GRTE	17	0.5	3	0.5	0
HOGR	61	1.9	23	4.0	+0.36
RUDU	11	0.3			-1.00
PIGR	10	0.3	11	2.0	+0.74
CANV	18	0.6	14	2.5	+0.61
RIDU	2	0.1			-1.00
Total	3159	100.0	561	100.0	

Table 59. Continued.

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[1]See Table 57 for species names, REDH=Redhead, RUDU=Ruddy Duck, RIDU=Ring-necked Duck.

[2]Total number of individuals of each species counted on the study area on 8, 15, 22, 29 May 1976 and 7, 13, 20 May 1977. In this survey 343 wigeons were also counted. See Appendices 3 and 4 for survey data.

[3]See Ivlev (1961). >0=more encounters than expected by population density; <0=less encounters than expected by population density; 0=as many encounters as expected by population density.

Wigeons avoided encounters with dominant species. They showed avoidance in 9.1-40.0% of their encounters with Canvasbacks, Mallards, coots, Horned Grebes and Pied-billed Grebes. Wigeons avoided subdominants only twice (0.5% of encounters); once with a Gadwall, and once with a Northen Pintail. Subdominant species were observed avoiding wigeons four times (1.0% of encounters); Gadwalls twice, a shoveler once, and a Blue-winged Teal once.

DISCUSSION

Territoriality

Interspecific variation in site tenacity in Anas species has led to controversy over Hochbaum's (1944) contention that waterfowl are territorial. Sowls (1955), Dzubin (1955) and others found that boundaries between 'territories' of some species were difficult to identify and preferred to call these areas home ranges (Odum and Kuenzler 1955).

Nonetheless, pairs of many duck species show site tenacity (Seymour 1974a), spend a high proportion of their time in restricted areas (Dwyer 1974, Poston 1974, Seymour 1974b) and show aggression toward trespassing conspecifics. Titman (1983) pointed out that although neighbouring Mallard territories overlapped, rarely did pairs use these common areas concurrently. This behavior fits the definition of territoriality as proposed by Tinbergen (1957).

Under this definition, wigeons were territorial. Wigeon territories were defended vigorously by the paired male and even unpaired males were not tolerated. GFATD and displays were an important element of defense.

McKinney (1973, 1975) and Derrickson (1978) proposed that the degree of mobility, as measured by territory size, is indicative of the site tenacity in waterfowl. Wigeon areas were small relative to most other Anas species studied so far (see review in Nudds 1980), substantiating that they have a strong territorial system similar to that of the shoveler (Seymour 1974b). As with most other duck species (Sowls 1955, Drewien 1968, Poston 1974, Dwyer 1974, Gilmer et al. 1975, Titman 1983), the mobility of wigeons decreased during the Prelaying and Laying stages.

Adaptive radiation and economic defendability of resources (e.g., food, mates, space, nest sites, etc.) (Brown 1964, Emlen and Oring 1977) have been proposed to explain the diversity of mating systems in dabbling ducks (McKinney 1973, 1975, Nudds 1980). Those individuals which most efficiently balance the costs and benefits experienced while acquiring resources in inter- and intraspecific competition, are favored by a greater relative representation in the gene pool.

Territoral Costs

Individuals incur costs when they defend territories. Wigeon and other waterfowl are sociable and occur in flocks year round except during the breeding season. It has been demonstrated that flocking may reduce vulnerability to predators (Goss-Custard 1970, Lazarus 1978, 1979) and

enhance foraging efficiency (Krebs et al. 1972, Krebs 1974, Krebs and Cowie 1976). These benefits are lost when birds space themselves out onto territories.

Also important negative factors were the time and energy requirements of territorial defence and the risk of injury while involved in aggressive encounters. Most of these costs were borne by the male. In addition, because males did not provide any direct parental investment, they sacrificed more than females by spacing out onto territories which limited the number of females they could fertilize.

Territorial Benefits

The benefits gained by individuals defending territories have been summarized for birds by many workers (Nice 1941, Hinde 1956, Davies 1978, etc.). As with costs, benefits differed in degree and consequence for male and female wigeons.

Exclusive Access to Mates

The process of early pair formation during the winter in wigeon promoted the combination of healthy, compatible mates (Chapter 5). Because forced copulation was a strategy employed by some males on the breeding grounds, a female could be inseminated by a male whose 'quality' she had been unable to evaluate. Therefore, it would be in her interest to copulate only with her mate or go through the costly process of finding a better one.

Territorial defence provided by the male reduced the chances of forced copulation. A female could identify males successful at forced copulation by being mounted by a male who was able to penetrate the defenses of the territory and her own evasive actions. However, being inseminated by such a male could actually result in increasing her fitness should her resultant offspring also inherit these genes. Thus, at some point (i.e. when mounted) it would be beneficial to succumb to such a male, particularly if the female also ran the risk of injury by not cooperating.

Once coition occurred, the male inflicting forced copulation abandoned the female and provided her with no further investment, except possibly additional copulations. If a cuckolded paired male "protected" himself by abandoning his mate there would be less benefit for the female to cooperate with a male perpetrating forced copulation at any point, for she would not obtain the other benefits arising from the pair bond. However, there was no evidence that paired males reacted this way. This would also be adaptive, for a single forced copulation might or might not fertilize any eggs.

Paired males gained no advantages and could have been levied considerable losses if their mate was inflicted with forced copulation by another male. As indicated by the skewed sex ratio, females were in short supply. Males invested time and energy in acquiring a mate and may not have been able to get another one (Chapters 4 and 5). Thus, a male should have attempted to ensure that all of his mate's offspring were sired by him. Spacing out onto territories reduced the chance that another male would succeed in mounting his female.

Barrett (1973), Barash (1977) and Burns et al. (1980) found that forced pair copulations occurred in several duck species. These often soon followed a rape attempt on the female and may have been a means of avoiding cuckoldry by introducing sperm competition. Although FPC in wigeon did not seem to be related to rapes by other males, they did occur frequently during egg-laying. Females might avoid frequent copulations by their mate if this would lead only to energy expenditure and not also to a greater chance of fertilization. As mentioned, it might be advantageous for a female to be fertilized by forced copulation. However, it would be in the greater interest of the male to maintain his own fresh sperm, whether before or after forced copulation, in his mate's oviduct should cuckoldry be a threat (i.e., prior to and during egg-laying).

Exclusive Access to Food

There is considerable evidence that wetlands are unequal in productivity and that habitat selection by ducks is affected by this variability (Patterson 1976, Joyner 1980, Kaminski and Prince 1981a,b). There is no information yet available, however, to show that food per se in natural habitats limits duck numbers.

The nutritional requirements of female reproduction are high (Krapu and Swanson 1975, Ankney and MacInnes 1978, Drobney 1980, Krapu 1981) and female condition affects productivity (Spurr and Milne 1976b, Ankney and MacInnes 1978). Although male wigeons relied heavily on their body reserves at this time, anything affecting female productivity would also affect their fitness.

Stenger (1958), Krebs (1971) and Cody and Cody (1972) demonstrated that bird territory size can be correlated with food density. Nudds (1980) showed that in ducks, territory size correlated with species body size and speculated that this was related to food dispersion. Further work, preferably of an experimental nature, is warranted to identify the importance of food availablility and competition in affecting territoriality in ducks.

Protection of Food For Young

Although young wigeons have large and specific nutritional demands (Sugden 1973), territoriality does not seem important to ensure its availability to them. Except in rare cases, males did not accompany the brood and territories were not defended at this time. Often the female moved the young long distances overland to larger, deeper potholes than those available on the original territory (Wishart, unpubl. data, Smith 1971). Thus, broods might spend little or no time on the territorial area that was originally defended by the male.

Protection of the Female's Time and Energy

Even if food is available, time is required to obtain it. Foraging time is affected by food dispersion and availability, and by food selectivity and foraging efficiency of the individual. Due to their small body size and habit of nesting late, wigeon females relied on food resources obtained on the breeding grounds (see also Calder 1974, Afton 1978, 1979). Harassment by sexually active males (those trying to either

perpetrate forced copulation or form pair bonds) would reduce the amount of time the female could devote to feeding (see Ashcroft 1976). Female wigeons reacted by trying to escape or hide. If discovered they were chased, often in flight, and energy reserves were further diminished.

Isolation on a territory defended by the male undoubtedly reduced the disturbance suffered by the female. In an artificially crowded Mallard population, Titman and Lowther (1975) found a high incidence of sexual harassment of females which resulted in their reduced productivity.

Even during incubation, particularly in early nesting pairs, female wigeons were molested by males. Females relied on incubation recesses to feed and thus reduce the negative energy balance they experienced through this stage. This would help to ensure that they would complete incubation successfully and be attentive of the young once they hatched. Thus, territoriality and extended attentiveness by the male (Ashcroft 1976) would seem to be adaptive for both sexes as long as other sexually active males were present. Afton (1979) found that a female shoveler whose mate died early in incubation of their clutch, deserted four days later when another pair established their territory on the same area. This underlines the male's importance to successful nesting.

Reduced Nest Predation

Tinbergen *et al.* (1967) demonstrated that clumped, immobile prey were subject to higher predation than if they were spaced more widely. McKinney (1965c) proposed that one benefit that accrued to territorial

ducks was lower predation of their nests. This hypothesis is supported by the tendency for some normally territorial duck species to nest almost colonially in predator-reduced habitats (Hammond and Mann 1956, Duebbert 1966, Vermeer 1968, Duebbert and Lokemoen 1980). However, further testing of this hypothesis for waterfowl is necessary.

Rendezvous Site

When members of pairs were separated (e.g., female at the nest, male in territorial defence, etc.) they relocated each other on the territory. The predictability of the rendezvous site would reduce searching time, and permit quick reformation of the pair. This was important, not only directly from a movement-energy standpoint, but it also reduced the harassment suffered by the female when she was left alone. It may also have ensured the male's priority in inseminating new eggs should a renesting attempt have been necessary. Therefore, this benefit is closely linked with others that were discussed above.

Advantages of Obtaining a Territory Early

Male ducks pairing overwinter generally follow their mate back to the area where as a juvenile she learned to fly (see McKinney 1965c and Blohm 1978, for reviews). Of 21 female wigeons I banded in 1976, 3 were reported shot by hunters and at least 9 returned to the study area in 1977. As a result, because the female was initially more familiar with the area, it was likely she who originally set the limits of the pair's movements.

Earlier arrival and presence by a pair in an area seemed to ensure their dominant status there, relative to other conspecifics. Seymour (1974b) found experimentally that a female shoveler restrained in another male's territory could not be defended successfully by her original mate. Similar results were obtained when testing captive wigeons (Wishart, unpubl. data). Thus, birds migrating early and selecting territories first would seem to be at an advantage in defending these areas and retaining their use through the breeding season.

The advantage during an encounter between two pairs competing for a territory would not necessarily go to the largest and strongest male. However, the male who attacked the female of the other pair first probably succeeded most often in winning the disputed area. This occurred because females flushed quickly if attacked by a male at this time and their mates always followed them. Therefore, a male's vulnerability lay in the presence of his female and usually aggression by a male was directed at this weakness (see also Titman 1983).

Pairs that had a territory and were stationed there held an initial advantage in its defence. An alert male was aware of any conspecifics that attempted to land on his area and he communicated this to his mate. If she remained motionless or hid, she avoided detection by other males. Her mate then was free to leave her and attract attention away from her location by attacking the trespassers.

Even if the chased pair attempted to return to the area after being pursued, they were at a disadvantage as long as the resident female

remained hidden, and less vulnerable than the chased female. It would not be in the interest of the intruders to persist in returning once chased, because this would only lead to the added consumption of time and energy and leave the female open to forced copulation or risk of injury.

This emphasizes the importance of the ability of the resident male to invest in alert behavior. If negligent, his female might be chased before he could detect the presence of intruders and the advantage of being resident would be reduced. Once chased, his female would use time and energy in attempting to escape and might eventually be raped. In addition, investment of considerable energy and time might be necessary to regain the territory or obtain a new one.

At Moose Jaw, where wigeons nest at high densities, pairs dispersed onto territories soon after they arrived in spring, in some cases two to four weeks before egg-laying began. This further indicates that pairs settling on territories early would have an advantage, if suitable habitat were limited.

Pairs that trespassed on areas dominated by pairs that settled earlier were vulnerable to attack. This would be energetically costly but movement might be necessary if suitable habitat for nesting were limited. The peak in frequency of GFATD coincided with a time in mid-May, soon after most pairs had dispersed from flocks. Theoretically, a pair should attempt to evaluate a number of vacant areas before finally settling. Once accomplished, area-restricted movement would be adaptive in order not only to defend the area from other settlers, but also to avoid costly attacks by neighbouring pairs.

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Pairs unable to obtain a territory early might eventually have settled on a suboptimal area or been forced to wait until an area defended by a more dominant pair was vacant. However, late-nesting pairs probably were less productive (see Spurr and Milne 1976a,b, Batt and Prince 1979) and may have been forced to molt and migrate later than other birds. Those unable to obtain a territory might not breed (Seymour 1974a) (e.g., during drought) supporting the contention that duck populations can be density dependent (Dzubin 1969).

Economic Defendability

What factors influenced the pattern of spacing and territory establishment by wigeons? With a specialized bill for grazing, wigeons are less efficient dabblers, relative to other Anas (Chapter 2). Except in late spring they were herbivorous feeding predominantly on seeds, vegetation and rootlets (Chapter 1). Much time was spent feeding on shore or in fields. At Moose Jaw, these upland feeding areas were adjacent to most wetlands and interspersed with native rangeland used for nesting. In the Prelaying and Laying stages, wigeons consumed aquatic invertebrates and this helped to meet their protein requirements for egg production (Chapter 1). Wigeons selected large invertebrates and these were obtained primarily by picking rather than straining (Chapter 1).

Although I saw wigeons occasionally feed in small temporary ponds, most of their activity occurred on larger, more persistent wetlands between May and mid-June. In Alberta, Smith (1971) also found wigeon

pairs using semipermanent ponds most frequently as did Stewart and Kantrud (1973) in North Dakota.

Deeper ponds provide greater densities of the aquatic macrophytes selected by wigeons for food (Stoudt 1971). Sugden (1973) also found wigeons feeding in deeper water, unlike other dabblers, and believed that this was due to the vegetation they preferred being found more abundantly away from shoreline emergents. Krull (1970) demonstrated that macrophytes also provide excellent substrate for large populations of the invertebrates eaten by wigeons (Chapter 1). Stoudt (1971) recognized that wigeons preferred habitats less subject to drought and reported that populations in southern Saskatchewan and Alberta fluctuated relatively little during wet-dry cycles that spanned 13 years (see also Boyd 1981).

Therefore, the preference by wigeons for more environmentally stable and predictable habitats for breeding permits a more stationary existence once these areas are located. The Moose Jaw study area had a large number of semipermanent and permanent ponds (persistent). Within the study area also, there occurred a high interspersion of native pasture and cropland. Steep slopes precluded the use of farm machinery in many areas and this, along with light agricultural grazing pressure, permitted the existence of abundant, dense upland nesting cover. Annual rotation of silage and feed grain crops provided additional habitat and

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supplementary food for late nesters. I believe that it was the proximity of these various kinds of habitat which encouraged wigeon and other duck species to nest here in such high numbers. The juxtaposition of resources permitted wigeons to nest on small territories which could be defended efficiently from conspecifics. A comparitive study of wigeon territoriality in a population using more natural habitat (without agriculture) (e.g., Mackenzie River Valley) should be conducted.

Wigeon Mating System Relative to that of Other Species of Dabbling Ducks

Wigeon males used GFATD as the primary means of defending territories. Relative to other Anas, characteristics of these flights were most similar to those of the Gadwall, as described by Titman and Seymour (1981).

Chases involving females were fast and vigorous and of relatively short duration. Trespassers were effectively evicted and once concluded, the male usually returned directly to rejoin his mate. Chases were directed at the female and physical contact among the participants was common. Paired males whose mate was being chased frequently defended them physically or attempted to stay between them and the chasing male. This was similar to behavior patterns of Northern Shoveler, Blue-winged Teal, and Gadwall (group 1) with strong site attachment and persistent pair bonds (Titman and Seymour 1981). By contrast, species such as Mallard, American Black Duck and Northern Pintail (group 2) normally do not defend their mates and may not even follow them on GFATD.

Similar to group 1, male wigeons were also intolerant of lone males (either paired or unpaired) entering their territories. Aggressive Chin-lifting displays (Tandem-swimming) often were given (Chapter 4). Tandem-swimming usually led to GFATD, which although less aggressive than those for shovelers (Seymour 1974c) and Blue-winged Teals (Stewart and Titman 1980), were effective in territorial defence.

Interpecific Interactions

Wigeon males also protected females from possible competition with other waterfowl species. Most conflicts with other ducks occurred at close range while feeding and may have been due to competition for a specific food patch. All duck species so far studied in detail rely heavily on invertebrates as a protein source during egg formation (see Chapters 1 and 2 for a review). Although species differ in nest timing (Bellrose 1976), overlap is still great due to the propensity to renest. However, due to variation in bill and neck structure, body size and foraging strategy (Goodman and Fisher 1962, Nudds 1980, Chapter 2), overlap in preferred foods by sympatric ducks is reduced.

Interspecific aggression may also occur in species that feed on mobile prey that are liable to disturbance from other individuals, (Davies and Green 1976, Davies 1978). Thus, aggression among ducks may assist in spacing individuals and permit more efficient feeding.

Other conflicts took place at shoreline clearings, rocks, muskrat houses, logs, etc. used by all waterbirds as loafing sites. Although loafing sites on most ponds did not seem to be limited, certain of them

were preferred and used as foci of the territory (see also Seymour 1974a, Titman 1983).

Dominant species had priority over subdominants to these resources and usually took them without physical hostility. Dominance was related to body size as found also by Bailey and Batt (1974). Males were larger than females (Bellrose 1976), and generally more aggressive. However, coots and grebes did not fit this pattern. Their dominant status probably was related to their 'weapons' (i.e., sharp bills and strong feet) (see Shields and Bildstein 1979) and attack method (i.e., grebes dived and attacked with the bill from below). Aggression by coots and grebes may have been related to food competition. However, during winter, wigeons regularly pirated food from coots with little retaliation (Wishart, unpubl. data). Aggression seemed to be most intense around floating nest structures built by coots and grebes. If not protected, ducks might have used these structures as loafing sites and destroyed eggs. Wigeons were more aggressive than expected by their size. This again might be related to weaponry (i.e., short strong goose-like bill) (see Chapter 2).

Breeding Strategies

Unpaired Males

Males without mates moved widely over the area and most left the study area soon after I captured them. These birds followed a strategy of attempting to break existing pair bonds in order to obtain a mate. Once pairs had spaced out onto territories one or two lone males associated with a pair for brief or extended periods and attempted to

follow the female. Courtship occurred but no attempts at forced copulation were seen.

Other observers have recorded unpaired male Northern Shovelers (Poston 1974, Seymour 1974b), Blue-winged Teals (Drewien 1968), Gadwalls (Dwyer 1974), American Black Ducks (Seymour and Titman 1979) and Northern Pintails (Derrickson 1977) following a similar strategy. Bailey et al. (1978) observed unpaired male Blue-winged Teals trying to mount females, however, these birds gave courtship displays and their primary intent also seemed to be to pair with the female.

Paired females of all duck species avoid unpaired males during the breeding season, Incite and show aggression toward them. Paired males, of some species (including wigeon) defend their mates and attempt to drive unpaired males away. Winter pair bonds may be broken by unpaired males (Weidman 1956), however, documentation of this in breeding ducks using marked birds is rare (but see Stewart and Titman 1980, and above). Bonds might be broken more frequently in late-nesting species like wigeon or in renesting pairs of all species when pair bonds are waning (but see Humburg et al. 1978).

Paired male wigeons invested considerable time and energy in guarding their mates. Males arriving on the breeding grounds in poor condition might be less attentive. Some wigeons did not pair until just before spring migration (Chapter 5) and these bonds might be unstable and easily disrupted. By moving widely and testing persistently a number of pairs, an unpaired male might eventually succeed in acquiring a mate.

Elder and Weller (1954) found that domestic Mallards could store sperm and produce fertile eggs up to 17 days after copulation. Burns et al. (1980) demonstrated that forced copulation in captive Mallards could lead to fertilization and Blohm (pers. comm.) found that unpaired male Gadwalls produced motile sperm. Assuming that wigeons behaved similarly, why then did unpaired males apparently not (or rarely) attempt to force copulation on females?

Attempts at forced copulation by single males probably would not be successful due to intervention by the paired male (Wishart and Knapton 1978, Bailey et al. 1978) and lack of cooperation by the female (see above). By attempting to attract (court) females rather than show aggression (forced copulation) they might eventually be more successful in dislodging a paired male.

Although unpaired males were seen joining several ongoing GFAFC and were among groups of males apparently searching for females, I did not see them attempting forced copulation. In general, paired males were larger and dominant to unpaired males (Chapter 5, Paulus 1980). In an attempt at forced copulation on a female involving both paired and unpaired males, it is probable that only the most dominant would be successful. Unpaired males might opportunistically copulate or attempt to pair with a female once other rapists departed, and gain experience assisting them in future encounters.

Unpaired males left the breeding grounds early in the spring and presumably molted before the breeding individuals (Oring 1968). Those

doing so might also have arrived early on the wintering grounds and had an advantage in acquiring a mate for the next breeding season (Chapter 5).

Paired Males and Females

Wigeons showed characteristics of a strong pair bond. In the Prelaying stage males spent much time attending the female closely. Even while the female was at the nest, males spent much time alert and continued to be intolerant of conspecifics entering the territory. When the pair was separated, males vocalized regularly. These calls (Slow Whistles) probably were individually recognizeable (Klint 1980a, Chapter 4) and seemed to function in reuniting the members of the pair. Paired males did not call as frequently when absent from the territory and ceased if conspecifics entered it. Females on the nest able to recognize these correlations may have used male calling as a cue in timing incubation recesses to when the male was present (i.e., calling). This would reduce the amount of harassment suffered from other sexually active males and permit efficient use of recesses for feeding (see Afton 1980).

During the Laying period, male wigeons continued to defend their territories but often their first reaction was to avoid encounters with trespassers. This indicated a strong attachment to the female at a time when the male was most vulnerable to cuckoldry. Leaving the female to chase intruders would be risky because origins of GFATD could be detected from great distances and might have been cues to the location of unattended females vulnerable to forced copulation. Females hiding while males were absent and the short direct nature of most wigeon GFATD,

likely reduced this danger. Shovelers and Blue-winged Teals characteristically use shorter GFATD and rely also on long-distance displays as alternatives to GFATD. Thus, females of these species are even less vulnerable to forced copulation (McKinney 1970, Titman and Seymour 1981).

Even outside of the Laying period females often hid when their mates were in GFATD. This was adaptive because by avoiding potential harassment, nutrient reserves would be conserved and channeled into production (egg-laying, incubation, brood care, renest attempts, etc.). Females hid more frequently when lone males trespassed, possibly reflecting their greater vulnerability to males not accompanied by a female. Lone males did not have the liability of a mate present at whom the defending male could direct a pursuit. Thus, they were harder to evict from the territory and became particularly persistent if they detected the female's location.

Oring (1964) using unmarked birds observed that five male wigeons in Idaho abandoned their mates between day 3-8 of incubation. Since then it has been accepted generally that wigeon pair bonds were weak and of short duration (Bellrose 1976, Palmer 1976a, Johnsgard 1978) (but see Stoudt 1971, Hochbaum 1973 and Cramp 1977).

Wigeons in southern Saskatchewan showed a different pattern. Males usually stayed with females into late incubation and in several cases until eggs pipped. I and others have presented evidence that some males remain paired even into brood rearing. W.G. Leitch (pers. comm.) near

my study area observed over 25 years at least 6 male wigeons attending females with young. McClanahan (1942), also in southern Saskatchewan, reported four observations made on 12 June 1941 of male wigeons attending females with broods of five to nine young. In one case a male feigned injury when approached, while the female led the brood away. Similar observations have been made rarely for other duck species (Bezzel 1959, Chura 1962, Oring 1964, Raitasuo 1964, Dzubin in McKinney 1965c, Harrison 1967, Lord 1979).

The male I collected, as well as those observed by McClanahan (1942) were attending broods that had hatched recently. Dzubin (in McKinney 1965c) also observed that Mallard males attended broods most frequently during early, mild springs. Although Oring (1964) provided few details of local weather and habitat conditions, these variables affecting bird condition may be responsible for the variation in pair bond duration between Idaho and Saskatchewan wigeons.

The fitness of an individual is measured by the number of reproducing offspring (and other relatives) he has (see Hamilton 1964). Trivers (1972), Dawkins and Carlisle (1976), Maynard Smith (1977) and others have emphasized the differing and sometimes conflicting life strategies paired males and females follow to maximize their fitness.

In wigeon where offspring are precocial, care by both parents may not lead to greater fledging success than if one parent remains with them (Kear 1970). In this case, it is in the interest of one parent to desert the pair bond early and the other to remain with the young.

Because egg production and incubation are energetically costly, it is unlikely that a female could hatch a brood and then renest successfully. Males on the other hand may have a chance of fertilizing additional eggs by pairing with and/or forcing copulation on renesting or late nesting females. Under these conditions Maynard Smith (1977) has shown it to be more likely to have evolved that the male will be the first to abandon.

The point at which pair bond dissolution occurred seems to be a point of conflicting interest between males and females. As long as females were vulnerable to predators and harassment from other ducks, it would be in their interest to be paired. However, use of excessive time and energy in maintaining the bond would negate the benefits of having a mate. Precopulatory Head-pumping by the female, particularly during incubation, may have been an uncostly means of 'coyly' maintaining male attentiveness past the stage of her fertility. Unpaired males avoided being cuckolded by such behavior by following a strategy of forced copulation rather than attempting to pair with females other than their own.

It would be in the male's interest to attend the female as long as the net effect of this behavior increased his fitness. Male attendance and territorial behavior occurred generally before the young hatched and this does not fit Triver's (1972) definition of parental investment. However, male attentiveness likely affected the female's time-energy budget which in turn would influence her productivity. Thus, male investment affected that by the female and was an indirect form of

parental investment. The use of this broader definition allows a clearer understanding of the evolution of social systems in species with precocial offspring.

There were opposing "pressures" acting upon paired birds which ultimately determined their reproductive effort. Males in poor condition may have been unable to adequately defend their mates and territories and abandoned the female early. It would be in the female's interest to identify and reject these males in the winter courtship process before accepting them as mates (Chapter 5). An important value of the bond was the protection from sexual harassment provided by the male for his female. This value was reduced as the number of sexually active males in the population decreased. This suggests why pair bond length was related more directly to the calendar rather than the stage of incubation of an individual pair. An early nesting pair (relative to other conspecifics) might be open to harassment even once eggs hatched, whereas a late nesting or renesting female might be undisturbed even in early incubation.

Most males departed from the study area by the last week of June and no nests were initiated after 18 June. Thus, males attending females after the end of June would probably be operating inefficiently, although they still would be providing some benefit (i.e., surveillance for predators and guarding against interspecific competition).

As the season progressed wigeon males were less attentive and moved about more widely. Forced copulations occurred opportunistically but usually seemed to involve considerable investment of time and energy.

Such a strategy adopted too early (before incubation) might expose mates to harassment and forced copulation.

Forced copulation is most common in early nesting species such as Northern Pintail (Derrickson 1977) and Mallard (Titman 1983). This partially may be a function of the prolonged period over which egg-laying can occur in these species. Should a male Mallard mate with a successful early nesting female there still may be up to four weeks where other females in the population are nesting or renesting. The opportunities for stolen copulations under such a reproductive timetable are greater. Conversely, in later species such as wigeon, the nesting season was compressed. Females were more synchronous in laying and there was less opportunity for renest attempts to occur. Under these circumstances, forced copulation would be less likely to be a dominant strategy.

Energy demands and niche resources are important factors affecting the mating systems of Anas species. McKinney et al. (1978) and Ball et al. (1978) found that the African Black Duck, a river specialist, maintained territories year round and might re-mate annually with the same female. For this species, suitable habitat seemed limiting and some individuals unable to obtain territories did not breed. Climate within the range of this species was moderate, freshwater habitats did not freeze, and territories provided most of the requisites for year round existence. Under these conditions, it would be in the interest of individuals to defend their territories continuously or run the risk of losing them to other birds and possibly foregoing subsequent reproduction.

Wigeon and other species that breed in temperate climates where water freezes must abandon their territories annually and migrate to other favorable habitats. While the female cares for the young, the male accumulates nutrient reserves and undertakes a molt migration (Chapter 3). The female often molts on the breeding grounds and so at this time pair bonds are severed with little liklihood of renewal for the next year. The necessity to obtain a new mate each year and the great competition for available females has resulted in strong sexual selection. More experienced males with larger nutrient reserves compete more successfully for mates (Chapter 5, Paulus 1980) during the winter courtship period. Males able to molt and migrate early probably are at an advantage in this regard. Thus, there would be a great advantage for males to abandon their mates as early as possible in the present breeding season so as to also have a greater chance of breeding in the next season. This pressure in opposition to those selecting for extended pair bonds ultimately is likely responsible for the variation in pair bond stability among individuals.

Why are Wigeon Monogamous?

Unlike mammals, monogamy is the dominant mating system in birds (Lack 1968b). Polygyny occurs but it is most likely to arise in species without direct parental care by males (Orians 1969). Wigeon young are precocial and males generally abandoned the female before the eggs hatched. Despite this, wigeons had a seasonally monogamous mating system.

Trivers (1972) has proposed that the sex making the greatest parental investment determines the characteristics of the mating system (see Wittenberger and Tilson 1980). In wigeon, because of the skewed sex ratio and the greater reproductive investment by females, they are the 'controlling' sex. While polygyny may be advantageous for males, it is not for females.

Wittenberger and Tilson (1980) simplistically attributed monogamy in Anatidae to the tendency of males to sequester females. Lack (1968b) speculated that monogamy in most duck species results because of the advantages of winter pairing.

The African Comb Duck (Carinini) is a tropical species with a polygynous mating system (Seigfried 1978). Unlike the wigeon, this species is non-migratory and pairing occurs on the breeding territory that is acquired beforehand by the male. Territory quality (e.g., presence of tree holes for nesting) varies and females may find it advantageous to join an already paired male if he holds a high quality area. Competition and harassment by unpaired males probably limits harem size (Siegfried 1978).

Unlike the Comb Duck, wigeons paired over winter (Chapter 5). Mate selection was based directly on individual qualities not on those of the territory (Chapter 5) which also was probably selected by the female. Due to competition it is unlikely that a male could have formed a bond and maintained it with two or more females at the same time. While defending one mate the other(s) might be forced to depart (e.g., in a GFASD).

It is advantageous for female wigeons to home to a familiar area to nest. It is unlikely that in a large winter flock a male would be able to associate with two females from the same breeding area. If the females did not cooperate by migrating together, the male would have to select which one to follow. Thus, females could easily restrict the occurrence of polygyny by being philopatric.

Once on the breeding grounds competition for territories was intense. Unpaired males were also threats to a territory holder and they invested considerable time and energy in guarding. A male likely would not be able to defend more than one mate. Wigeon flight was quick and manouverable, and with a functional penis, forced copulation was a viable reproductive strategy, even within this monogamous system.

Under polygyny, there would be more unpaired males and competition for females would be even greater. This might lead to a higher incidence of successful forced copulation by unpaired males. Males paired with two females could conceivably sire fewer offspring than those with only one. Females would also suffer greater harassment in this situation and as a result might have less nutrient reserves to invest in offspring. With these constraints it seems apparent that polygyny would not be a viable strategy for wigeons of either sex.

GENERAL SUMMARY

Chapter 1. - Feeding Ecology of the American Wigeon

1. Wigeons of both sexes fed primarily on nutritious leafy vegetation and were more herbivorous than other Anas species studied so far.
2. Invertebrates, primarily insects, were eaten during the breeding season until the molt started. Females ingested up to 40% animal foods and males 20%, during Laying.
3. Seeds were important foods at most stages but were eaten most from Early Arrival through Molt. Cultivated grains in upland habitats were eaten in spring and fall.
4. Important foods were listed for all stages of the annual cycle.
5. Wigeons favored particular foods.
6. Nutritional quality of wigeon diets was assessed over the annual cycle in relation to their biological needs.
7. Wigeon feeding behavior was described quantitatively for the breeding season. Most feeding occurred during the early morning and late evening and continued after dark.
8. Birds spent a high proportion of time feeding on land, particularly in the late evening.
9. Feeding on land increased over the spring to a high during Prelaying but declined thereafter.
10. Wigeons usually fed at the water's surface or just below it and tip feeding was relatively uncommon. Their feeding behavior changed only slightly over the season in relation to their needs for territorial defence and brood rearing.
11. Wigeons were aggressive and opportunistic foragers.

Chapter 2. - The Morphological and Physiological Adaptations of the American Wigeon to its Diet.

1. Wigeon were distinguished from other Anas species using discriminant analysis ordination of bill characteristics. This suggested bill specialization to the same degree as the shoveler but in the opposite direction.
2. Wigeon bills were pointed, and relative to body size, were short and vaulted, similar to those of geese. This structure permits increased closing power to be exerted at the tip, thus facilitating grazing.
3. Wigeons were deemed to be inefficient strainers compared to other Anas species due to their wide lamellar spacing on the bill (1.07 mm) and their short pointed bill structure.
4. Gizzard grit weighed most during Molt and through Winter and was made up primarily of small rock fragments (<0.50 mm in diameter).
5. Large grit over >2.0 mm in diameter dominated in gizzards during early spring.
6. At all stages, except during Laying and Prelaying, digestive organs of males were larger than those of females.
7. Largest digestive organs generally occurred during Molt except for the liver which was heaviest during spring and fall migration.
8. Gizzard grit characteristics changed in relation to diet indicating that wigeons were capable of selection based on fragment size.
9. Changes in digestive organ sizes also correlated with changes in diet, suggesting adaptation for increased digestibility.
10. Large fragments were more abundant in gizzard grit during stages when seeds dominated in the diet. Small grit correlated positively with increased consumption of invertebrates, and large proportions of

small grit with increases in herbaceous foods.

11. A decrease in organ size correlated with increased ingestion of soft animal foods.

Chapter 3. - Chronology of Molt in the American Wigeon

1. A description of wigeon molt chronology was derived using living, collected and museum specimens.
2. Juveniles proceeded slowly through the prejuvenal, prebasic I and prealternate I molts during their first fall and winter.
3. The molting chronology of individuals was variable.
4. Juvenal wing feathers were not replaced until after an individual's first breeding season.
5. The pattern and timing of molts over the year differed for males and females.
6. Females underwent part of the prealternate molt of body contour and down feathers during late winter and early spring.
7. Prebasic molt of females did not begin until late Brood Rearing.
8. Males had a protracted prealternate molt in late winter also but most of this occurred in the previous summer.
9. Most females that nested successfully probably molted on breeding areas, whereas males undertook a molt migration to larger marshes.
10. The peak of wing feather molt occurred in late July for males and in August for females. This began after all pterylae except the caudal had finished the prebasic molt.

11. Distal remiges were the last to molt.
12. The sex-related differences in molt pattern were discussed in relation to differential parental investment, and to other aspects of the mating system.

Chapter 4. - Social Displays and Vocalizations of American Wigeon

1. Wigeon displays performed during pair formation, and used for bond maintenance and territorial defence, were described quantitatively.
2. Courtship displays highlighted colorful plumages on the heads, wings and rumps of males and served to attract females and intimidate other males.
3. There was directional bias in some male displays which increased their signalling effect.
4. Females used displays to indicate mate preference and these influenced male displays and other behavior.
5. Aggression and Group Flights among competing males were dominant aspects of wigeon courtship.
6. Characteristics of displays or downy plumage suggested a close association of the wigeon with the blue-winged ducks, Gadwall and Falcated Duck.
7. Wigeon vocalizations and the contexts in which they occurred were described.
8. Several wigeon calls seemed to be recognizable individually and the advantages of such recognition by mates and offspring were discussed.

Chapter 5. - Pairing Chronology and Mate Selection in the American Wigeon

1. Wigeon sex ratios in winter were 52.4-59.6% males, similar to that during spring.
2. During the winter, some juvenile males proceeded slowly into their alternate plumage.
3. Not all birds took part in courtship or paired concurrently suggesting that individual traits in addition to photoperiod acted as proximate timers of this behavior.
4. Some winter pair bonds were ephemeral.
5. Pairing chronology differed between years but on average, for the years studied, it was similar between British Columbia and Texas.
6. Males in incomplete alternate plumage rarely courted females and I saw none that was paired.
7. Juvenile males were less capable than adults at acquiring mates.
8. Paired males were structurally larger than unpaired males in Early Winter but had smaller lipid reserves. I hypothesized that males successful in pairing had used lipid reserves in establishing and maintaining a pair bond.
9. Paired males were larger than unpaired males and had heavier breast muscles, and lipid and protein reserves over the latter parts of winter and during early spring.
10. A similar pattern occurred in an experimental flock of captive wigeons.
11. I concluded that disparate sex ratios in wigeon are a natural phenomenon which have been responsible for sexual selection acting on

males. This and the need to migrate between wintering and breeding habitats have probably selected for pairing over winter.

12. Male characteristics on which mate choice was based in winter were the same as those important for successful reproduction (i.e. aggressiveness, good condition, large size, flying ability and experience).

13. I discussed mate selection and pairing chronology in terms of individual reproductive cost-benefits.

Chapter 6. - Reproductive Biology, Behavior and Mating System of the American Wigeon

1. Wigeons arrived on their breeding areas between 11-19 April.

2. Birds remained in small flocks through April but aggression occurred among pairs coming closer than 2-3 m. Home range size averaged 25.3 ha.

3. Territories averaged 7.8 ha and comprised two wetlands during Prelaying.

4. There was sequential use of some territories by different pairs.

5. Regular use by wigeons occurred 65.4% of the time on persistent wetlands and only 34.6% on unpersistent wetlands. Irregular use occurred 13.5% of the time on unpersistent wetlands and 82.5% on unpersistent ponds.

6. Most wigeons showed a persistent pair bond. Males abandoned females, on average, by 25 June, 26.6 days after the onset of egg-laying. One male attended a female and a newly hatched brood.

7. Paired males used a home range averaging 19.9 ha, encompassing 4 wetlands during Incubation.
8. Time budgets of males and females were similar during Early Arrival but during Prelaying and Laying, females fed more and males spent more time alert. As a consequence, condition of females improved prior to egg-laying and that of males deteriorated over spring.
9. When females were at the nest, paired males vocalized (Slow Whistle) persistently and social interactions with conspecifics increased. During Incubation, male alert behavior declined when the female was at the nest.
10. Body reserves of females declined to a low of 206.7 kcal above starvation by the time broods hatched. Males reached a low of 425.3 kcal during Incubation.
11. Wigeon copulatory behavior was described. Forced pair copulation attempts occurred commonly, particularly during Laying.
12. Nest initiation occurred on 11 May in 1976, and 26 May in 1977, with peak nesting in both years about 1 June. Late nests were initiated about mid-June both years. One renest began on 3 June 1977, three days after the original nest was abandoned.
13. Nests were located an average of 42.5 m from the nearest wetland. Most were located in dense shrubby cover (snowberry, rose and Wolf-willow) or hay crops (Alfalfa, sweet clover).
14. Average clutch size was 8.6 eggs with adult females averaging 1.4 more eggs per clutch than juveniles in early nests.
15. Paired males used Group Flights to defend their territories. Males defended their females aggressively during these interactions and

contact in the air was common. Characteristics of GFATD were described.

16. Forced copulation attempts occurred commonly in wigeon.
17. The strategy of unpaired males was to attempt to break existing pair bonds. This was achieved once. Unpaired males ranged over an area averaging 61.8 ha encompassing 6 wetlands.
18. Wigeon were dominated only by Mallard and Canvasback among the waterbirds observed. Wigeon dominated other species more frequently that would be expected in relation to their body size.
19. Wigeon territorial behavior was similar to that of Gadwall and blue-winged ducks.
20. The evolution of territoriality, monogamy and breeding strategies of male and female wigeons was discussed in terms of net reproductive cost-benefits.

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Appendix 1. Common and scientific names of biota.[1,2]

Plants

Non Vascular

Filamentous algae	*Cladophora* spp.
Sea Lettuce	*Ulva fenestrata*
Moss	*Drepanocladus* spp.

Vascular

Pondweed	*Potamogeton pectinatus*
	P. gramineus
Horned Pondweed	*Zanichellia palustris*
Arrowhead	*Sagittaria* spp.
Grass	Graminea
White Top Grass	*Scolochloa festucacea*
Slough Grass	*Beckmannia* spp.
Sedge	*Carex* spp.
	C. atherodes
Spike-rush	*Eleocharis palustris*
	E. acicularis
Bulrush	*Scirpus acutus*
Lesser Duckweed	*Lemna minor*
Ivy-leaved Duckweed	*L. trisulca*
Rush	*Juncus* spp.
Dock	*Rumex maritimus*
Lamb's-quarters	*Chenopodium album*
Canada Anemone	*Anemone canadensis*

Appendix 1. cont'd

Water Buttercup	*Ranunculus subrigidus*
Gooseberry	*Ribes* spp.
Low Prairie Rose	*Rosa arkansana*
Wolf-willow	*Elaeagnus commutata*
Fireweed	*Epilobium angustifolium*
Water milfoil	*Myriophyllum exalbescens*
Water Celery	*Oenanthe sarmentosa*
Heart-leaved Alexanders	*Zizia aptera*
Snowberry	*Symphoricarpos albus*
Sow-thistle	*Sonchus arvensis*
Dandelion	*Taraxacum officinale*
Wooly Yarrow	*Achillea lanulosa*
Goldenrod	*Solidago* spp.
Wheat	*Triticum aestivum*
Oats	*Avena sativa*
Barley	*Hordeum vulgare*
Corn	*Zea mays*
Potato	*Solanum tuberosum*
Brussels Sprouts	*Brassica oleracea*
Lettuce	*Lactuca sativa*
Alfalfa	*Medicago sativa*
Clover	*Trifolium* spp.
Yellow Sweet Clover	*Melilotus officinalis*

Appendix 1. cont'd

Animals

Invertebrates

Hydra	Cnidaria
Round worm	Nematoda
Segmented worm	Annelida
Leech	Hirudinea
Snail	Lymnaeidae, Physidae
Mite	Araneae
Crustacean	Crustacea
Scud	Amphipoda
Seed shrimp	Ostracoda
Water flea	Daphinidae
Fish louse	Diaptomidae
Dragonfly	Odonata
Common skipper	Libellulidae
Narrow-winged damselfly	Coenagrionidae
Bug	Hemiptera
Water boatmen	Corixidae
Beetle	Coleoptera
Crawling water beetle	Haliplidae
Predaceous diving beetle	Dytiscidae
Water scavenger beetle	Hydrophilidae
Caddisfly	Trichoptera
Northern caddisfly	Limnephilidae

Appendix 1. cont'd

Fly	Diptera
Biting midge	Ceratopogonidae
Midge	Chironomidae

Vertebrates

Birds

Horned Grebe	*Podiceps auritus*
Pied-billed Grebe	*Podilymbus podiceps*
Black-crowned Night-heron	*Nycticorax nycticorax*
Canada Goose	*Branta canadensis parvipes*
Lesser Snow Goose	*Chen caerulescens*
Ross' Goose	*C. rossii*
White-fronted Goose	*Anser albifrons*
Shelduck	*Tadorna tadorna*
Mallard	*Anas platyrhynchos*
American Black Duck	*A. rubripes*
Gadwall	*A. strepera*
Northern Pintail	*A. acuta*
Green-winged Teal	*A. crecca*
Blue-winged Teal	*A. discors*
Cinnamon Teal	*A. cyanoptera*
Northern Shoveler	*A. clypeata*
American Wigeon	*A. americana*
Chiloe Wigeon	*A. sibilatrix*
Eurasian Wigeon	*A. penelope*

Appendix 1. cont'd

Falcated Duck	*A. falcata*
African Black Duck	*A. sparsa*
Chilean Teal	*A. flavirostris*
Wood Duck	*Aix sponsa*
Redhead	*Aythya americana*
Canvasback	*A. valisineria*
Lesser Scaup	*A. affinis*
Greater Scaup	*A. marila*
Common Goldeneye	*Bucephala clangula*
Bufflehead	*B. albeola*
Common Eider	*Somateria mollissima*
Swainson's Hawk	*Buteo swainsoni*
Bald Eagle	*Haliaeetus leucocephalus*
Northern Harrier	*Circus cyaneus*
Grouse	*Phasianidae*
Spruce Grouse	*Dendragapus canadensis*
White-tailed Ptarmigan	*Lagopus leucurus*
California Quail	*Callipepla californica*
Wild Turkey	*Meleagris gallopavo*
Common Moorhen	*Gallinula chloropus*
American Coot	*Fulica americana*
Ring-billed Gull	*Larus delawarensis*
Franklin's Gull	*L. pipixcan*
Great Horned Owl	*Bubo virginianus*
Black-billed Magpie	*Pica pica*
American Crow	*Corvus brachyrhynchos*

Appendix 1. cont'd

Great Tit	Parus major
Red-winged Blackbird	Agelaius phoeniceus
Mammals	
Coyote	Canis latrans
Red Fox	Vulpes vulpes
Muskrat	Ondatra zibethicus
Striped Skunk	Mephitis mephitis
Richardson's Ground Squirrel	Spermophilus richardsonii
Mink	Mustela vison
Weasel	M. spp.
Horse	Equus caballus
Cat	Felis catus
Dog	Canis familiaris

[1]Species are in phylogenetic order by kingdom with domesticated species at the end of each.

[2]Scientific nomenclature follows: Budd and Best (1969), Prescott (1969) and Hotchkiss (1972) for vascular plants; C. Tennent (pers. commun.) and Prescott (1969) for non vascular plants; Pennak (1953), Ward and Whipple (1959), Borror and DeLong (1964), Barnes (1974), Edmunds et al. (1976) and Wiggins (1977) for invertebrates; Johnsgard (1978) and A.O.U. (1982) for birds; and Banfield (1974) for mammals.

Appendix 2i. Weight of grit <0.25 mm in diameter over the annual cycle in gizzards of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	0.33	0.22 - 0.49	NS	14	0.24	0.13 - 0.46
EA	19	0.23	0.15 - 0.37	NS	10	0.19	0.10 - 0.35
PR	4	0.10	0.02 - 0.60	NS	4	0.28	0.07 - 0.86
LA	12	0.20	0.12 - 0.33	NS	16	0.20	0.12 - 0.32
IN	2	0.41		NS	6	0.48	0.19 - 0.86
BR	1	0.34		NS	13	0.36	0.21 - 0.63
PO					8	0.15	0.06 - 0.36
M1	4	0.15	0.05 - 0.50	NS	3	0.11	0.02 - 0.68
M2	11	0.06	0.03 - 0.14	NS	1	0.02	
M3	5	0.23	0.05 - 1.09	NS	1	0.25	
FM	2	0.04		*	3	0.63	0.08 - 5.00

[1]See Fig. 1 for definition of symbols.

[2]Dry weight in grams.

[3]NS=$P>0.05$, *=$P<0.05$, analysis of variance.

Appendix 2ii. Weight of grit 0.25-0.50 mm in diameter over the annual cycle in gizzards of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[1]	95% C.I.
WI	27	1.82	1.44 - 2.28	NS	14	1.45	1.02 - 2.06
EA	19	1.08	0.82 - 1.42	NS	10	1.19	0.83 - 1.72
PR	4	0.69	0.51 - 0.93	NS	4	0.70	0.08 - 6.29
LA	12	0.88	0.55 - 1.42	NS	16	0.73	0.53 - 1.01
IN	2	1.17		NS	6	1.23	0.99 - 1.54
BR	1	1.48		NS	13	0.92	0.65 - 1.30
PO					8	1.21	0.85 - 1.72
M1	4	1.77	1.11 - 2.82	NS	3	1.24	0.35 - 4.41
M2	11	1.29	0.93 - 1.79	NS	1	0.57	
M3	5	1.53	1.05 - 2.23	NS	1	1.84	
FM	2	1.49		*	3	2.15	1.17 - 3.97

[1]See Fig. 1 for definition of symbols.

[2]Dry weight in grams.

[3]NS=$P>0.05$, *=$P<0.05$, analysis of variance.

Appendix 2iii. Weight of grit 0.50-1.00 mm in diameter over the annual cycle in gizzards of male and female wigeons, 1976-8.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[1]	95% C.I.
WI	27	2.43	2.04 - 2.88	NS	14	1.95	1.46 - 2.60
EA	19	1.54	1.12 - 2.10	NS	10	1.54	1.07 - 2.21
PR	4	1.65	1.33 - 2.05	NS	4	2.02	1.12 - 3.67
LA	12	1.38	1.13 - 1.69	NS	16	1.22	0.97 - 1.53
IN	2	1.28		NS	6	1.05	0.38 - 2.92
BR	1	2.75		NS	13	1.04	0.62 - 1.74
PO					8	1.54	0.99 - 2.39
M1	4	2.33	1.80 - 3.03	NS	3	2.34	1.31 - 4.17
M2	11	2.89	2.44 - 3.42	NS	1	1.54	
M3	5	2.06	1.62 - 2.61	NS	1	2.15	
FM	2	3.06		NS	3	1.46	0.62 - 3.48

[1]See Fig. 1 for definition of symbols.

[2]Dry weight in grams.

[3]NS=$P>0.05$, analysis of variance.

Appendix 2iv. Weight of grit 1.00-2.00 mm in diameter over the annual cycle in gizzards of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\overline{X}$[2]	95% C.I.	Sig.[3]	N	$\overline{X}$[2]	95% C.I.
WI	27	0.44	0.33 - 0.59	NS	14	0.27	0.14 - 0.48
EA	19	0.35	0.21 - 0.56	NS	10	0.26	0.14 - 0.50
PR	4	0.25	0.06 - 1.05	NS	4	0.20	0.04 - 1.13
LA	12	0.22	0.13 - 0.38	NS	16	0.23	0.15 - 0.35
IN	2	0.28		NS	6	0.20	0.06 - 0.65
BR	1	0.24		NS	13	0.13	0.06 - 0.30
PO					8	0.22	0.13 - 0.38
M1	4	0.38	0.18 - 0.77	NS	3	0.26	0.07 - 0.98
M2	11	0.30	0.19 - 0.46	NS	1	0.46	
M3	5	0.49	0.16 - 1.47	NS	1	0.47	
FM	2	0.23		NS	3	0.14	0.01 - 6.07

[1]See Fig. 1 for definition of symbols.

[2]Dry weight in grams.

[3]NS=$P<0.05$, analysis of variance.

Appendix 2v. Weight of grit 2.00-3.00 mm in diameter over the annual cycle in gizzards of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	0.23	0.11 - 0.48	*	14	0.72	0.35 - 1.46
EA	19	0.20	0.11 - 0.37	NS	10	0.08	0.03 - 0.25
PR	4	0.79	0.37 - 1.67	NS	4	0.68	0.21 - 2.28
LA	12	0.45	0.20 - 1.01	NS	16	0.44	0.19 - 1.02
IN	2			NS	6		
BR	1			NS	13	0.47	0.20 - 1.13
PO					8	0.41	0.10 - 1.76
M1	4			NS	3	0.27	0.01 - 74.2
M2	11	0.82	0.13 - 1.18	NS	1		
M3	5	0.40	0.08 - 2.03	NS	1		
FM	2			NS	3	0.31	0.01 - 47.47

[1]See Fig. 1 for definition of symbols.

[2]Dry weight in grams.

[3]NS=$P>0.05$, *=$P<0.05$, analysis of variance.

Appendix 2vi. Weight of grit 3.00-4.00 mm in diameter over the annual cycle in gizzards of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	0.71	0.48 - 1.05	NS	14		
EA	19	0.40	0.23 - 0.72	*	10	0.12	0.05 - 0.28
PR	4	0.69	0.22 - 2.23	NS	4		
LA	12	0.55	0.26 - 1.14	NS	16	0.54	0.29 - 1.01
IN	2			NS	6	0.42	0.10 - 1.72
BR	1			NS	13	0.61	0.29 - 1.27
PO					8	0.49	0.17 - 1.47
M1	4	0.45	0.03 - 5.79	NS	3		
M2	11	0.76	0.42 - 1.40	NS	1	0.03	
M3	5			NS	1		
FM	2			NS	3		

[1]See Fig. 1 for definition of symbols.

[2]Dry weight in grams.

[3]NS=$\underline{P}>0.05$, *=$\underline{P}<0.05$, analysis of variance.

Appendix 2vii. Weight of grit 4.00-5.00 mm in diameter over the annual cycle in gizzards of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\overline{X}$[2]	95% C.I.	Sig.[3]	N	$\overline{X}$[2]	95% C.I.
WI	27			NS	14		
EA	19			NS	10		
PR	4			NS	4		
LA	12			NS	16		
IN	2			NS	6		
BR	1			NS	13		
PO					8	0.69	0.28 - 1.67
M1	4			NS	3		
M2	11			NS	1		
M3	5			NS	1		
FM	2			NS	3		

[1]See Fig. 1 for definition of symbols.

[2]Dry weight in grams.

[3]NS=$P>0.05$, analysis of variance.

Appendix 2viii. Weight of grit >5.00 mm in diameter over the annual cycle in gizzards of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27			NS	14		
EA	19	0.96	0.87 - 1.05	NS	10		
PR	4			NS	4		
LA	12	0.92	0.76 - 1.11	NS	16		
IN	2			NS	6		
BR	1			NS	13		
PO					8		
M1	4			NS	3		
M2	11			NS	1		
M3	5			NS	1		
FM	2			NS	3		

[1]See Fig. 1 for definition of symbols.

[2]Dry weight in grams.

[3]NS=$\underline{P}$>0.05, analysis of variance.

Appendix 2ix. Weight of total grit over the annual cycle in gizzards of male and female wigeons, 1976-78.

	Male				Female			
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.	
WI	27	5.41	4.64 - 6.31	NS	14	4.43	3.78 -	5.19
EA	19	3.87	3.43 - 4.37	NS	10	3.54	2.66 -	4.70
PR	4	2.92	2.24 - 3.80	NS	4	3.58	2.51 -	5.11
LA	12	3.06	2.48 - 3.77	NS	16	2.67	2.28 -	3.13
IN	2	4.59		NS	6	3.53	2.77 -	4.51
BR	1	4.80		NS	13	2.84	2.24 -	3.61
PO					8	3.47	2.90 -	4.14
M1	4	4.75	4.55 - 4.96	NS	3	4.06	2.57 -	6.40
M2	11	4.78	4.02 - 5.68	NS	1	2.60		
M3	5	4.61	3.39 - 6.26	NS	1	4.70		
FM	2	5.04		NS	3	4.52	1.84 -	11.13

[1]See Fig. 1 for definition of symbols.

[2]Dry weight in grams.

[3]NS=$P>0.05$, analysis of variance.

Appendix 2x. Length of small intestine over the annual cycle of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	159.4	149.7 - 169.8	NS	14	149.9	140.8 - 159.7
EA	19	152.2	145.1 - 159.6	NS	10	149.7	137.2 - 163.3
PR	4	126.7	107.4 - 149.5	NS	4	145.5	125.1 - 169.3
LA	12	141.3	129.8 - 153.8	NS	16	137.1	130.0 - 146.3
IN	2	155.9		NS	6	148.7	131.5 - 168.0
BR	1	149.0		NS	13	142.4	135.0 - 150.1
PO					8	143.9	134.7 - 153.9
M1	4	166.6	137.1 - 202.4	NS	3	145.4	119.2 - 176.5
M2	11	149.3	141.4 - 157.7	NS	1	150.0	
M3	5	158.1	145.0 - 172.4	NS	1	160.0	
FM	2	157.0		NS	3	150.7	113.3 - 200.4

[1]See Fig. 1 for definition of symbols.

[2]Length in cm.

[3]NS=$P>0.05$, analysis of variance.

Appendix 2xi. Weight of large intestine over the annual cycle of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	2.5	2.3 - 2.7	*	14	2.4	2.1 - 2.8
EA	19	2.5	2.2 - 2.8	NS	10	2.3	1.9 - 2.8
PR	4	1.8	1.3 - 2.5	**	4	2.4	1.7 - 3.6
LA	12	2.0	1.6 - 2.4	NS	16	2.6	2.0 - 3.2
IN	2	2.4		NS	6	2.9	2.2 - 3.9
BR	1	2.0		NS	13	2.8	2.3 - 3.3
PO					8	2.4	1.7 - 3.4
M1	4	3.5	2.5 - 4.7	NS	3	3.5	2.5 - 5.0
M2	11	3.4	2.9 - 4.0	NS	1	3.5	
M3	5	3.6	2.8 - 4.7	NS	1	3.0	
FM	2	3.2		NS	3	3.0	1.0 - 8.6

[1]See Fig. 1 for definition of symbols.

[2]Wet weight in grams.

[3]NS=$P>0.05$, *=$P<0.05$, **=$P<0.01$, analysis of variance.

Appendix 2xii. Length of large intestine over the annual cycle of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	9.7	9.0 - 10.5	NS	14	8.8	8.0 - 9.6
EA	19	9.7	9.4 - 10.1	NS	10	8.9	8.0 - 9.9
PR	4	8.1	6.2 - 10.4	*	4	8.7	7.8 - 9.8
LA	12	8.5	7.3 - 10.0	NS	16	9.6	8.6 - 10.8
IN	2	9.8		NS	6	9.9	8.5 - 11.6
BR	1	10.5		*	13	9.1	8.3 - 10.0
PO					8	9.1	7.6 - 10.9
M1	4	10.1	8.3 - 12.2	NS	3	10.0	7.1 - 14.1
M2	11	9.9	9.0 - 11.0	NS	1	8.0	
M3	5	10.0	9.1 - 10.9	NS	1	11.0	
FM	2	10.2		NS	3	9.4	6.1 - 14.5

[1]See Fig. 1 for definition of symbols.

[2]Length in cm.

[3]NS=$P>0.05$, *=$P<0.05$, analysis of variance.

Appendix 2xiii. Weight of combined ceca over the annual cycle of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	2.7	2.5 - 2.9	NS	14	2.5	2.3 - 2.7
EA	19	1.9	1.7 - 2.2	NS	10	1.8	1.7 - 2.0
PR	4	1.3	1.2 - 1.6	NS	4	1.5	0.9 - 2.5
LA	12	1.5	1.3 - 1.7	*	16	1.8	1.6 - 2.1
IN	2	1.8		*	6	1.8	1.5 - 2.1
BR	1	1.3		NS	13	1.8	1.6 - 2.1
PO					8	2.0	1.6 - 2.5
M1	4	2.2	1.6 - 3.2	NS	3	2.3	1.6 - 3.4
M2	11	2.5	2.2 - 2.9	NS	1	2.9	
M3	5	2.7	2.0 - 3.7	NS	1	2.2	
FM	2	2.6		NS	3	3.2	1.8 - 6.0

[1]See Fig. 1 for definition of symbols.

[2]Wet weight in grams.

[3]NS=$\underline{P}>0.05$, *=$\underline{P}<0.05$, analysis of variance.

Appendix 2xiv. Length of combined ceca over the annual cycle of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	45.2	43.1 - 47.4	NS	14	42.8	40.5 - 45.1
EA	19	39.6	36.4 - 43.1	*	10	33.6	31.6 - 35.7
PR	4	27.4	23.3 - 32.1	*	4	32.4	25.0 - 42.1
LA	12	34.9	30.9 - 39.3	NS	16	35.6	33.1 - 38.3
IN	2	43.5		NS	6	35.9	31.7 - 40.6
BR	1	37.9		NS	13	38.1	35.6 - 40.7
PO					8	37.0	34.7 - 39.4
M1	4	42.6	12.6 - 50.2	NS	3	38.4	32.5 - 45.3
M2	11	41.0	36.2 - 43.5	NS	1	39.0	
M3	5	48.2	38.6 - 55.0	NS	1	38.0	
FM	2	40.2		NS	3	37.7	34.5 - 41.3

[1]See Fig. 1 for definition of symbols.

[2]Length in cm.

[3]NS=$\underline{P}>0.05$, *=$\underline{P}<0.05$, analysis of variance.

Appendix 2xv. Weight of gizzard over the annual cycle of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	10.9	10.4 - 11.4	NS	14	9.6	8.7 - 10.7
EA	19	8.8	8.3 - 9.3	NS	10	7.8	7.0 - 6.9
PR	4	6.2	4.6 - 8.2	**	4	7.1	5.7 - 9.0
LA	12	5.7	5.0 - 6.5	NS	16	5.2	4.7 - 5.7
IN	2	8.8		NS	6	7.3	5.9 - 9.0
BR	1	9.0		NS	13	6.4	5.6 - 7.4
PO					8	7.5	6.7 - 8.5
M1	4	10.8	10.0 - 11.7	NS	3	9.2	5.4 - 15.5
M2	11	12.2	11.0 - 13.5	NS	1	9.2	
M3	5	12.8	10.4 - 15.6	NS	1	13.7	
FM	2	12.5		NS	3	11.9	10.4 - 13.6

[1]See Fig. 1 for definition of symbols.

[2]Dry weight in grams.

[3]NS=$P>0.05$, **=$P<0.01$, analysis of variance.

Appendix 2xvi. Weight of kidney over the annual cycle of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	3.6	3.3 - 3.8	NS	14	3.0	2.8 - 3.3
EA	19	3.0	2.8 - 3.3	NS	10	2.8	2.5 - 3.2
PR	4	2.2	1.8 - 2.6	*	4	2.7	2.3 - 3.1
LA	12	2.6	2.3 - 3.0	NS	16	2.9	2.7 - 3.1
IN	2	2.7		NS	6	2.9	2.5 - 3.4
BR	1	2.4		NS	13	2.4	2.1 - 2.7
PO					8	2.8	2.5 - 3.2
M1	4	3.3	2.1 - 5.1	NS	3	3.3	1.8 - 5.9
M2	11	4.0	3.7 - 4.3	NS	1	4.3	
M3	5	3.4	2.9 - 4.0	NS	1	3.1	
FM	2	3.1		NS	3	3.6	2.5 - 5.1

[1]See Fig. 1 for definition of symbols.

[2]Wet weight in grams.

[3]NS=$P>0.05$, *=$P<0.05$, analysis of variance.

Appendix 2xvii. Weight of liver over the annual cycle of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	18.4	17.2 - 19.6	NS	14	15.8	14.6 - 17.0
EA	19	24.7	20.9 - 29.1	NS	10	23.9	18.9 - 30.3
PR	4	12.0	8.7 - 16.5	NS	4	16.2	11.7 - 22.4
LA	12	12.7	11.0 - 14.6	**	16	18.3	16.5 - 20.2
IN	2	15.1		NS	6	16.3	13.9 - 19.1
BR	1	1.60		NS	13	12.8	11.4 - 14.4
PO					8	16.6	14.4 - 19.1
M1	4	21.4	16.8 - 27.3	NS	3	18.6	14.7 - 23.5
M2	11	22.8	20.6 - 25.3	NS	1	24.8	
M3	5	20.2	16.2 - 25.1	NS	1	23.1	
FM	2	29.8		NS	3	18.3	10.8 - 30.8

[1]See Fig. 1 for definition of symbols.

[2]Wet weight in grams.

[3]NS=$P>0.05$, **=$P<0.01$, analysis of variance.

Appendix 2xviii. Weight of pancreas over the annual cycle of male and female wigeons, 1976-78.

	Male				Female		
Stage[1]	N	$\bar{X}$[2]	95% C.I.	Sig.[3]	N	$\bar{X}$[2]	95% C.I.
WI	27	3.8	3.4 - 4.2	NS	14	3.2	2.9 - 3.5
EA	19	2.8	2.5 - 3.2	NS	10	2.3	1.9 - 2.8
PR	4	1.2	0.4 - 3.3	NS	4	2.1	1.4 - 3.1
LA	12	1.9	1.4 - 2.4	NS	16	2.2	1.9 - 2.5
IN	2	1.7		NS	6	1.8	1.2 - 2.7
BR	1	1.6		NS	13	2.0	1.6 - 2.4
PO					8	2.3	1.8 - 2.9
M1	4	3.7	2.9 - 4.8	NS	3	3.7	2.7 - 5.1
M2	11	4.4	3.6 - 5.2	NS	1	4.6	
M3	5	4.3	3.4 - 5.4	NS	1	5.8	
FM	2	3.0		NS	3	3.9	

[1]See Fig. 1 for definition of symbols.

[2]Wet weight in grams.

[3]NS=$P>0.05$, analysis of variance.

Appendix 3i. Number of some waterbird species observed on the Moose Jaw study area, spring, 1976.

Date	Social status[1]	Species[2]							
		MALL	NOPI	NOSH	BWTE	GADW	AMWI	GRTE	CANV
1 May	P	27	5	1	8	21	32		1
	M	51	15	3	5		7		
	F	3		1	1				
8	P	40	2	7	19	16	22	1	
	M	40	20		10	4	5		
	F	3	3						
15	P	23	8	3	33	23	14	2	1
	M	44	9	1	11	3	7		
	F								
22	P	13			40	26	15	1	
	M	77	17	8	26	4	17		
	F	2	1	6		1			2
29	P	13	2	2	26	13	11	1	1
	M	87	13	7	61	15	17	2	
	F	3	2		2	4			
5 June	P	12	3	5	14	15	6	1	1
	M	87	11	15	68	17	29	2	
	F	1		1	1		1		2

Appendix 3i. cont'd

Date	Social status[1]	Species[2] MALL	NOPI	NOSH	BWTE	GADW	AMWI	GRTE	CANV
13 June	P	17		2	6	2	5		
	M	59	6	5	56	22	16		
	F	6	2				1		1
19	P	9		3	11	4	4		
	M	42	1	5	44	24	20		
	F	3	4	1	1	1	1		1
26	P	3		1		10	5		
	M	24		1	24	13	10		
	F	5	1	1		1	3		1
1 July	P	1			6	13	1		
	M	13		1	7	7	1	1	
	F	6	1			2	6		1

[1]P=pairs, M=males without females, F=females without males.

[2]MALL=Mallard, NOPI=Northern Pintail, HOSH=Northern Shoveler, BWTE=Blue-winged Teal, GADW=Gadwall, AMWI=American Wigeon, GRTE=Green-winged Teal, CANV=Canvasback.

Appendix 3ii. Number of remaining waterbird species observed on the Moose Jaw study area, spring, 1976.

Date	Social status[1]	Species[2]								
		LESC	RIDU	REDH	RUDU	BUFF	COME	AMCO	PIGR	HOGR
1 May	P	45	1	1						3
	M	18								
	F									
8	P	41		5						6
	M	24						30	1	
	F	2								
15	P	25		5						3
	M	8						45	2	1
	F									
22	P	33		4						3
	M	9		1				34	2	3
	F	1								
29	P	31		4	5					
	M	18		1	1			38	1	3
	F									
5 June	P	46		10	6					
	M	29		3	2			35	1	4
	F	1			1					

Appendix 3ii. cont'd

Date	Social status[1]	Species[2]								
		LESC	RIDU	REDH	RUDU	BUFF	COME	AMCO	PIGR	HOGR
13 June	P	23		3						
	M	42		5	7			29		5
	F	3			1					
19	P	20		1	2					
	M	50			4			27		2
	F				1					
26	P	16		3	2					1
	M	59		1	5			16		
	F			3						
1 July	P	5		3						
	M	40			9					
	F			1						

[1]P=pairs, M=males without females, F=females without males. For AMCO, PIGR and HOGR single birds could not be sexed and were classified as males (data are missing for these 3 species on 1 July).

[2]LESC=Lesser Scaup, RIDU=Ring-necked Duck, REDH=Redhead, RUDU=Ruddy Duck, BUFF=Bufflehead, COME=Common Merganser, AMCO=American Coot, PIGR=Pied-billed Grebe, HOGR=Horned Grebe.

Appendix 4i. Number of some waterbirds species observed on the Moose Jaw study area, spring, 1977.

Date	Social status[1]	Species[2]							
		MALL	NOPI	NOSH	BWTE	GADW	AMWI	GRTE	CANV
14 Apr	P	119	36	2		7	32	13	
	M	28	10				4	21	
	F	3							
21	P	103	18	6	2	26	38	25	2
	M	19	3			4	5	17	
	F	3	1						
28	P	64	8	9	12	21	22	8	1
	M	34	1		7	3	3	5	
	F	1							
7 May	P	48	6	6	32	26	29	1	2
	M	51	16	7	8	3	5	3	
	F	2	2		1				
13	P	35	2	7	39	17	26		
	M	55	3	5	13	4	8		
	F	1	1						
21	P	42	5	2	31	24	22		4
	M	41	2	5	25	3	6		
	F		1						

Appendix 4i. cont'd

Date	Social status[1]	Species[2] MALL	NOPI	NOSH	BWTE	GADW	AMWI	GRTE	CANV
27 May	P	8	2	4	36	25	19		
	M	56	10	6	36	8	2		
	F	4				1			2
2 June	P	22	2	2	23	25	13		
	M	63	3	3	51	13	6		2
	F	8		1			1		
9	P	17			18	15	9		
	M	44	2	1	58	21	11		
	F	2	2	4					1
16	P	12		1	21	11	7		
	M	56		6	52	25	10	1	
	F	6			1				1
23	P	6			23	9	3	1	
	M	18		4	41	20	3	2	
	F	8	4		1	2	1		
30	P	1			13	4			
	M	10			36	13			
	F	11	4		5	5			1

Appendix 4i. cont'd

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[1]P=pairs, M=males without females, F=females without males.

[2]MALL=mallard, NOPI=Northern Pintail, NOSH=Northern Shoveler, BWTE=Blue-winged Teal, GADW=Gadwall, AMWI=American Wigeon, GRTE=Green-winged Teal, CANV=Canvasback.

Appendix 4ii. Number of remaining waterbird species observed on the Moose Jaw study area, spring, 1977.

Date	Social status[1]	Species[2]								
		LESC	RIDU	REDH	RUDU	BUFF	COME	AMCO	PIGR	HOGR
14 Apr	P	15	2	2			1			
	M	14	4	1		1		1		
	F									
21	P	27								
	M	20						3		
	F									
28	P	35	1	4						
	M	17		1				22	4	
	F									
7 May	P	62	1	4						2
	M	17						37	2	1
	F									
13	P	39		1						2
	M	14						6	1	2
	F									
21	P	71		2						3
	M	24						13	1	13
	F									

Appendix 4ii. cont'd

Date	Social status[1]	Species[2]								
		LESC	RIDU	REDH	RUDU	BUFF	COME	AMCO	PIGR	HOGR
27 May	P	59								
	M	33								
	F									
2 June	P	47	1	2	1					
	M	24								
	F									
9	P	53		1	1					
	M	26	1		2					
	F				2					
16	P	34		7	2					
	M	37		1						
	F			2	2					
23	P	41	1	1	1					
	M	28								
	F									
30	P	56								
	M	40								
	F	3								

Appendix 4ii. cont'd

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[1]P=pairs, M=males without females, F=females without males. For AMCO, PIGR and HOGR single birds could not be sexed and were classified as males (data are missing for these 3 species between 27 May and 30 June). A single American Black Duck was observed on 27 May.

[2]LESC=Lesser Scaup, RIDU=Ring-necked Duck, REDH=Redhead, RUDU=Ruddy Duck, BUFF=Bufflehead, COME=Common Merganser, AMCO=American Coot, PIGR=Pied-billed Grebe, HOGR=Horned Grebe.