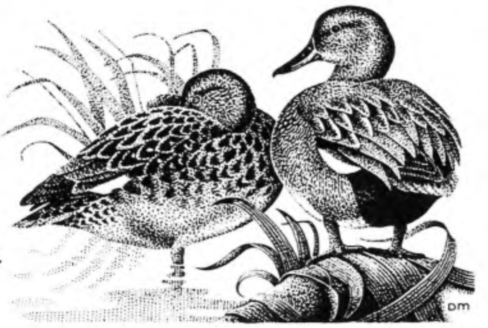
Weights of wild Mallard *Anas platyrhynchos*, Gadwall *A. strepera*, and Blue-winged Teal *A. discors* during the breeding season



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During 1976-81 we weighed several thousands of wild Mallard, Gadwall, and Blue-winged Teal in central North Dakota to examine duckling growth patterns, adult weights, and the factors influencing them. One-day-old Mallard and Gadwall averaged 32.4 and 30.4 g, respectively, a reduction of 34% and 29% from fresh egg weights. In all three species, the logistic growth curve provided a good fit for duckling growth patterns. Except for the asymptote, there was no difference in growth curves between males and females of a species. Mallard and Gadwall ducklings were heavier in years when wetland area was extensive or had increased from the previous year. Weights of after-second-year females were greater than yearlings for Mallard but not for Gadwall or Blue-winged Teal. Adult Mallard females lost weight continuously from late March to early July. Gadwall and Blue-winged Teal females, which nest later than Mallard, gained weight after spring arrival, lost weight from the onset of nesting until early July, and then regained some weight. Females of all species captured on nests were lighter than those captured off nests at the same time. Male Mallard weights decreased from spring arrival until late May. Male Gadwall and Blue-winged Teal weights increased after spring arrival, then declined until early June. Males of all three species then gained weight until the end of June. Among adults, female Gadwall and male Mallard and Blue-winged Teal were heavier in years when wetland area had increased from the previous year; female Blue-winged Teal were heavier in years with more wetland area.

Body weight is an important attribute of wild waterfowl, reflecting growth and development of young and general physical condition of adults. Waterfowl are most vulnerable before fledging; duckling mortality often ranges between 40 and 60% (Sargeant & Raveling in press). Increased weight tends to reduce the risk of mortality in several ways; heavier ducklings are less susceptible to some predators (Lack 1968), generally have greater body reserves to withstand food deprivation (Haramis *et al.* 1986), and can better tolerate weather extremes (Koskimies & Lahti 1964). Thus increased body weight may account for the lower mortality observed in older ducklings. Despite the evident importance of the topic, studies of growth in wild ducklings have been limited, probably because of the difficulty in capturing precocial young (Ricklefs 1973).

Body weight and physical condition influence the breeding biology of adult ducks. Heavier females tend to lay larger clutches (Krapu 1981, Cowardin *et al.* 1985) and renest more readily after losing a clutch (Cowardin *et al.* 1985, Swanson et al. 1986). Furthermore, higher body weights have been associated with greater survival probabilities (Haramis *et al.* 1986, Pollock *et al.* 1989).

The objectives of this paper are as follows:

1) To describe the patterns of growth in weight of wild Mallard *Anas platyrhynchos*, Gadwall *Anas strepera*, and Blue-winged Teal *Anas discors* ducklings.
2) To examine patterns of weight change of adult ducks during the breeding season.
3) To relate duckling growth and adult weight to environmental conditions.

Unlike many previous studies of weights of ducklings and adult ducks, this one relied on wild, not captive, birds.

Methods

During 1976-81 we weighed several thousand Mallard, Gadwall, and Blue-winged Teal eggs, young, and adults. The work was conducted in central North Dakota in conjunction with a

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study of homing and reproductive strategies of these three species (Lokemoen *et al.* 1990). The study area encompassed 22.6 km^2 of moderately rolling landscape. About 10% of the surface area was wetland, and the uplands were about equally divided between native grassland and cropland.

Two measures of environmental conditions were made. Wetland area was measured as the total hectares flooded in May plus the total hectares flooded in July of the same year. The total hectares flooded in May and July better represent the average wetland conditions for a year than a single annual survey. Wetland change was the difference between wetland area of a year and wetland area of the previous year. We used the variable wetland change to indicate the hectarage of wetland that had dried or been flooded since the previous year. Wetland area in hectares and wetland change for the six years were as follows:

	Wetland area	Wetland change
1976	88	Unknown
1977	30	-58
1978	164	134
1979	199	35
1980	109	-90
1981	102	-7

Duck weights were obtained from arrival of the birds in late March or early April until late August or early September. Egg weights were measured at nests during laying and at the pipping stage. Weights of young were recorded at nests and on wetlands when young were captured with drive-traps (Cooch 1953), by night-lighting (Cummings & Hewitt 1964), or with decoy-hen traps (Sharp & Lokemoen 1987). Most adults were captured with rocket nets (Dill & Thornsberry 1950) or decoy-hen traps. Hens on nests were captured with long-handled dip nets or nest traps adapted from Salyer (1962). Weights were taken with Pesola spring scales, whose accuracy was regularly checked with known weights. Weights less than 100 g were recorded to the nearest gram and measurements over 100 g were made to the nearest 5 g.

The exact age, in days, of many young was known because the birds had been marked at hatching with web-tags (Alliston 1975). The age of unmarked young was estimated by feather-age classes described by Gollop & Marshall (1954). These birds were assigned an age equal to the midpoint of the appropriate feather-age class.

The age of many adult females was known because they had been marked as young or adults in a previous year. For unmarked females we distinguished those in their second year (SY) from those after their second year (ASY) using age classification systems developed by Krapu *et al.* (1979) for Mallard, by Blohm (1977) for Gadwall, and by Dane (1968) for Blue-winged Teal. We could not distinguish ages of adult males of any species.

Weights of flightless ducklings were fitted to growth curves by using nonlinear regression (procedure NLIN of SAS (SAS Institute, Inc. 1987)). Ages were estimated from feather-age classes. To determine the asymptotes of the curves, weights of some adults were used in the model-fitting, and an age of 320 days was ascribed to them. We used only early-breeding-season adult weights: before 15 April for Mallard and before 5 May for Gadwall and Blue-winged Teal. Resulting curves gave a general pattern of duckling growth. We examined departures from the pattern by computing residuals from the model (observed weights minus predicted values) by species and sex, and used these in an analysis of variance to seek effects due to wetland area, wetland change, and year.

For Gadwall, we had enough data to compare actual weights and predicted weights of known-age ducklings. Predicted values were taken from the growth curve model based on ages estimated from feather-age classes. We also calculated expected weights for young flying Mallard (average age 56 days) and Gadwall (50 days). To determine if the attainment of flight had any effect on weight gain, we compared actual weights of flying young with those predicted from the growth curve.

Weights of adults were grouped by 10-day intervals beginning with 27 March-5 April. Each 10-day interval was coded by its midpoint. Intervals with <10 measurements were grouped with adjacent ones and the weighted average date was used for the coded date.

We used the General Linear Models Procedure (SAS Institute, Inc. 1987) to test for relationships between adult weights and several explanatory variables. These variables included age (for females only), a variable indicating whether or not the bird had been captured on a nest (females only), 10-day interval, year, wetland area, and wetland change. Models were developed by successively eliminating non-significant ($P>0.05$) variables. Averages of adult weights were expressed as estimated population marginal means, which accounted for the unbalanced sample sizes (SAS Institute, Inc. 1987:600).

Results

Weights of eggs and hatchlings

Table 1. Average weights (in g), sample sizes (n), and standard deviations (S.D.) of Mallard eggs and ducklings, by sex and age.

		Females			Males		
Class[a]	Age	Mean	n	S.D.	Mean	n	S.D.
Fresh egg[b]		49.3	27	3.5			
Pipped egg[b]	0	45.5	302	3.9			
Ia[b]	3.5	32.4	36	2.4			
Ib	9.5	115.3	6	37.3	92.2	4	11.5
Ic	15.5	265.0	2	91.9	215.0	3	5.0
IIa	22.0	288.9	14	60.5	343.2	11	75.3
IIb	30.5	401.2	20	92.2	460.3	30	93.4
IIc	40.5	575.0	22	152.9	648.4	19	128.4
III	50.5	774.3	38	124.9	863.9	31	102.1
Flying	56.0	740.0	5	114.9	817.1	7	91.4

[a] Age classes as defined by Gollop & Marshall (1954).
[b] Not separated by sex.

Freshly laid Mallard eggs from three clutches averaged 49.3 g (Table 1). After one week of incubation, eggs averaged 46.3 g (n = 18), with weights declining another 0.8 g at pipping. One-day-old young (42% of which were dry and 58% of which were damp) weighed an average of 32.4 g. That weight loss of mainly shell, membrane, and moisture represented an average decline of 34% from newly laid eggs and 29% from pipped eggs.

Table 2. Average weights (in g), sample sizes (n), and standard deviations (S.D.) of Gadwall eggs and ducklings, by sex and age.

		Females			Males		
Class[a]	Age	Mean	n	S.D.	Mean	n	S.D.
Fresh egg[b]		43.1	20	1.7			
Pipped egg[b]	0	39.0	439	3.5			
Ia[b]	3.5	30.4	75	2.3			
Ib	10.5	99.3	40	24.2	93.7	27	13.0
Ic	16.5	186.6	40	45.5	188.0	63	48.1
IIa	23.0	287.6	94	50.8	294.0	89	49.9
IIb	33.0	380.7	91	74.9	406.6	131	83.0
IIc	41.5	484.5	55	60.5	556.1	55	81.5
III	47.5	573.0	33	60.0	616.9	50	69.8
Flying	50.0	552.9	7	44.2	606.4	14	41.4

[a] Age classes as defined by Gollop & Marshall (1954).
[b] Not separated by sex.

Gadwall egg weights declined 10% from freshly laid eggs to pipping (Table 2). After hatching, young in the nest (25% dry, 75% damp) weighed an average of 30.4 g, indicating losses of 29% from fresh eggs and 22% from pipped eggs. We did not obtain fresh egg weights for Blue-winged Teal, but there was a 33% decline in weight between pipped eggs and one-day-old young (all dry) in the nest (Table 3).

Table 3. Average weights (in g), sample sizes (n), and standard deviations (S.D.) of Blue-winged Teal eggs and ducklings, by sex and age.

		Females			Males		
Class[a]	Age	Mean	n	S.D.	Mean	n	S.D.
Pipped egg[b]	0	27.2	22	5.2			
Ia[b]	3.0	18.1	21	3.2			
IIa	17.5	162.0	5	40.2	166.2	8	40.0
IIb	26.0	203.5	13	22.1	206.7	9	25.5
IIc	33.5	261.3	41	30.5	269.0	56	37.2
III	38.5	281.9	93	29.4	301.3	97	34.4

[a] Age classes as defined by Gollop & Marshall (1954).
[b] Not separated by sex.

Growth of ducklings

Although male ducklings weighed more than female ducklings beginning with the Class II stage (Tables 1-3) variability was considerable and sex differences were not significant (P>0.05).

We fit three growth curves to the data for flightless young of each species and sex: logistic, Gompertz, and Richards (e.g. Ricklefs 1973, Richards 1959). We found that the logistic curve provided a better fit than the Gompertz curve, and was as good as the Richards curve, which requires estimation of an additional parameter for shape. We accordingly used the logistic model:

$$W(t) = \frac{A}{1 + be^{-rt}},$$

Where $W(t)$ is the weight at age t, A is the asymptote, r is the growth rate, and b reflects the weight at hatch (t = 0) relative to the asymptotic weight.

Initially we fitted the logistic model for each species and sex. We found that, within a species, the sexes had similar parameter estimates, except for the asymptote. We then fitted a single model for each species, with asymptote depending on sex. Estimates of the parameters obtained are presented in Table 4, and fitted curves are shown in Figure 1.

For Mallard and Gadwall ducklings, residuals from the logistic model varied by year (P<0.0001), but effects due to sex and the sex-year interaction were not significant (P>0.10). For Blue-winged Teal, the main effect due to sex was not significant, but the year effect and

Table 4. Estimates of parameters of the logistic equation fitted to weights of Mallard, Gadwall, and Blue-winged Teal flightless ducklings. *A* is the asymptote, *r* is the growth rate, and *b* reflects the weight at hatch (t = 0) relative to the asymptotic weight. Standard errors are in parentheses.

Parameter	Mallard	Gadwall	Blue-winged Teal
A (females)	1076 (10.0)	785 (6.7)	365 (3.2)
A (males)	1210 (7.2)	840 (5.7)	384 (2.7)
r	0.0692 (0.0030)	0.0700 (0.0014)	0.0750 (0.0045)
b	13.45 (1.58)	10.40 (0.47)	5.14 (0.78)

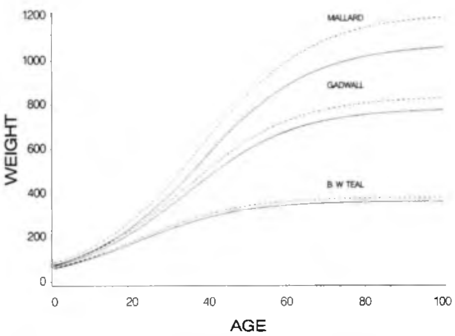

Figure 1. Logistic curves fitted to weights of flightless Mallard, Gadwall, and Blue-winged Teal ducklings and projected to age 100 days, by sex. Weights are in grams and age is in days. Solid lines represent females and dashed lines represent males.

sex-year interaction were significant (P<0.005). Some, but not all, of the annual variation could be attributed to variation in wetland area or wetland change. Mallard and Gadwall tended to be heavier than expected in years when wetland area was extensive (P = 0.048, P = 0.0007, respectively) and when wetland area increased from the previous year (P = 0.003, P = 0.025). No such trend was evident for female Blue-winged Teal, and for male Blue-winged Teal only wetland change was significant (P = 0.001). Blue-winged Teal ducklings, however, were weighed in only three years.

The variation in weight of individuals within the same feather-age class was high (Tables 1-3). The coefficients of variation (standard deviation/mean) often exceeded 20% for Class II Mallard and 15% for Class II Gadwall and Blue-winged Teal. Potential sources of variation include measurement error in weighing, inaccuracy of ageing the birds from plumage, variation of ages within feather-age class, and true variation in weight among individuals of the same age.

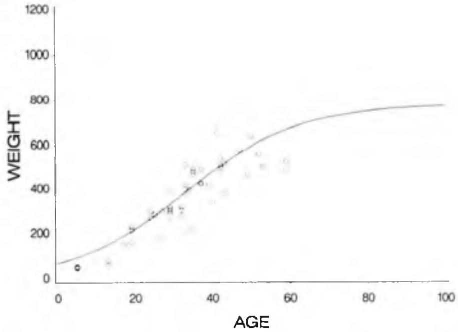

Figure 2. Weights of known-age female Gadwall ducklings plotted against fitted logistic growth curve. Weights are in grams and age is in days.

Some insight into the importance of this last source of variation was obtained by examining weights of 62 female and 50 male Gadwall ducklings of known age (numbers of the other species were too small to analyze). Ducklings of the same age and sex varied greatly in weight as shown by the display of female weight variation in Figure 2. High weight variability even occurred within broods. For broods recaptured 19 to 41 days after hatching, the average difference among female broodmates was 24 g (range 0-140 g), and among male broodmates was 46 g (range 0-95 g). The difference between broodmates regardless of sex averaged 57 g, and ranged from 0 to 180 g. Weights of known-age Gadwall ducklings led to another unexpected finding. Actual weights were significantly lower than values predicted from the logistic curve based on ages estimated from feather-age classes (P = 0.003 for females, P = 0.053 for males, Fig. 2).

Flying young

Flying Mallard and Gadwall young of both sexes weighed less than the younger Class III young and less than the logistic model predicted. The differences between actual values (Tables 1 and 2) and the predicted values (Mallard female = 841.2 g and male = 945.4 g; Gadwall female = 597.7 g and male = 639.5 g) were consistent, but the overall test not significant (P = 0.12), probably because of small samples.

Adults

ASY Mallard females weighed significantly (P<0.001) more ($\bar{x}$ = 1020 g, n = 173) than SY females ($\bar{x}$ = 973 g, n = 177). Average weights of females (ASY and SY were combined because patterns were similar for both ages) changed significantly through the breeding season (P<0.001, Fig. 3). From a peak of 1104 g during the 30 March period, females declined steadily to 895 g during the 17 July period. During those 109 days, Mallard females lost an average of 209 g (19% of their initial weight), or 1.9 g per day. Weights of females captured on nests (n = 109) averaged 64 g lower (P<0.001) than those of females captured during the same times but not on nests (n = 241). There was no relationship between female weights and wetland change or wetland area (P>0.05), but there was significant annual variation in weights (P<0.001, Fig. 4). Females were lightest in the drought year of 1977 ($\bar{x}$ = 951 g) and heaviest in 1976 ($\bar{x}$ = 1061 g) and 1978 ($\bar{x}$ = 1046 g).

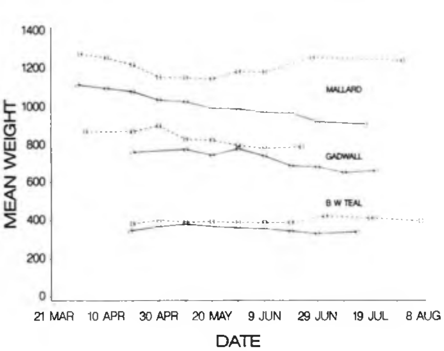

Figure 3. Average weights (estimated population marginal means) of adult ducks by 10-day period of the breeding season, for three species. Circles denote females and squares denote males.

Male Mallard weighed an average 1206 g (n = 660) and outweighed females during each period of the breeding season (Fig. 3). Male weights declined significantly (P<0.001) during the early portion of the breeding season until the 20 May period. From the peak weight of 1277 g during 31 March period males lost an average of 132 g in 50 days (10%), or 2.6 g per day. After 20 May males generally gained weight through the end of June. Male weights showed significant (P<0.004) annual variation (Fig. 4), much of which could be explained by the fluctuation in wetland condition between years. Male weights tended to be greater in years when wetland area increased from the previous year (P<0.001). Male weights increased an average of 0.14 g for each added hectare of flooded wetland.

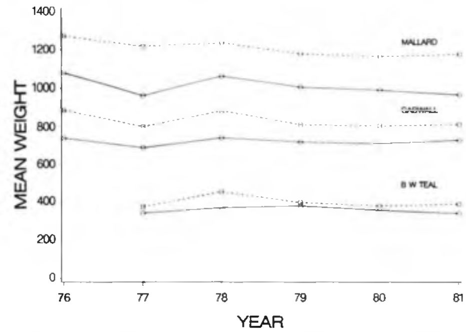

Figure 4. Average weights (estimated population marginal means) of adult ducks by year, for three species. Circles denote females and squares denote males.

Weights of female Gadwall did not differ significantly by age (P>0.05); the overall average was 722 g (n = 346). However, average weights of females did change significantly through the breeding season (P<0.001). Their average weights increased from 747 to 781 g from April through the end of May, after which they declined to 651 g in the 9 July period (Fig. 3). From their peak weight near the end of May to the low on 9 July, average weights declined 130 g (17% of the average peak weight), or 3.3 g per day. Gadwall females captured on nests were significantly lighter (58 g less) than those captured at the same time but not on nests (P<0.001). The annual weight variation of Gadwall females was largely associated with the change in wetland area from the preceding year (P = 0.004). For each hectare increase in wetland area, female weights increased an average of 0.15 g.

Male Gadwall averaged 835 g (n = 344), outweighing females by 16%. Average weights of males changed significantly (P<0.001) through the breeding season (Fig. 3). From earliest captures through the 20 April period male weights averaged 873 g. Average weights increased to 904 g during the 30 April period and then declined to 783 g by the 9 June period, an average loss of 121 g (13%) or 3.0 g per day. Weights of male Gadwall varied significantly from year to year (P<0.001), with higher weights in 1976 and 1978 than in other years (Fig. 4). The annual weight fluctuation was not accounted for by variation in wetland area or wetland change.

Weights of female Blue-winged Teal did not differ significantly by age (P = 0.13); ASY and SY females had an overall average of 348 g (n

= 255). Like Mallard and Gadwall, Blue-winged Teal females showed significant weight variation through the breeding season (P<0.001, Fig. 3). Average female weights increased from 339 g during the 19 April period to 374 g in the 10 May period and then declined to 323 g in the 29 June period. Females thus lost an average of 51 g (14%), or 1.0 g per day between early May and late June. Female teal began gaining weight again during the 10-day interval in mid-July, after the nesting season. Females captured on nests weighed an average of 34 g less than those captured elsewhere at the same time (P<0.001). Female weights were positively related to wetland area (P = 0.001); for each added hectare of wetland in a year hen weights averaged 0.20 g greater.

Male Blue-winged Teal weighed an average of 397 g (n = 313), or 14% more than the average female. Although male weights varied significantly through the breeding season (P = 0.006), changes were small and rather erratic (Fig. 3). Average weights increased from the 20 April period to the 30 April period, and generally declined until late June. From a peak average weight of 403 g during the 30 April period, male weights declined for the next 50 days but losses averaged only 13.8 g or 3%. Male weights were significantly related to wetland change (P = 0.021), but there was an additional effect due to year (P = 0.004, Fig. 4). Each additional wetland hectare was associated with an average weight increase of 0.16 g.

Discussion

Weights of eggs and hatchlings

The average of unincubated Mallard eggs we weighed (49.3 g) was similar to the 46 g modal weight reported for eggs of wild birds (46.0) in Russia (Dement'ev & Gladkov 1967) and the 50.0-51.3 g range reported for eggs from captive birds in Manitoba (Batt & Prince 1978). The 34% weight decline we noted between fresh eggs and day-old young was similar to the 37-40% loss noted by Prince *et al.* (1970). The 13.1 g loss between pipped eggs and day-old young closely compared with the 12 g loss recorded by Kear (1965). In her study she noted that this weight was regained after about 48 hours.

The average weight we calculated for fresh Gadwall eggs (43.1 g) was similar to the average of 42.1 g observed by Dement'ev & Gladkov (1967) for eggs from wild Gadwall. The 29% weight decline we documented between fresh Gadwall eggs and one-day-old young was more than the 22 to 24% noted by Dement'ev & Gladkov (1967) for the same period.

In our study, one-day-old Blue-winged Teal weighed 33% less than pipped eggs. This weight decline was the largest of the three species, probably because all Blue-winged Teal nestlings were dry when weighed, whereas some Mallard and Gadwall were wet. The average weight of Blue-winged Teal nestlings we recorded (18 g) was the same as the average calculated by Southwick (1953) for one-day-old young.

Growth of ducklings

Weights of ducklings we captured varied greatly within feather-age class. At least part of this variation was due to true variation in weight among individuals of the same age. Dzubin (1959) alluded to wide variation in weight among Mallard and Canvasback *Aythya valisineria* within a feather-age class. Also, Southwick (1953) noted considerable variation in weights and plumages of hand-reared Blue-winged Teal of the same age.

Mallard and Gadwall in our study weighed about the same as hand-reared birds observed by Prince *et al.* (1970) and Oring (1968), respectively, up to about two weeks of age. After two weeks of age the females in our study weighed less than captive females studied by Prince *et al.* (1970) and Oring (1968). In contrast, body weights of young wild Mallard captured in Russia (Dement'ev & Gladkov 1967) were similar to ours. It appears that captive birds gain weight faster and have less variability in development compared with wild birds. These differences probably reflect greater energy expenditures of birds in the wild. Owen (1969) calculated that wild birds needed to expend 13% more energy during maturation than captive birds.

Mallard and Gadwall young gained weight faster in years with good wetland conditions, presumably because of the superior feeding habitat in those years. Favourable wetland habitat can aid duckling growth and survival in two primary ways. First, it provides increased invertebrate food for nesting hens, which in turn may lay larger eggs (Eldridge & Krapu 1988). Larger eggs yield larger young (Pehrsson 1982), which may be better able to survive harsh environmental conditions (Koskimies & Lahti 1964). Second, a larger invertebrate food base will enhance duckling weights directly. Little published information exists on the direct effects of food supplies on duckling weight changes, but Street (1977) found decreased duckling survival on infertile ponds and Oring (1968) noted that well-fed ducklings attained flight sooner.

Flying young

The mean weights of flying young Mallard and Gadwall for both sexes weighed less than the younger Class III ducklings and less than values predicted from the growth curves. Although samples were small and the overall test only approached significance, we suspect that there is an actual weight loss associated with the onset of flight. The period when young birds are making trial flights and finishing primary feather growth may be the time of highest energy demand. Although weight loss at fledging is not easily documented in either wild or pen-reared waterfowl, other authors have noted weight losses during this period. Veselovsky (1953) recorded weight declines of Mallard ducklings when flight feathers began growing and when young began to fly. Sugden *et al.* (1981) found weight declines in Lesser Scaup *Aythya affinis* and Mallard reared in captivity and Weller (1959) noted a weight loss in captive Redhead *A. americana* at the time of first flight.

Variation in adult weights by sex and age

Breeding-season weights of males were greater than females for all three species, the differences ranging from 14% of the female average weight in Blue-winged Teal to 21% in Mallard. This well-known sexual dimorphism (e.g. Kear 1970, Johnsgard 1975) is accentuated during the egg-laying and incubation phases of the breeding season, when females encounter heavy demands on their energy reserves.

We found weight differences between SY and ASY females only for Mallard. Batt & Prince (1978) and Krapu & Doty (1979) also found age-related weight differences in female Mallard. For female Gadwall, we suspect that weight differences existed but were undetected because the ageing method we used incorrectly classified an unknown portion of ASY females as SY females (Lokemoen *et al.* 1990).

Seasonal change in adult weights

Weights of all three species changed through the breeding season. The onset of weight changes varied by species in accordance with the phenology of breeding. For Mallard, which begin nesting shortly after arrival, the weight loss began immediately in April. For Blue-winged Teal, which are mid-season nesters, the decline began in late May. For Gadwall, which are late nesters, the loss was not apparent until June. Typically 10% of the nests were initiated in our study area by 26 April for Mallard, 8 May for Blue-winged Teal, and 20 May for Gadwall. The weight loss of female Mallard began some two weeks before the 10% nest initiation date whereas female Gadwall and Blue-winged Teal weight loss began two to three weeks after the 10% nest initiation date. Similarly, Krapu (1981, Fig. 1) did not find weight gains by female Mallard in spring but he recorded stable weights followed by weight loss during nesting. Mallard females may lose weight earlier in the breeding cycle than other species because they have less time between arrival and nesting to acquire nutrients and fewer nutrients are available.

From spring peaks to post-nesting lows, Mallard females in our study averaged a 19% drop in weight, Gadwall a 17% drop, and Blue-winged Teal 14%. These declines compare to weight losses during incubation of 18% for Mallard, 16% for Gadwall, and 12% for Blue-winged Teal found by Gatti (1983). The consistency between his figures and ours for each species suggests that percent weight loss is less in smaller-bodied ducks. The energy demands of nesting were emphasized by the weight differences between females on and off nests: 6% for Mallard, 8% for Gadwall, and 9% for Blue-winged Teal.

Males showed significant weight changes during the breeding season but followed a pattern somewhat different from females. Losses began one 10-day period earlier than females, except for the Mallard, in which the change in both sexes was apparent from the beginning. The declines also ended earlier for males than for females. Male Mallard began gaining weight by the end of May and male Blue-winged Teal by early July. We did not detect an increase by male Gadwall, perhaps because we captured too few of them after mid-June.

Earlier weight declines for males are not surprising as males spend more time than females from spring arrival to incubation defending a space for mating, feeding, and possibly nesting (McKinney 1965, Siegfried 1974). At this time males spend more time in movement and mate-guarding activities and less in feeding than do females (Dwyer 1975, Stewart & Titman 1980, Titman 1981). When females begin incubating, males become less active and begin to gain weight. Oring (1969) found that male Gadwall gained weight rapidly after deserting their mates. Females continue to lose weight until late summer because their breeding-season activities - including incubation, possibly renesting, and brood rearing - continue longer than males.

Annual variation in adult weights

Annual variation in weight was apparent in all species and sexes. In general, the highest average weights occurred in 1976 and 1978, lowest weights in 1977, and intermediate values in the other years. Sample sizes were sometimes small, however, and in 1976 no Blue-winged Teal were captured. Some of the annual variation could be attributed to wetland area in a particular year or to the change in wetland area from the previous year. Female Blue-winged Teal weights were heavier in years with greater wetland area. This result seems to fit well with the strategy of this species not to home but to seek good wetland habitat each spring (Lokemoen *et al.* 1990). We found higher weights for male Mallard and female Gadwall in years when the wetland area had increased from the previous year. We suspect that favourable wetland conditions help ducks gain weight because they can feed in the newly flooded feather-edge where food is highly available. We found heavier weights in years with good wetland conditions, despite the fact that energy-expensive breeding activities were probably greater in those years (Cowardin *et al.* 1985).

This study relied to a major extent on data collected by a host of summer technicians who are named elsewhere (Lokemoen et al. 1990). We appreciate the work and advice provided during this study by Harold F. Duebbert. We thank Pamela J. Pietz, who provided detailed editorial comments on the manuscript, and Jane E. Austin, who provided beneficial insights on earlier drafts. We also thank Michael D. Schwartz, who drafted the figures.

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