EFFECTS OF BODY WEIGHT AND AGE ON THE TIME OF PAIRING OF AMERICAN BLACK DUCKS

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ABSTRACT.—I used captive young and adult American Black Ducks (*Anas rubripes*) during October–February 1984–1985 to test whether body weight and age affected time of pair-bond formation. Eighty ducks were marked individually, and 10 ducks (6 males and 4 females, half of each age class) were assigned to each of 8 experimental pens. Ducks in 4 pens received an *ad libitum* diet of commercial duck food, and ducks in the other 4 pens received a restricted ration of the same food. During early winter ducks in both groups gained weight, but ducks on the restricted diet gained less than birds on the *ad libitum* diet; peak winter weight of ducks on the *ad libitum* diet averaged 22% greater than initial body weight compared with 6.5% for ducks on the restricted diet. In late winter ducks on the restricted diet lost 28.7% of peak winter weight, and ducks on the *ad libitum* diet lost 19.3%. Weight loss of ducks on the *ad libitum* diet began before weather conditions became severe and coincided with a reduction in food consumption. This result supports the idea that weight loss of waterfowl in late winter is controlled endogenously. Individuals on the *ad libitum* diet paired earlier than those on the restricted diet, and pair bonds were stronger. Adults of both sexes paired earlier than young ducks, but differences for females were not significant statistically. Age and energy constraints are factors that can affect intraspecific variation in pairing chronology. *Received 8 July 1985, accepted 22 December 1985.*

FORMATION of pair bonds by North American ducks (Anatidae) generally occurs before birds arrive at spring breeding areas (Palmer 1976, Bellrose 1978). Courtship behavior and pairing chronology in fall and winter have been reported for many species (e.g. Weller 1965, Smith 1968, Soutiere et al. 1972, Armbruster 1982, Hepp and Hair 1983, Paulus 1983). These data indicate that time of pairing can vary both within and among species. Dabbling ducks (*Anas* spp.), for example, generally initiate courtship and establish pair bonds earlier than diving ducks (*Aythya* spp.).

Many factors have been proposed to explain variation in time of pairing. Young individuals may pair later than adults (McKinney 1965), and age-related parameters such as time of alternate plumage development (Weller 1965, McKinney 1970) and intensity (Bossema and Kruijt 1982) or form (Dane and Van der Kloot 1964, Korschgen and Fredrickson 1976) of reproductive displays may affect time of pairing within species. Delays in courtship and pair-bond formation also may be related to energetic constraints, resulting in intraspecific differences in pairing chronology (Wishart 1983, Brodsky and Weatherhead 1985). Temporal variation in pairing among species may be caused by differences in time of nesting (Weller 1965, Armbruster 1982), foraging strategies (Paulus 1983), and male-male competition (Spurr and Milne 1976).

Compared with unpaired conspecifics, paired ducks are dominant (Paulus 1983, Hepp and Hair 1984) and thus occupy more favorable winter habitats in which thermoregulatory costs may be lower (Jorde et al. 1984). Further, paired females improve their foraging efficiency by having a male in attendance (Ashcroft 1976). Because these benefits may help in accumulating nutrient reserves, time of pairing may be related to subsequent reproductive success (Hepp 1984) and survival. If the benefits of pairing result in higher probabilities of reproducing or surviving, then it is not clear why some individuals and species delay pair-bond formation. Pairing involves costs and benefits that may vary intra- and interspecifically. For example, high dominance rank may be important only if resources, such as food, are defen-

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TABLE 1. Amount of food (g·bird^{-1}·day^{-1}) in the *ad libitum* and restricted diets and average daily temperature, 1984-1985. Values are means ± SE. Time periods are the intervals between consecutive dates on which American Black Ducks were weighed.

Time period	n[a]	*Ad libitum* diet	Restricted diet (% of *ad libitum* diet)	Daily temperature (°C)[b]
3-19 Oct	6	119.6 ± 12.0	116.4 ± 2.8 (97)	16.1 ± 0.5
20 Oct-1 Nov	11	111.5 ± 6.0	81.6 ± 3.1 (73)	18.6 ± 1.0
2-15 Nov	13	140.8 ± 6.3	110.8 ± 4.3 (79)	8.7 ± 0.9
16 Nov-5 Dec	18	132.5 ± 4.7	85.5 ± 7.3 (64)	4.6 ± 0.7
6-19 Dec	12	116.0 ± 9.6	40.4 ± 6.2 (35)	7.0 ± 1.4
20 Dec-14 Jan	25	97.6 ± 6.7	32.9 ± 1.4 (34)	4.2 ± 1.2
15-28 Jan	13	54.2 ± 6.0	71.8 ± 2.0 (132)	−4.1 ± 1.3
29 Jan-11 Feb	13	80.6 ± 6.4	63.5 ± 1.2 (79)	−1.1 ± 0.8
12-28 Feb	16	108.0 ± 7.7	54.7 ± 2.0 (51)	6.9 ± 1.4

[a] Number of days between weighings that were used in calculating mean *ad libitum* and restricted diets.
[b] Values are means of the average daily temperatures [(maximum + minimum)/2] from nearby Baltimore-Washington International Airport (39°11'N, 76°40'W) and include every day in the time period.

sible. Variation in the economics of pairing, therefore, may produce temporal differences in pair-bond formation. An interesting area of research concerns the factors that affect trade-offs between costs and benefits of pairing, and that may ultimately determine the pairing chronology of waterfowl.

In this study using young and adult American Black Ducks (*Anas rubripes*), I manipulated food availability, and therefore weight (i.e. nutrient reserves), during fall and winter to test the effects of age and body weight on time of pair-bond formation.

METHODS

The study was conducted from October 1984 through February 1985 at the Patuxent Wildlife Research Center (PWRC) in Laurel, Maryland. Adult (2 yr) and young (hatched in May 1984) American Black Ducks from a captive breeding colony at PWRC were used. All adults were known to have nested in 1984, and young ducks were hatched in an incubator from eggs collected from captive pairs.

The experimental design consisted of 8 pens (4 control : 4 treatment) that were built in a small man-made impoundment and that varied in size (mean 18.1 m long × 6.8 m wide × 2.0 m high; range 16.1-21.3 × 6.1-7.3 × 2.0 m). Each pen contained areas of open water and dry land. On 18-19 September, 80 ducks were marked individually with nasal saddles and assigned in groups of 10 (6 males and 4 females, half of each age class) to the 8 pens. When assigning ducks to experimental pens, former mates as well as former broodmates (adults and young) were separated, and young were not placed with either parent. Visual barriers were placed between pens. From 19 September to 3 October, ducks were allowed to adjust to the new pens and were given an *ad libitum* diet of commercial duck food (Beacon Duck Developer, Beacon Milling Company, Cayuga, NY). To avoid effects of prior experience on social behavior and development of pair bonds, young Black Ducks were exposed only to members of their brood from time of hatching until they were selected for use in the study. Ducklings from individual clutches were brooded separately for 6-8 weeks after hatching and then transferred to outdoor pens, where they again were isolated visually from other broods of ducklings.

Experimental and control individuals received the same commercial duck food (Beacon Duck Developer). After 3 October, the control group received an *ad libitum* diet, while the treatment group was given less than *ad libitum*. Food consumption of ducks in the control group was measured daily; the restricted diet was calculated based on the average daily food consumption of ducks in the *ad libitum* group. The objective of food restriction was to reduce the weight of ducks in the treatment group by 20-25% (approximately 200-300 g). Because some natural foods (roots and rhizomes of vegetation at the land-water interface) were available in the pens, the restricted diet sometimes was as low as 34% of *ad libitum* (Table 1) to attain the desired weight loss.

Ducks were weighed to the nearest 10 g between 0900 and 1300 twice a month using a Pesola spring scale. The day before weighing, all 8 pens received an equal amount of food to reduce variation in weights caused by differences in amounts of undigested foods.

Courtship behaviors were monitored daily, and pair status of each female was determined weekly. Pair bonds were defined as either weak or strong based on the following chronology of pairing events: (1) a male and female associated infrequently and exhibited no courtship displays, (2) association between the male and female was more frequent and some-

TABLE 2. Percentage of weight change ($\bar{x}$ ± SE) of experimental American Black Ducks, 1984-1985.[a]

	Ad libitum diet	Restricted diet	$F(1,6)$[b]	P
3 Oct-15 Nov	13.9 ± 1.3	5.4 ± 0.7	34.8	0.001
3 Oct to peak winter weight[c]	22.2 ± 1.4	6.5 ± 0.4	106.7	0.001
Peak winter weight to 28 Feb	−19.3 ± 1.2	−28.7 ± 0.2	53.3	0.001
3 Oct-28 Feb	−1.5 ± 0.8	−23.7 ± 0.5	552.3	0.001

[a] Values are the percentage weight change occurring in the time period {e.g. for 3 Oct-15 Nov, % change = [(weight on 15 Nov − weight on 3 Oct)/weight on 3 Oct] × 100}.

[b] A split-plot ANOVA tested differences in percentage weight change between *ad libitum* and restricted groups. Effects of pen, age, sex, and all possible combinations on weight change were tested, but no significant ($P > 0.05$) differences were found.

[c] Date of peak winter weight was 5 Dec for ducks on restricted diets and on 19 Dec for ducks on *ad libitum* diets.

times was accompanied by courtship displays, but no mutual displays (e.g. female inciting and male turning-back-of-head, mutual head pumping, and copulation), (3) the male and female displayed mutually and always were closely associated, and (4) the male defended his mate during feeding or courtship. Categories 1 and 2 were classified as weak and categories 3 and 4 as strong pair bonds.

Split-plot ANOVAs were used to test for differences in weight changes and in time of pairing. Time of pairing for both weak and strong pair bonds was measured in weeks from the start of the study, and these data were ranked before proceeding with the analysis (Conover and Iman 1981). Values are presented as $\bar{x}$ ± 1 SE.

RESULTS

Food restriction and weight changes.—The degree to which food was restricted varied throughout fall and winter (Table 1). Initially, differences in body weight between the restricted and *ad libitum* groups were not large because Black Ducks on the restricted diet supplemented their ration of commercial duck food with naturally occurring foods within pens. Early in the study (3 October to 15 November), however, ducks on the restricted diet gained a significantly ($P < 0.001$) smaller proportion of initial body weight than birds on the *ad libitum* diet (Table 2). In addition, peak winter weights of ducks on the *ad libitum* diet reflected a greater percentage of weight increase than peak weights of ducks on the restricted diet (Table 2). Food was restricted more during 16 November to 5 December (Table 1); mean weight of individuals on the restricted diet increased, but not as much as that of the control group (Fig. 1). Food restriction was greatest from 6 December to 14 January (Table 1), causing a sharp drop in mean weight of ducks in the restricted group. In January and February, birds on the restricted diet lost a significantly ($P < 0.001$) greater proportion of peak winter weight than ducks on the *ad libitum* diet (Table 2).

Black Ducks on the *ad libitum* diet also lost weight in late winter (Fig. 1). Peak weights of ducks on the *ad libitum* diet occurred on 19 December and declined thereafter. Weight loss of birds in the *ad libitum* group coincided with a decrease in food consumption (Table 1). Reductions of weight and food consumption were greatest during 15-28 January, which was also the coldest part of the winter (Table 1). To prevent excessive weight loss due to lowered food consumption by birds in the *ad libitum* group, individuals in the restricted group were given 132% of the *ad libitum* diet during 15-28 January. Mean weights of restricted birds at this time were lower than those of the control group, and additional food restriction may have caused some mortality. At the end of the study (28 February), ducks on the restricted diet had lost almost 25% of initial body weight, while the weight of individuals in the control group remained approximately the same (Table 2).

Pairing chronology.—Black Ducks initiated courtship activity in October, and birds on the *ad libitum* diet paired earlier than those on the restricted diet. At the end of October, 75% of control females were paired (all strong bonds), compared with 50% of females on the restricted diet (4 were strong bonds) (Fig. 2). Ducks in the *ad libitum* group continued pairing during November, and by the end of December, 94% of females in this group were paired. In January and February, weak pair bonds of females on the *ad libitum* diet strengthened, but the percentage of paired females remained the same

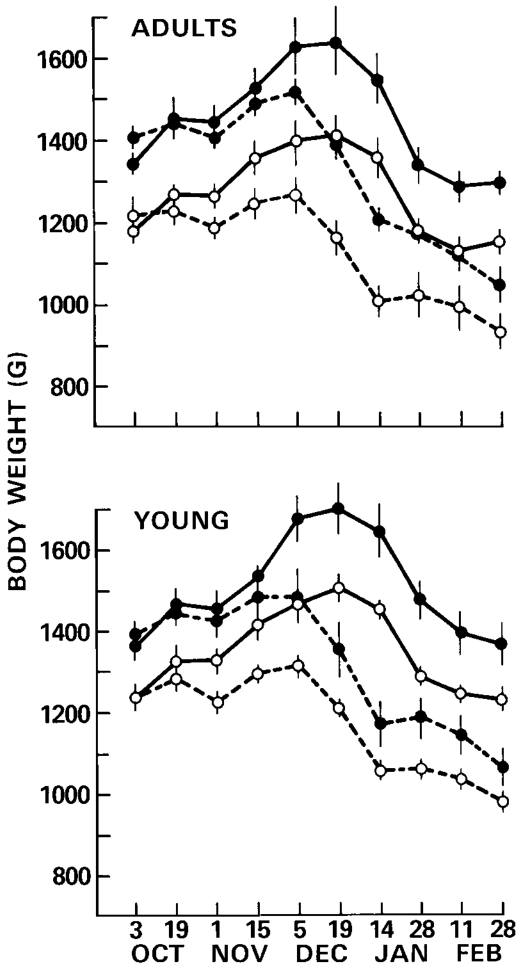

Fig. 1. Mean body weights of adult and young American Black Ducks. Vertical lines on each side of means represent standard errors. Closed circles = males, open circles = females, solid lines = *ad libitum* diet, and dashed lines = restricted diet.

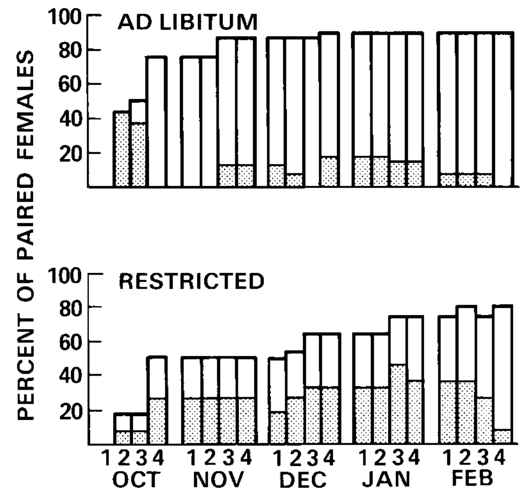

Fig. 2. Percentage of paired females by treatment group. Shaded bars = weak pair bonds and open bars = strong pair bonds.

(Fig. 2). For birds on the restricted diet, no pairs formed in November, but pairing continued during December–February (Fig. 2). The time required to form pair bonds was less for the *ad libitum* group than for ducks on the restricted diet (weak bond: 5.1 ± 0.9 vs. 10.7 ± 1.4 weeks, $P < 0.01$; strong bond: 6.7 ± 1.2 vs. 15.4 ± 1.5 weeks, $P < 0.05$) (Table 3).

Adult females formed both weak and strong pair bonds earlier than young females (Table 4), but differences were not significant (Table 3). Pairing chronology of males, however, was significantly ($P < 0.05$) related to their age (Table 3). Adult males formed both weak and strong pair bonds earlier than young males (Table 4). The interactions of male or female age with treatment were not significant ($P > 0.05$) (Table 3).

DISCUSSION

WEIGHT CHANGES

Body weight of Black Ducks given food *ad libitum* increased during autumn, peaked in mid-December, and decreased afterwards. These results are consistent with conditions generally observed in other species of ducks (Owen and Cook 1977, Peterson and Ellarson 1979, Whyte and Bolen 1984). The percentage of peak winter weight that was lost in late winter (19%) by ducks on the *ad libitum* diet also was similar to weight losses (15–20%) reported for Black Ducks wintering in Maine (Reinecke et al. 1982).

Because food was readily available, and because weight and food consumption started to decline before the coldest part of the winter, weight loss in late winter probably reflects a regulated loss of weight (see King and Murphy 1985, Mortensen and Blix 1985) similar to weight reductions in some bird species during incubation (Sherry et al. 1980). Cold weather or reduced food availability in winter, or both, may increase the rate of weight loss (see Dugan et al. 1981), but my data show that body weight

TABLE 3. Analysis of variance for effects of diet and age on time of pairing of American Black Ducks.[a,b]

Source	df	Time to weak bond (*F*)	Time to strong bond (*F*)
Treatment	1,6	14.01***	9.40**
Pen (treatment)	6,19	0.20 NS	0.60 NS
Female age	1,19	1.16 NS	0.72 NS
Male age	1,19	3.96*	4.73**
Treatment × female age	1,19	0.24 NS	0.15 NS
Treatment × male age	1,19	0.03 NS	0.02 NS
Female age × male age	1,19	0.10 NS	0.08 NS

[a] Analyses are on ranked data.

[b] * = $P < 0.10$, ** = $P < 0.05$, *** = $P < 0.01$, NS = not significant.

of Black Ducks will decline in late winter regardless of weather conditions or food availability. Dugan et al. (1981) also concluded that late-winter weight loss of Black-bellied Plovers (*Pluvialis squatarola*) was controlled internally and that weight changes during fall and winter reflected temporal variation in the benefits and costs of maintaining energy reserves. Perry (1985) showed that weight loss of several species of ducks in late winter was similar for individuals kept in either indoor or outdoor pens and fed an *ad libitum* diet, which also strongly suggests that weight losses of waterfowl in late winter are endogenously controlled.

Weight fluctuations of waterfowl during fall and winter result from changes in levels of nutrient reserves. Increases in body weight of female Black Ducks during fall, for example, are correlated strongly with increases of lipid and protein reserves (Reinecke et al. 1982). Changes in body weight of Mallards (*Anas platyrhynchos*) in fall and winter correspond to variation in amounts of lipid reserves (Whyte and Bolen 1984). Accumulation of energy reserves during fall and early winter is extremely important, and waterfowl may use reserves to supplement daily energy expenditures as energy demands increase in late winter (Raveling et al. 1972, Hickey and Titman 1983). Individuals with insufficient energy reserves may need to forage more actively to survive and, if food is unavailable, they may have a greater probability of dying from starvation because of shorter fasting endurances. Recent studies reported that ducks with small energy reserves in fall and early winter had lower survival probabilities (Pollock et al. in press, Hepp et al. 1986). Selection probably has favored the storage of large reserves by waterfowl before times when energy demands are likely to be high or food availability to be reduced.

PAIRING CHRONOLOGY

Timing of courtship and pair-bond formation of Black Ducks on the *ad libitum* diet was similar to that of wild Black Ducks, which generally initiate courtship in early autumn (Johnsgard 1960). In North Carolina courtship began in early October, and 97% of females were paired in November (Hepp and Hair 1983).

Age.—Adult Black Ducks paired earlier than young ducks, but differences were greater for males than females. This supports McKinney's (1965) suggestion that adults in the tribe Anatini pair earlier than yearlings. Blohm (1982), for example, showed that in spring yearling male Gadwalls (*Anas strepera*) were paired significantly less frequently than expected. Age-specific variation in reproductive displays (Dane and Van der Kloot 1964, Korschgen and Fredrickson 1976, Bossema and Kruijt 1982), plumage growth (McKinney 1970), or neuroendocrine development (Dittami 1981, Ottinger 1983) may be responsible for the early pairing of adult males. Most studies have concentrated on the effects of age on pairing chronology of males, but female age also may influence time of pairing. Because there were no differences in the percentages of weight change, delayed pairing of young Black Ducks was not caused by age-specific differences in nutritional status (see Wishart 1983). It is more likely that later pairing by young ducks was caused by differences in neuroendocrine development, experience, or dominance status.

Diet.—Black Ducks on the *ad libitum* diet paired significantly earlier than those on the restricted diet. Supplemental feeding has been shown to advance the time of breeding in many bird species (Källander 1974, Yom-Tov 1974, Ewald and Rohwer 1982, Davies and Lundberg 1985). Differences in pairing chronology of Black Ducks, however, were caused by delays in pairing of the restricted group and not by unusually early pairing times of ducks on the *ad libitum* diet.

TABLE 4. Time ($\bar{x}$ ± SE, in weeks) of weak and strong pair-bond formation by age and sex class for American Black Ducks given an *ad libitum* or restricted diet.[a]

	Ad libitum diet		Restricted diet	
	Adult	Young	Adult	Young
Male				
Time to weak bond	3.2 ± 0.5	10.0 ± 4.1	8.9 ± 1.7	14.2 ± 4.1
Time to strong bond	4.6 ± 0.8	12.1 ± 4.0	12.0 ± 3.0	20.5 ± 1.5
Female				
Time to weak bond	3.2 ± 0.4	6.9 ± 1.8	8.9 ± 2.5	12.5 ± 2.3
Time to strong bond	4.6 ± 0.8	8.7 ± 2.1	14.0 ± 2.0	16.7 ± 1.5

[a] Times (weeks from beginning of the study, 3 October) to pairing are means of means in each pen (n = 4).

High dominance rank associated with early pairing may help to acquire important energy reserves (Paulus 1983, Hepp and Hair 1984), but pairing activity entails costs that may reduce levels of endogenous reserves (Wishart 1983). A threshold level of nutrient reserves may have to be established before individuals participate in autumn and winter courtship activities (Murton and Westwood 1977: 152, Wishart 1983). It is generally acknowledged that maintenance requirements must be satisfied before time and energy are allocated to breeding activities (King 1974). The effects of nutrient reserves on reproductive activities, however, are documented better for breeding birds. Levels of certain energy reserves may influence both the "decision" to breed (Alisauskas and Ankney 1985) and the time of breeding (Jones and Ward 1976, Boersma and Ryder 1983). Common Eiders (*Somateria mollissima*), for example, may not breed in some years because of poor physical condition (Coulson 1984).

During the time of peak pairing activity in October and November, Black Ducks on the restricted diet gained proportionately less weight than did ducks on the *ad libitum* diet. They probably also spent more time feeding, because they supplemented their restricted ration with natural foods. Therefore, they had less time and energy available for courtship and maintenance of pair bonds, which may have caused delays in pairing. Brodsky and Weatherhead (1985) showed that variation in the onset of courtship and time spent in reproductive activity of Black Ducks wintering in Ontario was related to differences in habitat quality. Ducks spent more time courting and initiated courtship behavior earliest at sites where energy was abundant and the constraints on time and energy were the least. Reduced food availability and low energy reserves may prevent individuals from allocating time and energy to pair-bond formation.

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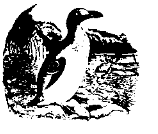
100 Years Ago in The Auk



From a review by David S. Jordan of the first edition (1886) of "The A.O.U. Check-List of North American Birds" (1886, Auk 3: 394):

"It is true, as the authors of the 'Code' have insisted, that 'nomenclature is a means and not an end in science.' But the experience of ornithologists have [sic] shown us that in systematic zoölogy and zoögeography, this means is one absolutely essential to any end of importance. A system of nomenclature based on common fairness and common sense, and stable, because above the reach of individual whim or choice, is as necessary to success in this kind of work as a sharp scalpel is to good work in anatomy.

"So long as no rules superior to the caprice of the individual or the tradition of some museum are recognized, so long is systematic work a mere burlesque, and our schemes of classification anything but a mirror of nature.

"But besides the positive advances made by the ornithologists, from which others may profit when the time comes, there is something for us to learn from the results of their less fortunate experiments.

"An illustration of this may be taken from the last Check-list of Dr. Coues. This work is in many respects most valuable. In it, however, so much learning and labor has been expended in the mending and remodelling of scientific names, as fairly to bring purism in that regard to *reductio ad absurdam.*

"Hence the Committee on the new code, with Dr. Coues at its head, now declares that 'a name is only a name, and has no necessary meaning,' and therefore no necessarily correct orthography. After this experience, the work of strengthening the lame and halting words is hardly likely to be continued in other fields of science.

"Another illustration may be drawn from the excessive multiplication of genera, a stage through which ornithology has naturally passed, and which other sciences, profiting from this experience, may possibly be able to avoid."