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ORIGINAL PAPER

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Intermittent fasting during winter and spring affects body composition and reproduction of a migratory duck

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Abstract We compared food intake, body mass and body composition of male and female black ducks (*Anas rubripes*) during winter (January–March). Birds were fed the same complete diet ad libitum on consecutive days each week without fasting (control; nine male; nine female) or with either short fasts (2 day.week^{-1}; nine male; nine female), or long fasts (4 day.week^{-1}; eleven male; twelve female). We continued treatments through spring (March–May) to measure the effect of intermittent fasts on body mass and egg production. Daily food intake of fasted birds was up to four times that of unfasted birds. Weekly food intake of males was similar among treatments (364 g.kg^{-1}.week^{-1}) but fasted females consumed more than unfasted females in January (363 g.kg^{-1}.week^{-1} vs. 225 g.kg^{-1}.week^{-1}). Although both sexes lost 10–14% body mass, fasted females lost less mass and lipid than unfasted females during winter. Total body nitrogen was conserved over winter in both sexes even though the heart and spleen lost mass while the reproductive tract and liver gained mass. Intermittent fasting increased liver, intestinal tissue and digesta mass of females but not of males. Fasting delayed egg production in spring but did not affect size, fertility or hatching of the clutch. Females on long fasts were still heavier than controls after laying eggs. Thus black ducks combine flexibility of food intake with plasticity of digestive tract, liver and adipose tissue when food supply is interrupted during winter. Females modulate body mass for survival and defer reproduction when food supply is interrupted in spring.

Keywords Eggs · Fasting · Fat · Intestine · Liver

Abbreviations *C* constancy · *M* contigency · *Ie* environmental information factor · *DM* dry matter · *OM* organic matter · *P* predictability

Introduction

Variation in environmental conditions and food supply select for phenotypic plasticity and may ultimately lead to genotypic change. An ability to contend with fluctuating resources may have facilitated the evolution of migration in birds (Rappole 1995; Chesser and Levey 1998). For example, both a genotypic response to season and a phenotypic response to recent temperatures and thermoregulatory demands (Bednekoff et al. 1994; Rogers et al. 1994) affect total body lipid of small birds. Fluctuating availability of food stimulates lipid deposition before migration in autumn (Totzke et al. 2000) and may predispose migrants to retain greater levels of body lipid during winter than non-migratory conspecifics in the same area (Winker et al. 1990).

Responses to resource variability are affected by trade-offs between survival factors during winter (non-breeding) and between survival and fecundity in the spring (breeding; Sibly and Calow 1986). For example, increased lipid mass may reduce the risk of starvation but impair mobility and increase risk of predation in winter (Bednekoff and Houston 1994), whereas egg production and incubation can deplete body tissues to critical limits (Ankney and MacInnes 1978) or impair subsequent reproduction in spring (Carey 1996). Reproductive investment may be constrained by proximate

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factors such as the availability of endogenous or exogenous nutrients for egg laying, incubation and brood rearing (Drent and Daan 1980; Ankney et al. 1991; Drobney 1991). However, investment in eggs may ultimately be limited by the time required for incubation, growth and survival of young in environments where food availability is highly seasonal (Arnold and Rohwer 1991; Sedinger et al. 1995).

The ability to predict the availability of resources through cues such as photoperiod or rain attenuates the risk to survival or reproduction (Wingfield et al. 1992). Colwell (1974) divided the probability of finding foods or resources in an environment (predictability; P) between variance in time (constancy; C) and dependence on time (contingency; M). For example, an equatorial staging ground where food is constantly available on arrival each year is just as predictable as an arctic breeding ground where food is only available after the summer solstice long after birds have nested. As contingency increases in relation to constancy, recent environmental cues and food availability become more important in modulating commitments of activity and tissues to seasonal reproduction (Hahn et al. 1997).

Foraging time of waterfowl may be limited by predation pressure (Ydenberg 1999), regular environmental changes such as photoperiod or tide, and irregular changes in temperature, visibility, wind speed and water level associated with storms (Lovvorn 1994). Many birds feed and fast intermittently during migration, at winter refuges and on spring breeding grounds. Intermittent feeding and fasting impose a repeated change from digestion, absorption and anabolism after feeding, to catabolism and digestive quiescence during each fast. Black ducks (*Anas rubripes*) can compensate for lost feeding time in autumn by increasing daily rates of food intake to 2.5 times the unfasted rate within 48 h (Barboza and Jorde 2001). Digestive function also resumes rapidly after the fast because high daily intakes of food reduce metabolizability of energy and protein only by 3% and 9%, respectively, in black ducks. Although some birds can increase rates of food intake to eight times maintenance levels at thermoneutrality (McWilliams and Karasov 1998; Kvist and Lindström 2000), metabolizable intakes may be insufficient when energy and nutrient demands are increased for growth (Lepczyk et al. 1998; Kitaysky 1999) or for mass gain, migration and thermoregulation (Hume and Biebach 1996; Barboza and Jorde 2001).

We measured responses of black ducks to intermittent food availability during winter when thermoregulatory costs may be high, and during spring when demands for female reproduction are greatest. We chose yearling birds because we believed that this age group would be most sensitive to fluctuations in feeding. Mortality rates are highest for black ducks during their first winter (Conroy et al. 1989; Blandon 1992), and winter survival may depend on lipid reserves established in autumn (Haramis et al. 1986) when young birds are growing and also preparing for migration. We increased the daily variance in food availability by reducing frequency of ad libitum feeding each week without changing food quality or overall abundance. This treatment maintains predictability of feeding (P) by reducing constancy (C) and increasing the contingency (M) of fed and fasted states on consecutive days during each week (Colwell 1974). We describe long-term responses to intermittent availability of food by measuring food intake, body composition and egg production. We minimized short-term behavioral responses to variance in the risk and rewards of foraging (Bateson and Kacelnik 1999) by preventing predation and maintaining food quality without limiting the quantity of food provided.

Materials and methods

Animals and experimental design

Black ducks were part of a captive colony founded with eggs collected from Nova Scotia and New Brunswick, Canada, and were thus minimally influenced by introgression with mallards (*Anas platyrhynchos*; Avise et al. 1990; Hanson and Ankney 1994). Birds were studied at Laurel, Md., USA, which is within both the wintering and breeding ranges for the species (Bellrose 1980). Experiments were performed from January 1997 through June 1997 on birds hatched in 1996. Birds were held outdoors in covered pens 4.5 m×9.0 m×2.3 m high with 4.0 m diameter flow-through ponds (Jorde et al. 1995). Sexes were segregated and housed in groups of four for 2 months before the experiment. We used three treatment regimes: daily feeding (control; 9 males in three pens, 9 females in three pens), fasting for 2 consecutive days each week (short-fasts; 9 males in three pens, 9 females in three pens) or fasting for 4 consecutive days each week (long-fasts; 11 males in four pens, 12 females in four pens). Birds were killed at two points in the experiment (3 males, 3 females per treatment, each from different pens) before treatments commenced in January (Julian day 8), and at the end of winter in March (Julian day 73) to compare the effects of winter and intermittent feeding on body composition (Fig. 1).

Breeding pairs were assigned in March (Julian day 74) within treatment groups on the basis of minimum relatedness. Each pair was housed in individual pens through laying, incubation and hatching. Nests were checked each day to record laying date, number of eggs and hatching. Eggs were candled at between 6 days and 10 days incubation to assess fertility. Similar measures of egg production were made on 29 experienced breeding pairs (> 1-year-old) in the same colony to compare the performance of yearlings with untreated birds. Clutches laid by yearling females were weighed after candling. Sixteen infertile eggs were collected from two clutches laid by yearlings at 6 days incubation on 2 separate days (day 105, day 113) and stored at –20 °C for chemical analysis. Eggs were lyophilized and ground through 1.25-mm mesh in a Wiley mill (Thomas Scientific, Philadelphia, Pa., USA) before analysis by the same methods used for body tissues (see below). The average composition of these eggs was used to estimate the commitment of nutrients to the clutch and to compare that to the total amount of lipid and N in the female at the end of March (Julian day 73). Although egg composition does change subtly within clutches and between females, this variation is small in comparison with the number of eggs laid (Carey 1996).

Food intake and body mass

Food was provided in covered pans floating on water, which prevented consumption of food by pestilent rodents or small birds. Uneaten food was replaced with fresh food provided at the same

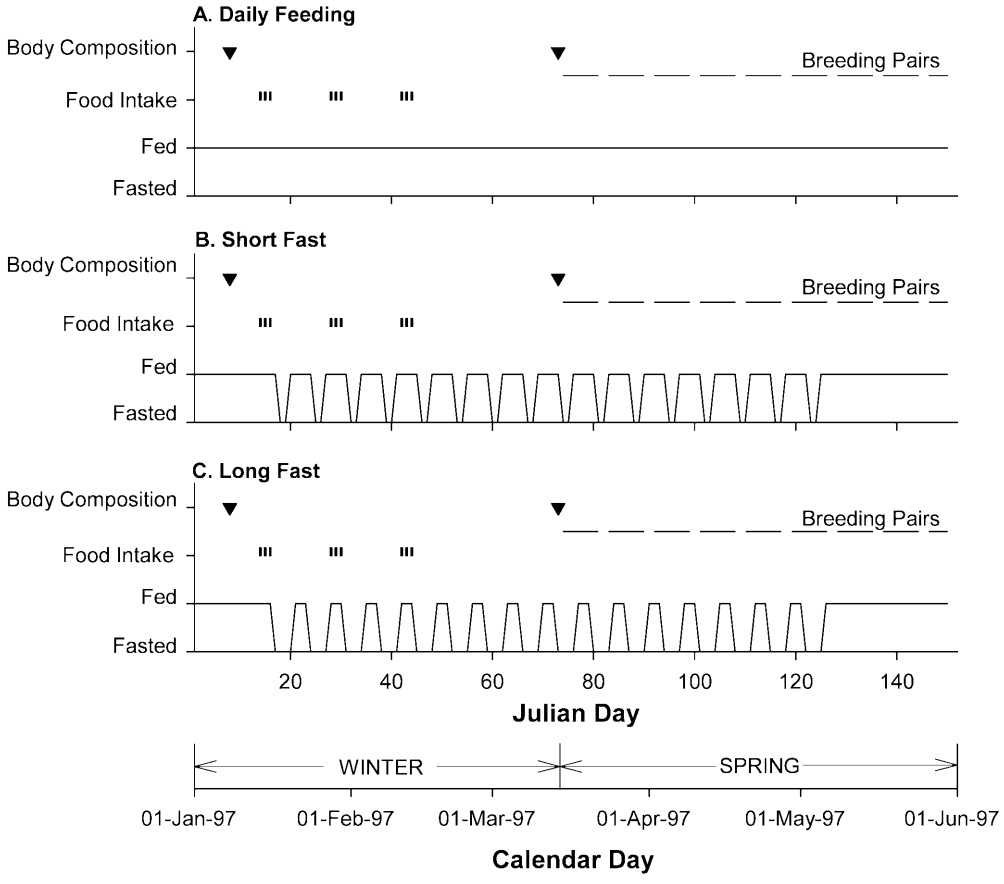

Fig. 1A–C. Timeline for experiments on male and female black ducks during winter (Julian day 1 on January 1 to March 14) and spring (Julian day 74 on March 15 to Julian day 152 on 1 June). Birds were segregated by sex and held in groups until March 15 when pairs were formed for breeding (*dotted line*). Subsets of birds were killed (*filled triangles*) on Julian day 8 and Julian day 73. *Solid lines* indicate days on which food was provided ad libitum to each treatment group: daily feeding (**A**); short fasts (**B**; 2 days.week^{-1}); long fasts (**C**; 4 days.week^{-1}). *Vertical marks* indicate days on which food intake was measured in all groups: before treatment (Julian day 14–16) and after treatment for 2 weeks (Julian day 28–30) and 4 weeks (Julian day 42–44), respectively

time each morning. Ducks were fed extruded pellets of complete diets based on standards for domestic waterfowl (National Research Council 1994). Three diets were provided at different stages: growth (Mazuri no. 5641; PMI Feeds, St Louis Mo.), maintenance (no. 5642), and breeding (no. 5640). These formulations included cereals (wheat, corn, oat) and concentrates (meat and bone meal, soybean meal, milk whey) with vitamin and mineral premixes. All birds were raised on the grower diet from hatching to wing molt. Manufacturer's guaranteed analysis of the grower diet was no less than 20% crude protein and 3% crude fat, but no more than 6.5% crude fiber and 7% ash on an air-dry basis. The maintenance diet was offered from autumn through winter. Manufacturer's guaranteed analysis of this product was no less than 14% crude protein and 3% crude fat, but no more than 4.5% crude fiber and 6% ash on an air-dry basis. Breeder diet was provided immediately after pairing in March (Julian day 74) and throughout incubation. Manufacturer's guaranteed analysis of the breeder diet was no less than 17% crude protein and 2.5% crude fat, but no more than 6% crude fiber and 10% ash on an air-dry basis. Breeding birds were also provided with ground oyster shell ad libitum to ensure adequate eggshell formation.

Body mass was recorded (±1 g) each week during winter (January–March) by confining birds in a tube placed on an electronic balance. All animals were weighed on the same day before providing fresh food in the morning to minimize effects of gut fill on body mass. Fasted groups were weighed at the end of the feeding cycle, that is, at the start of the fasting period on the first morning of 2 days or 4 days without food. Body mass was also recorded during the breeding season at the end of treatment in May (Julian day 129) and 14 days later on Julian day 143 (Fig. 1).

Treatments were started on Julian day 17 (Fig. 1). Intakes were estimated for each pen over 3 consecutive days immediately before starting the treatments (Julian days 14, 15 and 16) and after 2 weeks (Julian days 28, 29 and 30) and 4 weeks (Julian days 42, 43 and 44) of treatment (Fig. 1). Uneaten food was dried to constant mass in a fan-forced oven at 55 °C. Subsamples (20 g) of food offered to birds were also dried each day. Intakes were the difference between the dry mass of food offered and that remaining the following day. Weekly intake of dry matter (DM) was calculated as the product of the mean daily intake of birds in the pen and the number of feeding days in the week (i.e., control = 7 days fed.week^{-1}; short-fasts = 5 days fed.week^{-1}; long-fasts = 3 days fed.week^{-1}).

Food offered to birds was sampled before treatment (Julian day 1–3, and 14–16) and after 2 weeks and 4 weeks of treatment (Julian days 28–31 and 42–44, respectively). Daily samples of dry food offered were combined within weeks and ground through a no. 20 mesh (1.25 mm) in a Wiley Mill before analysis. DM, ash, lipid and N (crude protein) were assayed by the same methods used for homogenized tissue below. Gross energy content was measured in an adiabatic bomb calorimeter (Model no. 1261, Parr, Moline Ill.). Acid detergent fiber was extracted by the method of Van Soest et al. (1991).

Body composition

Birds were killed by cervical dislocation in January (Julian day 8; before treatment) and in March (Julian day 73; before pairing and after 8 weeks treatment; Fig. 1). All animals were killed before providing fresh food in the morning. Each body was wrapped in two layers of plastic and stored in a plastic bag at –20 °C. Wrapped carcasses were thawed at 3 °C for dissection. Dimensions of the bill (culmen to post-nares) and the leg (tarsus) were recorded with Vernier calipers (±0.1 mm). Feathers were removed and estimated as the mass lost on weighing the plucked bird. The following sections were removed and weighed (± 0.01 g): skin with subcutaneous adipose tissue, breast muscles (pectoralis and supracoracoideus), omental adipose tissue, heart, liver, spleen with pancreas, kidneys, and reproductive tract. The digestive tract was

dissected from omental adipose, weighed and ligated to isolate the esophagus and proventriculus, gizzard (ventriculus), small intestine, colon, and ceca. Each segment was weighed and measured for length (±1 mm) by laying the intact segment flat on a plastic cutting board. Digestive tract contents were temporarily displaced from the mid-point of the segment to measure the flat width at that point. Nominal areas of small intestine, ceca and colon were calculated as twice the flat width multiplied by the length (Barboza 1995). Segments were emptied of digesta and weighed to measure tissue mass and to calculate the mass of digesta content by difference.

Tissues were combined into the following five groups for chemical analysis: breast muscles, viscera (heart, liver, pancreas, spleen, kidneys, reproductive tract, empty digestive tract segments), omental adipose tissue, skin and musculoskeleton (remaining appendicular skeleton). Combined tissues were stored at –20 °C in two layers of plastic. Tissues were thawed at 3 °C and homogenized in a stainless steel blender (Model no. 5010, Waring, New Hartford Conn.) or meat grinder (Model EC33, General, Murfreesboro Tenn.). Water contents of feathers and homogenized tissues were determined by drying to constant mass in a forced convection oven at 55 °C. Homogenized tissues were lyophilized for further analysis. Ash was determined by combustion at 550 °C in a muffle furnace for 4 h. Lipid was assayed by extraction with petroleum ether (Dobush et al. 1985) in a modified Soxhlet procedure (Model no. HT6 Soxtec, Tecator, Foss North America, Silver Spring Md.). Nitrogen was determined by an elemental analyzer (Model no. CNS 2000, Leco, St Joseph Mich.) and expressed as crude protein in food on the assumption that 100 g crude protein contained 16g N (Robbins 1993). Nitrogen was also calculated as a proportion of lean organic matter (OM; DM minus lipid and ash) in tissues as this fraction approximates total protein and nucleic acid if carbohydrate content is assumed to be small. Feathers and digesta were excluded from summation of chemical composition, that is, total lipid and N in the body were calculated only from homogenized tissues.

Statistical analyses

Statistics were calculated and analyzed with programs in SYSTAT version 10.0 (SPSS, Chicago Ill.). Data expressed as proportions or percentages (e.g., moisture content of lipid-free tissue, N in lean OM) were transformed to the arcsine of the square root to meet assumptions of normality (Zar 1974) for analysis of variance (ANOVA). Data with unequal variance between groups were transformed to natural logarithms for ANOVA. Univariate comparisons of dimensions and chemical composition of body components were limited because these variables were inter-correlated. Therefore, we prepared four multivariate sets of data to analyze distributions of mass among all dissected tissues (body mass factors), of mass among internal organs (visceral mass factors), of mass, length and surface area along the digestive tract (digestive factors) and of lipid, protein and ash in body fractions (composition factors). Correlation matrices were sorted into three principal components (factors), which were rotated to orthogonal axes to provide a score for all subjects on each factor (1–3). Variables were ranked to describe the three variables that explained the most variance in each factor. Multivariate factors and key variables (e.g., liver mass) were subsequently tested by ANOVA for experimental effects.

We tested effects of sex, treatment and pen (nested within treatment) by ANOVA. Effect of time was tested as repeated measures of food intake or body mass in the same animals or as an effect of period for comparisons of body composition between animals. ANOVA included interactions between sex and time, treatment and time, and between sex and treatment in the General Linear Model. Post hoc tests of ANOVA used Bonferroni's adjustments for multiple pair-wise comparisons between times and treatment groups. Statistical significance was determined as less than 5% probability of Type I error ($P < 0.05$). All means are reported with one standard deviation (±SD).

Results

Feeding

The maintenance diet was 93.9 ± 1.1% DM which contained 5.6 ± 0.1% N (15.6 ± 0.1% crude protein), 1.6 ± 0.2% lipid, 6.9 ± 0.2% acid detergent fiber, and 6.1 ± 0.2% ash. Gross energy content of the diet was 18.23 ± 0.03 kJ.g^{-1} DM.

Ambient temperatures were similar in January and February when food intakes were measured: average minima –6.9 ± 4.3 °C; average maxima 7.7 ± 1.7 °C. Food intakes of males did not change during January and February from 0 weeks to 4 weeks of treatment (Fig. 2a). Similar weekly intakes of males between treatments (364 ± 65 g.kg^{-1}.week^{-1}) were the result of increased daily food consumption between fasts. After 2 weeks treatment, unfasted males consumed 53 ± 6 g.kg^{-1}.day^{-1} whereas males on short and long-fasts consumed 70 ± 23 g.kg^{-1}.day^{-1} and 124 ± 17 g.kg^{-1}.day^{-1}, respectively, on each day that food was available.

Although food intakes of females were lower than those of males before treatment (290 ± 112 g.week^{-1} vs. 407 ± 94 g.week^{-1} per bird; $P = 0.035$), food intakes of females increased during January ($P = 0.003$; Fig. 2b) and were similar between sexes after 4 weeks treatment (443 ± 81 g.week^{-1} per bird). Fasting also increased weekly food intakes of females after 2 weeks treatment ($P = 0.049$; Fig. 2b). During this same period, daily food consumption by unfasted control females was 33 ± 6 g.kg^{-1}.day^{-1}, whereas fasted females consumed 65 ± 12 g.kg^{-1}.day^{-1} and 131 ± 19 g.kg^{-1}.day^{-1} on short and long-fasts respectively.

Body mass and size

Both sexes lost body mass between January and March ($P < 0.05$) but males were heavier than females throughout winter ($P < 0.001$; Fig. 3) and lost proportionately less of their initial mass (10.8 ± 5.2% vs. 14.4 ± 6.5%; $P = 0.010$) between January (Julian day 10) and March (Julian day 73). Although males on short-fasts tended to lose less mass than other males to day 37 ($P = 0.099$), those birds subsequently lost mass more rapidly so that all groups of males ended winter at the same average mass (Fig. 3a). Females lost mass in a similar pattern through the 1st week of treatment but females on long-fasts lost less mass and ended winter heavier than control females fed daily through 8 weeks of treatment (Fig. 3b).

Males killed for compositional analysis were similar in body mass between January (Julian day 8; 1401 ± 49 g) and March (Julian day 73; 1311 ± 130 g), whereas females sampled for body composition were lighter in March (1058 ± 118 g) than January [1298 ± 158 g; $P = 0.018$; see Appendix (Table 2)]. Structural elements of the body such as the length of the limbs and

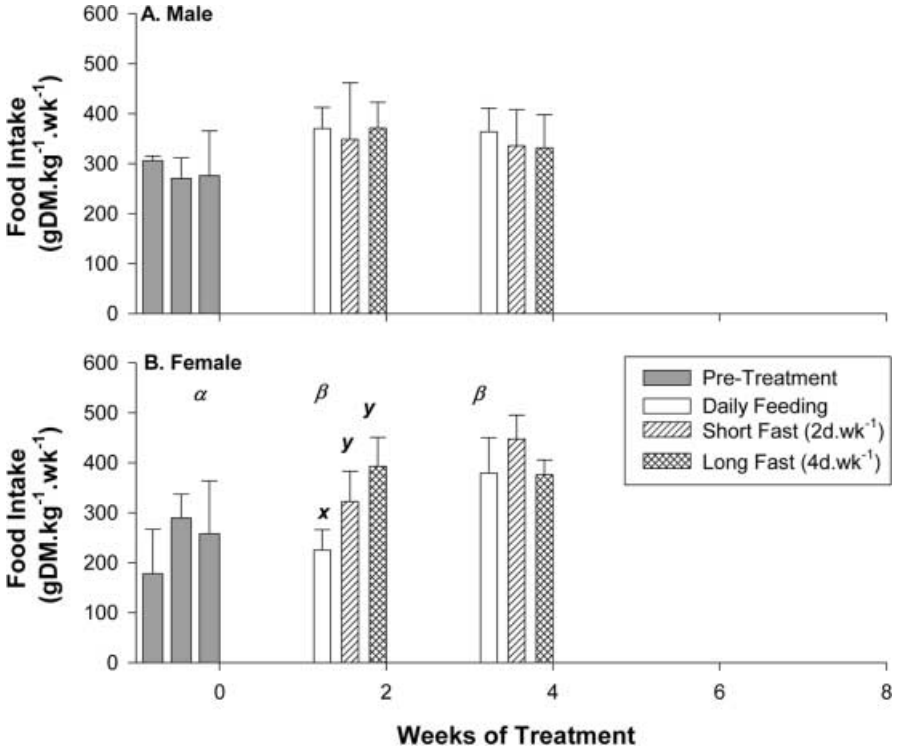

Fig. 2. Weekly food intakes [g dry matter (DM).kg^{-1} body mass; mean ± SD] of male (**A**) and female (**B**) black ducks in outdoor pens during January (pre-treatment, days 14–16) and after 2 weeks (days 28–30) and 4 weeks (days 42–44) of treatment when food was provided daily or intermittently with short-fasts (2 days.week^{-1}) or long-fasts (4 days.week^{-1}). *Different letters* indicate significant differences ($P < 0.05$) between times (α, β) or treatment groups (x, y)

head did not differ between months, treatment groups or pens. Males were heavier than females ($P < 0.001$) and had longer bills (48.5 ± 1.3 mm vs. 45.1 ± 1.6 mm; $P < 0.001$) and legs (45.5 ± 1.4 mm vs. 42.7 ± 1.1 mm; $P < 0.001$).

Partitioning body mass

Changes in body mass were partitioned among three body mass factors (Fig. 4). Factor 1 represented seasonal declines associated with heart, skin and omental adipose (Fig. 4a). Heart mass of males changed from 11.2 ± 1.5 g to 10.3 ± 1.3 g between January and March while that of females changed from 10.7 ± 1.5 g to 8.9 ± 0.9 g over winter [see Appendix (Table 2)]. Skin mass also changed over winter from 307.7 ± 34.7 g to 256.1 ± 88.8 g in males, and from 324.7 ± 94.3 g to 155.0 ± 69.0 g in females. Differences between the sexes in body mass factor 2 (Fig. 4b) for both January and March were associated with greater mass of breast muscles, musculoskeleton and feathers in males than in females: breast muscles 257.5 ± 12.2 g vs. 233.1 ± 13.9 g; musculoskeleton 604.9 ± 26.3 g vs. 516.2 ± 37.4 g; feathers 94.1 ± 6.4 g vs. 85.8 ± 6.9 g. Seasonal increases in mass were reflected in body mass factor 3 (Fig. 4c) which was associated with kidney, liver and reproductive tissue. Kidney mass changed from 5.3 ± 0.6 g to 5.9 ± 0.8 g in males from January to March whereas female kidney mass was 5.1 ± 0.6 g and 5.9 ± 0.9 g at the start and the end of winter, respectively. Reproductive tissues increased in size between January and March in both sexes (Fig. 4d). All females killed in March had commenced ovarian development and were undergoing pre-basic molt. Reproductive tissue was similar in mass and development among females in March (Julian day 73); average diameters of the three largest ovarian follicles were 5.8 ± 0.7 mm, 7.4 ± 2.6 mm and 4.8 ± 0.7 mm for control, short-fast and long-fast females, respectively. In contrast, reproductive tissues of males were heavier in birds on short-fasts than in either unfasted or long-fast birds at the end of winter (Fig. 4d).

Tissues of the kidney, reproductive tract and liver were also associated with the first factor partitioning mass of visceral organs (Fig. 5a). Differences between the sexes in visceral mass factor 2 were associated with the size of tissues such as the hindgut (ceca plus colon): males 2.8 ± 0.3–2.5 ± 0.4 g; females 2.3 ± 0.3–2.4 ± 0.6 g in January and March, respectively [see Appendix (Table 3)]. Factor 2 was also affected by changes from January to March in the spleen (plus pancreas) of both males (4.7 ± 1.0 g to 3.3 ± 0.6 g) and females (4.2 ± 1.3 g to 2.9 ± 0.9 g). Effects of fasting enhanced seasonal changes in visceral factor 3 associated with liver and small intestinal tissues especially among females (Fig. 5c). Long-fasts increased liver mass above that of unfasted females in March (Fig. 5d). Small intestinal tissue of females changed from 9.7 ± 1.1 g in January, to 10.2 ± 1.3 g, 12.7 ± 1.4 g and 13.8 ± 2.1 g in unfasted, short-fast and long-fast birds, respectively, in March. Liver mass of males (Fig. 5d) was also increased by fasting in March. However, scores of visceral mass factor 3 declined from January to March in males (Fig. 5c) and probably reflected a change in small intestinal mass from 12.1 ± 1.0 g in January to 9.4 ± 0.2 g, 11.1 ± 2.2 g

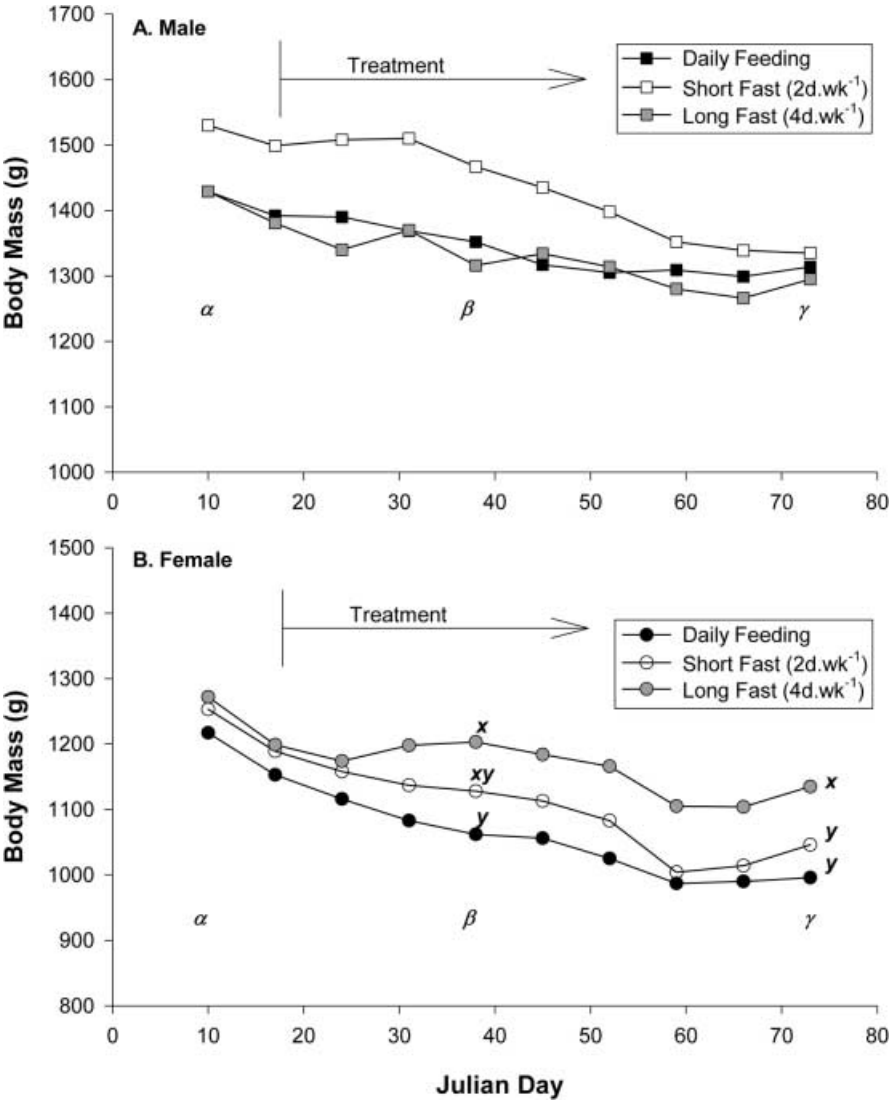

Fig. 3. Average body mass of male (**A**) and female (**B**) black ducks provided with food each day of the week (daily feeding) or intermittently with short-fasts (2 days.week^{-1}) or with long-fasts (4 days.week^{-1}) from January to March after 8 weeks treatment. *Different letters* indicate significant differences ($P < 0.05$) between times (α, β, γ) or treatment groups (x, y) at Julian days 10, 38 and 73 for each sex

and 12.3 ± 1.4 g in unfasted, short-fast, and long-fast birds, respectively, at the end of winter.

Partitioning digestive tract dimensions

Dimensions and contents of digestive tract tissues were partitioned among three gut factors which were associated with variation in the gizzard, intestinal area and intestinal mass respectively (Fig. 6). Scores for digestive factor 1 were greater for males than for females in both January (Julian day 8) and March (Julian day 73; Fig. 6a) which reflected the larger mass of the empty gizzard (26.9 ± 4.3 g vs. 20.6 ± 2.9 g) and its contents (6.0 ± 2.6 g vs. 4.8 ± 1.9 g) in males than in females. Declines in digestive factor 2 over winter were associated with changes in males for the nominal surface areas of the small intestine (128.5 ± 11.2 cm^2 vs. 112.5 ± 10.3 cm^2), ceca (30.7 ± 5.2 cm^2 vs. 22.2 ± 4.8 cm^2) and colon (14.0 ± 3.2 cm^2 vs. 11.5 ± 2.4 cm^2). Female scores for digestive factor 2 were similar to those of males (Fig. 6b) but were less affected by winter. Intestinal surface areas in females were 116.4 ± 12.1 cm^2, 24.6 ± 6.9 cm^2 and 12.4 ± 3.5 cm^2 for the small intestine, ceca and colon, respectively, in January and March. However, small intestinal content of females changed from 2.6 ± 1.0 g in January to 2.8 ± 0.9 g, 3.8 ± 1.3 g and 5.8 ± 0.9 g in unfasted, short-fast and long-fast birds, respectively, at the end of winter. Changes in contents and the mass of small intestine resulted in higher scores for digestive factor 3 in fasted females than in unfasted controls during March (Fig. 6c). Males were similar to females in scores of digestive factor 3 and in the mass of small intestinal contents in January (3.5 ± 1.2 g) and March (4.2 ± 1.4 g). The greater mass of the full digestive tract in males than in females probably reflected the greater size of the gizzard in males during January (Fig. 6d). However, increases in small intestinal mass and contents of fasted females reduced the difference between sexes in the mass of the digestive tract in March (Fig. 6d).

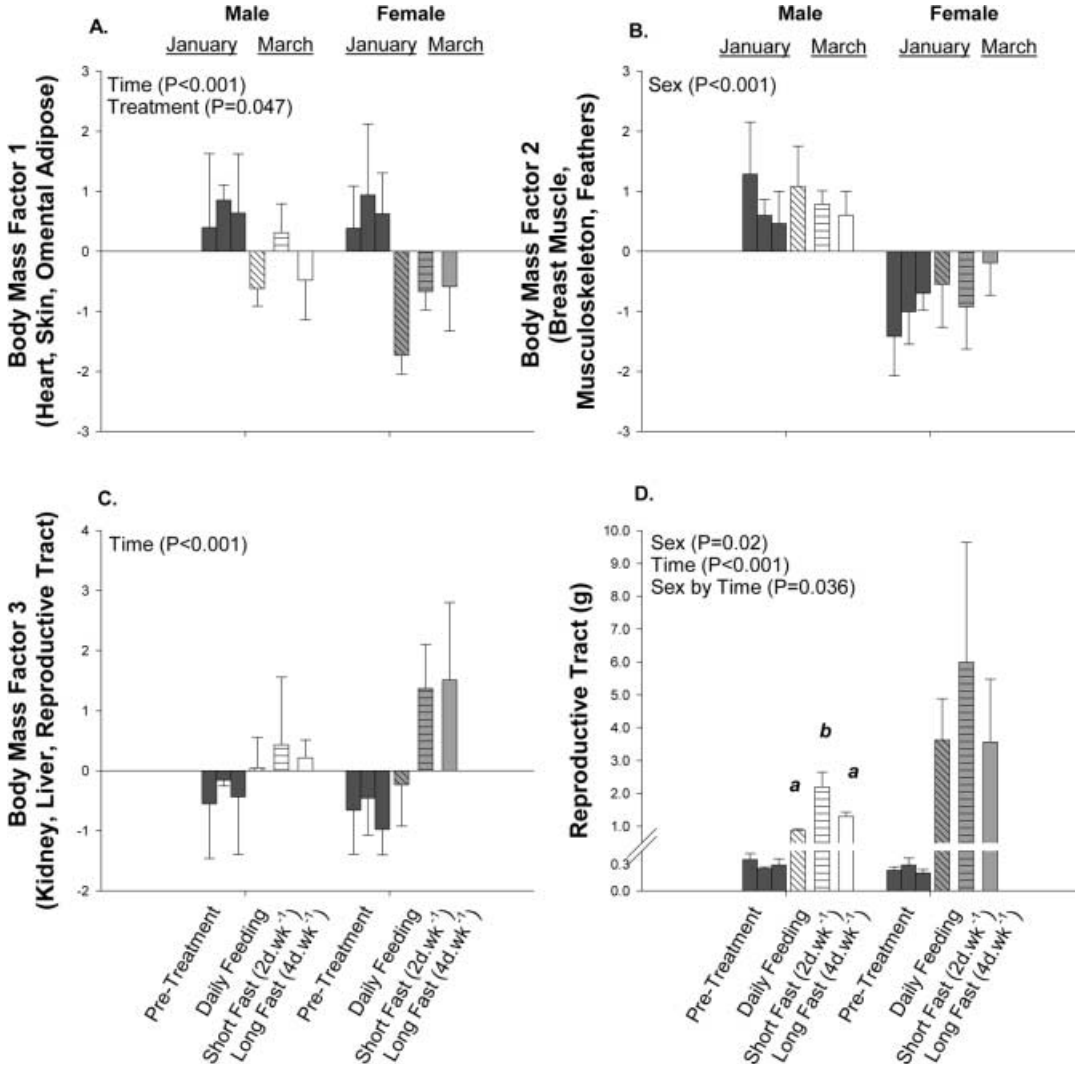

Fig. 4A–D. Body mass distribution of black ducks in January (Julian day 8; pretreatment) and March (Julian day 73) following daily or intermittent feeding with short-fasts (2 days.week^{-1}) or long-fasts (4 days.week^{-1}) for 8 weeks ($n = 18$ males, 18 females). Body mass factors 1 (**A**; heart, skin, omental adipose), 2 (**B**; breast muscle, musculoskeleton, feathers) and 3 (**C**; kidney, liver, reproductive tract) accounted for 30%, 22% and 19% of total variance, respectively. Body mass factors include mass of feathers, skin, breast muscle, musculoskeleton, full digestive tract, omental adipose, heart, pancreas and spleen, liver, kidney, and reproductive tract. The three variables ranked highest for each factor are listed on the *vertical axis*. Mass of reproductive tract tissue (g) is plotted in **D** for comparison with body factor 3

Body composition

Lipid, N and ash in body tissues were partitioned among three composition factors which were associated with fat depots, lean body size and lean organ mass respectively (Fig. 7). Most body lipid was attributed to skin ($56 \pm 7\%$), with $11 \pm 5\%$ in omental adipose tissue, $28 \pm 9\%$ in the musculoskeleton and only $3 \pm 1\%$ in the breast muscles (Fig. 8a). Although females lost more lipid than males between January and March (286 g vs. 95 g; Fig. 8a) lipid was mobilized in a similar fashion between sexes, with most lipid lost from subcutaneous (male 58%, female 64%) and omental (male 28%, female 18%) depots (Fig. 8a). Scores for composition factor 1 (Fig. 7a) indicated that declines in lipid depots were greatest for unfasted females between January and March.

Scores for composition factor 2 were associated with lean components of the body frame such as N in breast muscles and musculoskeleton which were greater for males than females (Figs. 7b, 8b). Musculoskeleton accounted for the largest proportion of body N ($65 \pm 3\%$) with only $20 \pm 3\%$ and $10 \pm 3\%$ in breast muscle and skin, respectively (Fig. 8b). Although N in viscera accounted for only $4 \pm 1\%$ of body N, visceral N was significantly greater in females on long-fasts than in unfasted controls in March (Fig. 8b) which contributed to a treatment effect on scores for chemical component 3 (Fig. 7c). This difference was probably associated with the greater size of liver and intestine in females on long-fasts [Figs. 5, 6; Appendix (Tables 2, 3)]. However, these changes in the allocation of N did not affect total body N of either sex between January and March (Fig. 8b).

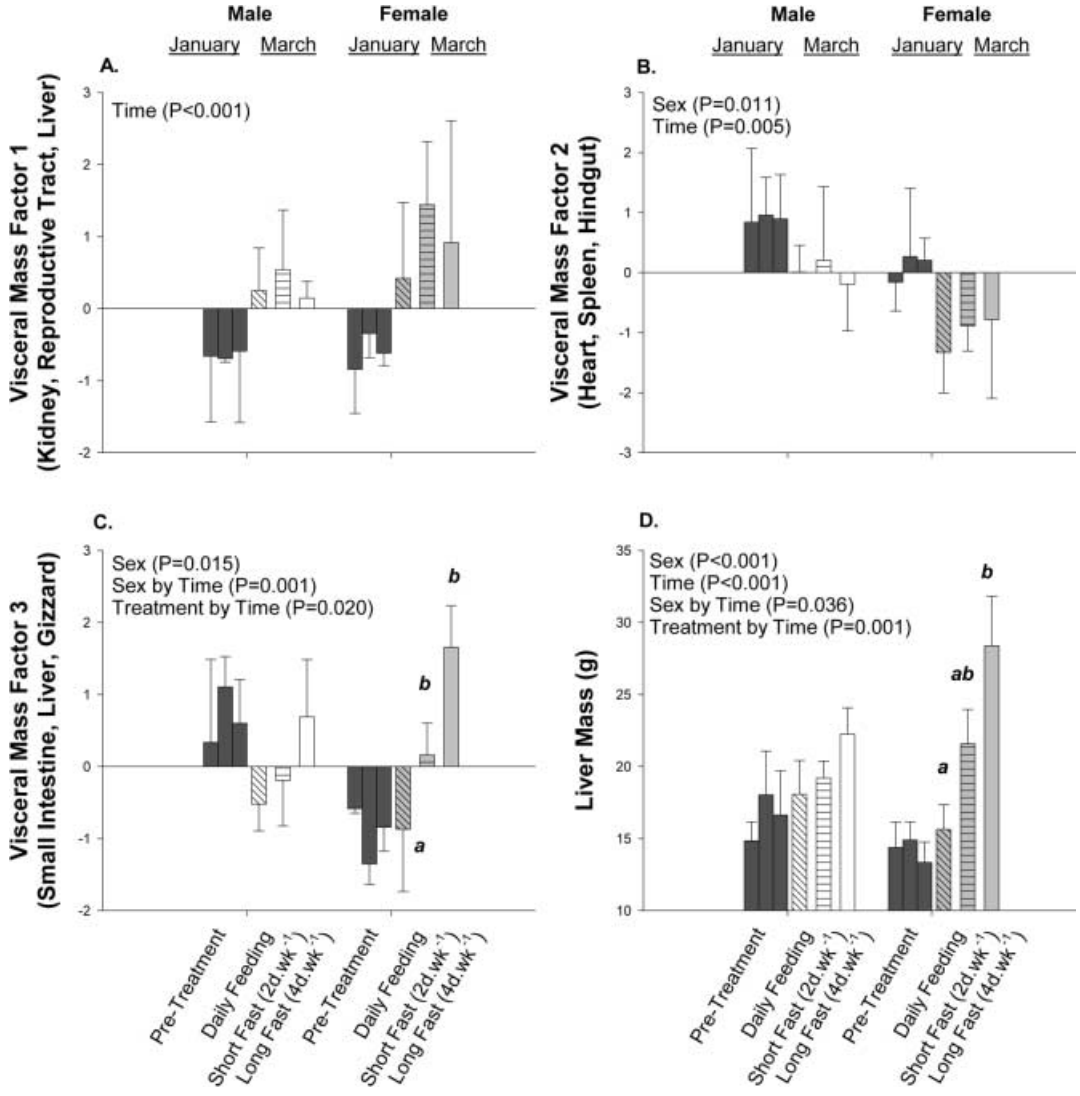

Fig. 5A–D. Distribution of visceral mass of black ducks in January (Julian day 9; pre-treatment) and March (Julian day 73) following daily or intermittent feeding with short-fasts (2 days.week^{-1}) or long-fasts (4 days.week^{-1}) for 8 weeks ($n = 18$ males, 18 females). Visceral mass factors 1 (**A**; kidney, reproductive tract, liver), 2 (**B**; heart, spleen plus pancreas, hindgut) and 3 (**C**; small intestine, liver, gizzard) accounted for 28%, 25% and 20% of total variance, respectively. Visceral mass factors include tissue mass of heart, pancreas and spleen, liver, kidney, reproductive tract, gizzard, small intestine and hindgut (ceca and colon). The three variables ranked highest for each factor are listed on the *vertical axis*. Mass of liver (g) is plotted in **D** for comparison with visceral mass factors 1 and 3

Composition of the lipid-free fraction of tissues varied subtly between sexes and months in winter. Water content of lean tissue in the whole body was significantly higher in females than males ($72.6 \pm 0.6\%$ vs. $72.2 \pm 0.6\%$; $P = 0.006$). Similarly, moisture in lean breast muscle was greater in females than males ($70.5 \pm 1.2\%$ vs. $69.4 \pm 1.0\%$; $P = 0.032$) but this measure decreased from January to March ($72.6 \pm 0.5\%$ vs. $72.3 \pm 0.7\%$; $P = 0.050$). Lean OM, a fraction assumed to be equivalent to crude protein, did not vary in N content with sex or with month. However, the average content of N in lean OM for breast muscle (9.9 ± 0.8 g N.100 g^{-1}) was lower than that of the whole body (13.6 ± 0.8 g N.100 g^{-1}), which was considerably lower than the value of 16 g N.100 g^{-1} typically used in converting N content to equivalents of crude protein in plant and animal feedstuffs.

Egg production and body mass

Intermittent fasting was associated with both an absence of egg production (no eggs laid in two of nine birds on long-fasts and one of six birds on short-fasts) and with delayed initiation of egg production (Fig. 9a). Cessation of treatment by feeding all birds each day resulted in the completion of clutches among birds from the long-fast group. Egg-laying females in all groups continued to lose mass during daily feeding, but females from the long-fast group remained heavier than other females at Julian day 143 (Fig. 9b). Body masses of males did not vary among groups at the end of treatments and were

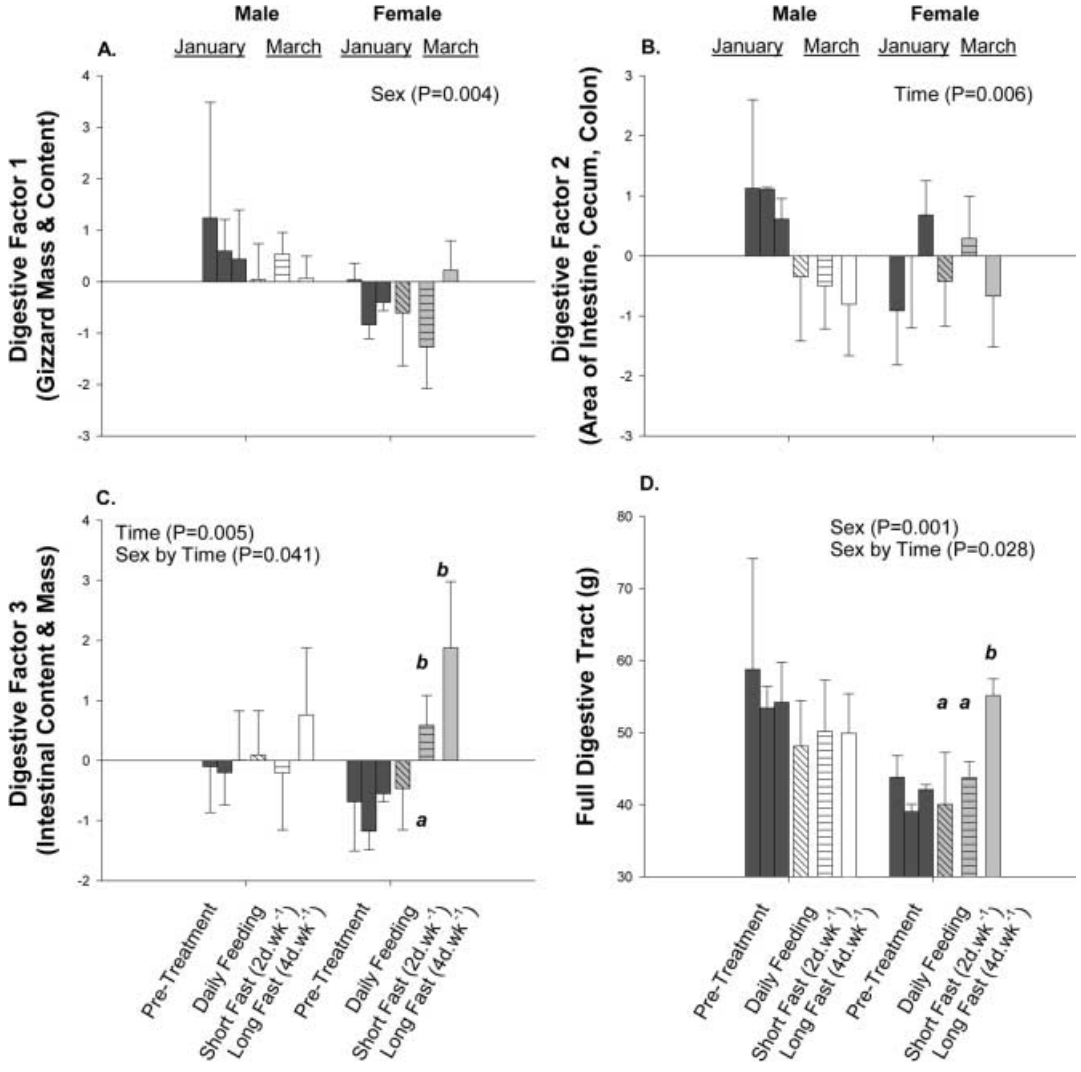

Fig. 6A–D. Distribution of mass and dimensions of digestive tract tissue of black ducks in January (Julian day 9; pre-treatment) and March (Julian day 73) following daily or intermittent feeding with short-fasts (2 days.week^{-1}) or long-fasts (4 days.week^{-1}) for 8 weeks ($n = 18$ males, 18 females). Digestive factors 1 (**A**; gizzard mass and content), 2 (**B**; areas of small intestine, ceca and colon) and 3 (**C**; small intestinal content and mass) accounted for 26%, 19% and 17% of total variance, respectively. Digestive factors include tissue mass and digesta content of gizzard, small intestine and hindgut, with the length and width of the gizzard and the nominal mucosal surface area of the small intestine, ceca and colon. The three variables ranked highest for each factor are listed on the *vertical axis*. Mass of full digestive tract (g) is plotted in **D** for comparison with digestive factors 1 and 3

unchanged by 14 days of daily feeding. Total numbers of eggs laid in the long-fast group were lower than those for control yearlings fed daily through winter but similar to the average clutch produced by older females in the same colony (Table 1). Rates of fertility and numbers of eggs hatched were similar between treatment groups of yearlings and similar to those of other birds that had bred previously in this colony (Table 1).

Average egg mass was 50.0 ± 3.8 g at 6–10 days of incubation. Infertile eggs sampled at this stage of incubation contained $38.2 \pm 3.3\%$ DM that was $5.5 \pm 0.1\%$ N, $33.2 \pm 0.2\%$ lipid and $24.7 \pm 0.8\%$ ash. Therefore, females deposited 19 g DM with 1.1 g N, 6.3 g lipid, and 4.7 g ash in the average egg, based on the assumption that fertility does not affect the composition of the egg. Nutrients deposited by the female in the average clutch were 72 g lipid with 12.0 g N in unfasted birds, 47 g lipid with 7.9 g N in short-fast birds and 34 g lipid with 5.6 g N in birds on long-fasts.

Discussion

Food intake and body composition

Both body size and reproductive effort affect seasonal food intake, body composition and metabolism of sexually dimorphic animals (Barboza and Bowyer 2000, 2001). Male black ducks were 8% larger than females in lengths of leg and bill, and 17% heavier in lean mass. Greater lean mass probably increased total energy demand and thus food intakes of males compared with females in January (Fig. 2). However, subsequent

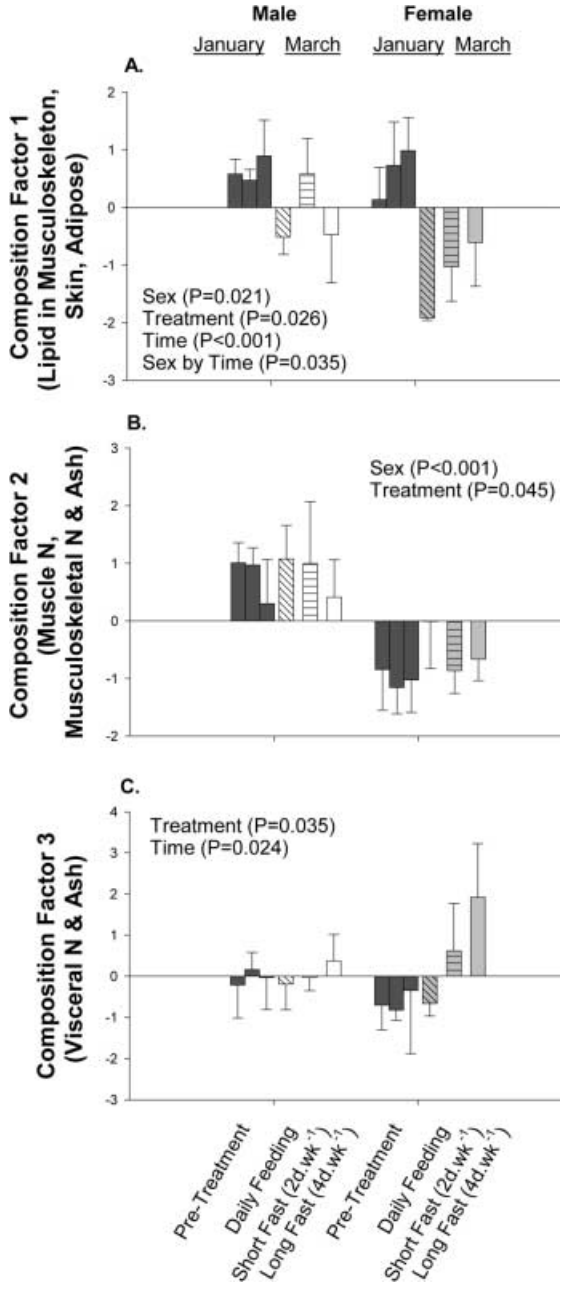

Fig. 7A–C. Distribution of body lipid, N and ash of black ducks in January (Julian day 9; pre-treatment) and March (Julian day 73) following daily or intermittent feeding with short-fasts (2 days.week^{-1}) or long-fasts (4 days.week^{-1}) for 8 weeks ($n = 18$ males, 18 females). Composition factors 1 (**A**; lipid in musculoskeleton, skin and omental adipose), 2 (**B**; N in breast muscle, N and ash musculoskeleton) and 3 (**C**; N and ash in viscera) accounted for 33%, 20% and 13% of total variance, respectively. Composition factors include lipid, N and ash in skin, breast muscle, musculoskeleton, omental adipose and internal organs. The three variables ranked highest for each factor are listed on the *vertical axis*

increases in food intakes of females were probably due to differences between sexes in the annual cycle of reproductive effort. Reproductive costs for males are greatest during competition for mates before winter whereas reproductive efforts of females are greatest during laying, incubation and brood care in spring.

Declines in body mass of unfasted birds (Fig. 3) through winter indicate an endogenous seasonal pattern in both sexes of black ducks. Concomitant reductions in the mass of heart and spleen are consistent with changes in the circulatory demands of tissues (Bethke and Thomas 1988). Winter mass loss has also been reported for wild black ducks and mallards (Reinecke et al. 1982; Whyte and Bolen 1984), but has usually been related to the effects of cold stress and increased energy demand. Body mass may also be regulated in relation to a genetic set-point for fitness that is dependent upon risks of weather and predation in each population (Rogers et al. 1994; Piersma et al. 1996; Gates et al. 2001). This suggestion is supported by body mass changes of male black ducks that were fed intermittently through autumn; resumption of daily feeding results in either loss or gain of body mass to a common level at the start of winter (Barboza and Jorde 2001). Similar body mass among treatment groups of males in this study (Fig. 2a) also suggests a seasonal set-point for the end of winter.

Body mass and composition are directly related to food intakes and daily energy expenditures. For example, female black ducks on long-fasts probably replenished small losses of mass by increasing daily food intake after 2 weeks treatment (Figs. 2, 3). This response is similar to those of small birds that increase food intake and the rate of daily mass gain when body mass has been reduced by acute cold stress (Bednekoff et al. 1994; Lilliendahl et al. 1996) or when feeding time is constrained (Ekman and Hake 1990; Bednekoff and Krebs 1995). However, weekly intakes of black ducks were similar among females after 4 weeks treatment at Julian day 42–44 (Fig. 2). Body mass remained constant in long-fast females, while control females continued to lose mass into March (Julian day 73; Fig. 3). The maintenance of a greater mass in female black ducks fed intermittently with long-fasts could reflect lower energy expenditure during each fast (Perry et al. 1986). Captive finches reduce energy expended on locomotion as energy demands increase with clutch size but these birds do not increase food intake (Williams and Ternan 1999). Although wild mallards reduce social activities at roost during periods of cold stress (Jorde et al. 1984), the suggestion of compensatory reductions in activity costs during fasting awaits confirmation by direct measures of energy expenditure in waterfowl fed intermittently during winter.

High food intakes between fasts increased digestive and absorptive loads of nutrients for black ducks by a factor of 2.3 in males and by 4.0 in females. This suggests that black ducks have reserve capacity for processing nutrients (Karasov and Hume 1997) if metabolizability of the diet was maintained in a similar fashion to that measured in males during autumn (Barboza and Jorde 2001). It is likely that intermittent feeding entrains secretory and metabolic responses of the liver and pancreas to anticipate the feeding cycle (Diaz-Muñoz et al. 2000). Increased mass of liver in fasted animals suggests a greater capacity

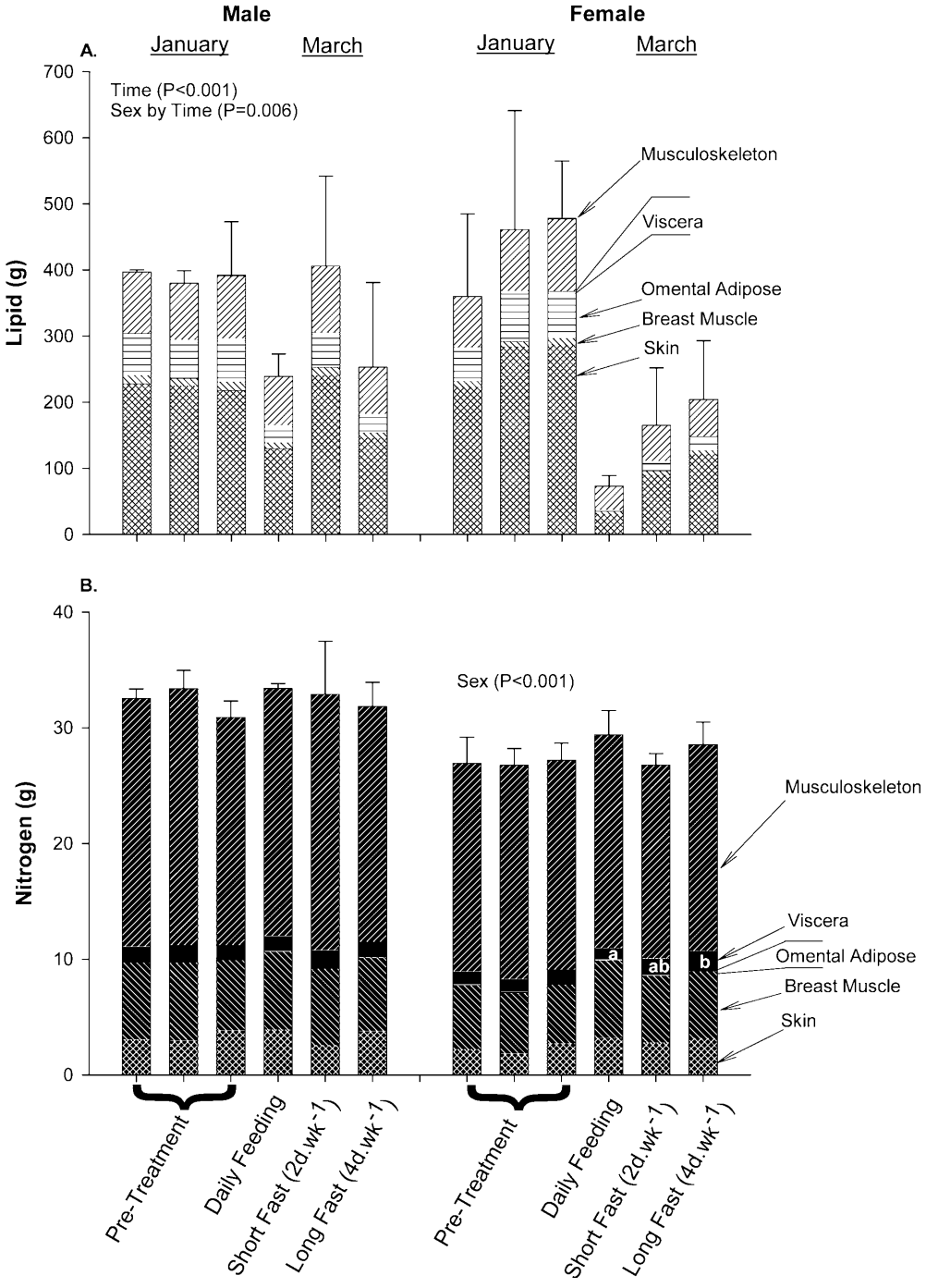

Fig. 8. Body lipid (**A**) and N (**B**) of black ducks in January (Julian day 9; pre-treatment) and in March (Julian day 73) following daily or intermittent feeding with short-fasts (2 days.week^{-1}) or long-fasts (4 days.week^{-1}) for 8 weeks ($n = 18$ males, 18 females). *Stacked shaded bars* from *horizontal axis*: skin, breast muscle, omental adipose, viscera and musculoskeleton. *Error bars* (+1 SD) only refer to totals. All lipid fractions except visceral lipid were significantly different ($P < 0.05$) between months for females. *Different letters* within bars indicate significant differences ($P < 0.05$) between treatment groups for visceral N in March

for hepatic metabolism in both males and females (Fig. 5d). This suggestion is supported by faster rates of dye clearance by the liver of female mallards during egg production when lipid flux and liver mass are increased (Patton 1978).

Food intakes of male black ducks were probably within the reserve capacity of the intestine because intestinal mass, content and nominal surface area were not affected by intermittent fasting (Figs. 5, 6). Fasting reduces intestinal activity and the absorptive surface of villi (Ferraris and Carey 2000) but resumption of feeding is accompanied by rapid restoration of the villi followed by proliferation of intestinal cells (Karasov and Hume 1997; Starck and Beese 2001). This suggestion is supported by increased rates of post-prandial protein synthesis in the digestive tract of chickens fed intermittently (Pinchasov et al. 1988). Increased mass and content of the small intestine in fasted female black ducks is consistent with responses to increased food intake (Kehoe et al. 1988; Starck 1996). Intestinal responses of females may, however, be influenced by reproductive schedule because intestinal length and nominal surface area did not increase with intermit-

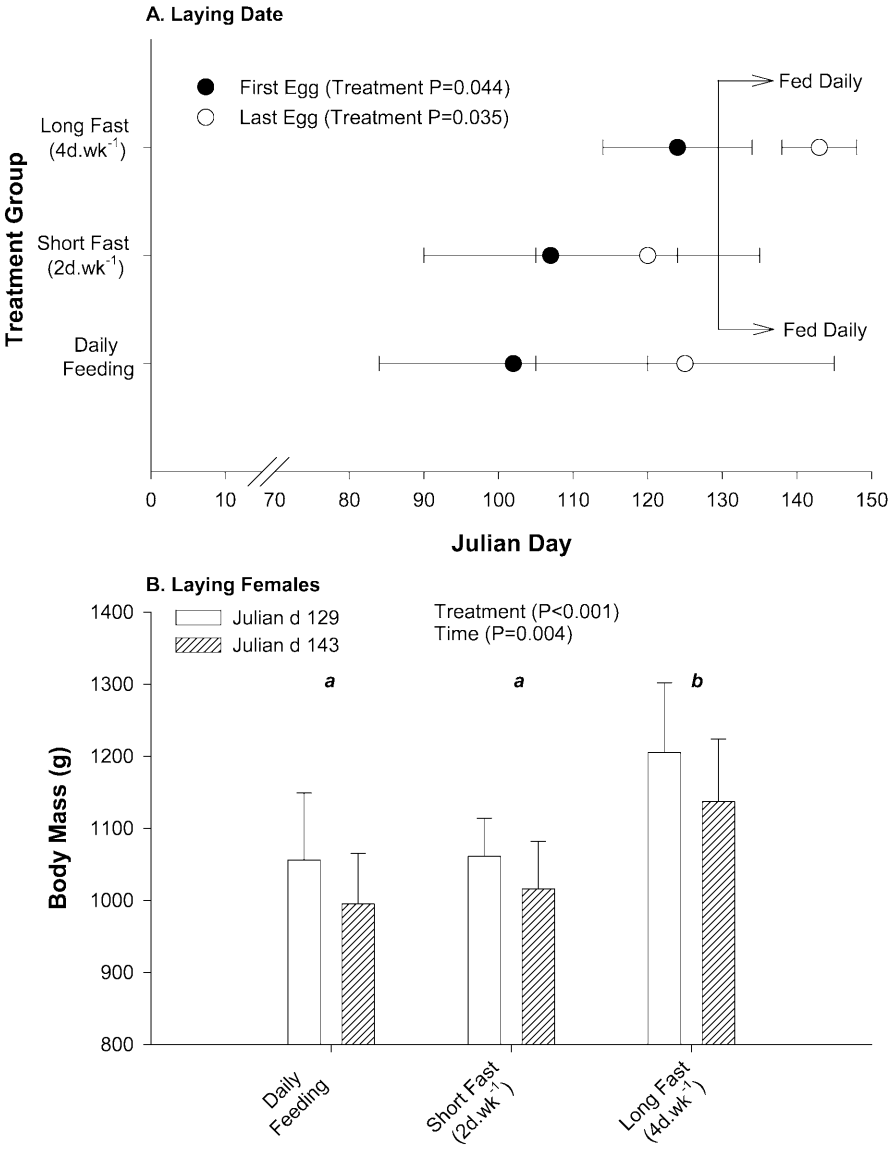

Fig. 9. Egg-laying dates and corresponding body masses of female black ducks following daily feeding ($n=6$) or intermittent feeding with short-fasts (2 days.week^{-1}; $n=5$) or long-fasts (4 days.week^{-1}; $n=7$). All birds were fed each day from day 129. Birds were weighed on day 129 and day 143

tent feeding. Increments in the length of intestine could reduce the peritoneal space to accommodate reproductive tissue and developing eggs at the start of spring.

Changes in body composition of black ducks in this study were not a consequence of food limitation (King and Murphy 1985). Mobilization of omental and subcutaneous lipid in black ducks through winter (Figs. 7, 8) does not indicate an energy deficit even though these depots are depleted by restricting food intake during autumn (Morton et al. 1994). Maintenance of similar feather mass and total body N within both sexes during winter (Fig. 8) and the gain in renal and gonadal tissue in March (Figs. 4, 5), suggest that dietary supplies of N also were not limiting. However, food restriction can limit energy and nutrient intake and therefore can deplete lean tissue in breast muscle of male black ducks (Morton et al. 1994) and delay prebasic molt in female mallards (Richardson and Kaminski 1992). Subtle differences between the sexes in the moisture content of lean tissues in black ducks may reflect changes at several levels, from the proportions of muscle fibers and connective tissue to the concentration of glycogen within cells (Rosser and George 1987; Evans et al. 1992; Saunders and Fedde 1994; Torella et al. 1996).

Breeding

Differences in body mass between female black ducks during egg production were probably due to sustained differences in lipid mass between the groups at the end of winter (Fig. 8). Greater body mass of females on long-fasts (Fig. 9) was not directly related to reproductive investment of lipid or N because fasted females either did not lay a clutch or produced a similar number of eggs to other groups of females (Fig. 9; Table 1). Investment of lipid in eggs was equivalent to 98%, 29% and 16% of body lipid content of control, short-fast,

Table 1. Reproductive output of captive female black ducks. Experienced birds were >1-year-old and fed daily throughout the winter and the breeding season. Yearling birds that were breeding for the first time, were fed daily or intermittently with short-fasts (2 days.week^{-1}) or long-fasts (4 days.week^{-1}) from Julian day 9 to Julian day 128. All birds were fed each day from day 128

Parameter	First breeding			Experienced breeders Daily feeding ($n=29$)
	Daily feeding ($n=6$)	Short-fast ($n=6$)	Long-fast ($n=9$)	
Total eggs laid	$11.3^{a}_{y} \pm 3.7$	$7.5^{ab}_{x} \pm 3.8$	$5.3^{b}_{x} \pm 3.2$	$7.9_{x} \pm 2.2$
Fertile (%)	36 ± 42	$54^{*} \pm 45$	$31^{**} \pm 41$	47 ± 36
Eggs hatched	3.8 ± 4.3	4.1 ± 4.2	1.7 ± 2.8	3.9 ± 3.1

* Excludes one non-layer, $n=5$
** Excludes two non-layers, $n=7$
[a, b] Different superscripts indicate significant differences ($P<0.05$) between treatment groups of yearlings
[x, y] Subscripts compare experienced breeders with yearlings

and long-fast females, respectively, at the end of winter. Similarly, N invested in eggs was equivalent to 41%, 30% and 20% of body N in control, short-fast, and long-fast females, respectively, during March. These data indicate that the availability of endogenous nutrients did not limit reproductive output of our black ducks. Body mass and reserves of lipid and N are related to fecundity in lesser snow geese (*Chen caerulescens*; Ankney and MacInnes 1978; Alisauskas and Ankney 1991) and other species that use nutritional "capital" from their body tissue to invest in female reproduction (Ankney et al. 1991). Although most birds deplete some body tissue during egg production, nutritional "income" from their diet is also used for reproduction (Carey 1996; Christians 2000). Ducks such as shovelers (*Anas clypeata*) use a combination of endogenous capital and dietary income for reproductive investment in the clutch and in incubation (MacCluskie and Sedinger 2000). It is likely that black ducks also follow this pattern by relying on dietary income to provision the clutch but retain endogenous reserves for subsequent incubation. Mass loss in incubation is relatively common among waterfowl (Ankney and MacInnes 1978; Raveling 1979; MacCluskie and Sedinger 2000), including black ducks (Reinecke et al. 1982) and mallards (Krapu 1981). This suggests that income-breeders may respond to intermittent food availability by increasing body mass, which would reduce the risk of starvation during incubation rather than support investment in eggs.

Although responses to intermittent feeding in black ducks may enhance adult survival, immediate reproductive output and survival of juveniles may be impaired. Body mass and size of females are related to early initiation of nesting in many waterfowl (e.g., Alisauskas and Ankney 1991; MacCluskie and Sedinger 2000), but the heaviest female black ducks (long-fast group) delayed nesting (Fig. 9). If time for maturation of juveniles were unchanged, fitness would be a function of variation in breeding interval and survival of juveniles and adults (Sibly and Calow 1986). Intermittent feeding would increase the breeding interval because delays in producing the first clutch would reduce the time for re-nesting and thus compromise reproductive output. Delayed hatching may also constrain juveniles because brood mortality of mallards increases with hatching date (Krapu et al. 2000), and growth is directly affected by changes in food abundance during spring and summer (Sjöberg et al. 2000). Nesting delays therefore defer reproductive investment and ultimately favor survival of the adult into the next breeding season.

Although restricted food intake can delay breeding in black ducks and mallards (Hepp 1986; Pattenden and Boag 1989), the same response to intermittent feeding indicates a direct effect of frequency of feeding on breeding because abundance or quality of food was not altered in our study. Furthermore, predictability (P) of feeding and fasting was not varied between treatment groups. Intermittent feeding altered the constancy (C) and contingency (M; Colwell 1974) of the fed and fasted states each day and therefore changed the environmental information factor ($Ie = M/C$; Wingfield et al. 1992). As Ie increases from 0 in daily feeding to 6 for short-fasts and 66 for long-fasts, environmental information becomes more important than initial cues such as photoperiod (Wingfield et al. 1992) when predicting the fed or fasted state of the animal. Consequently, reproductive commitments such as nesting and egg production may be more influenced by supplementary cues from the local environment. Photoperiod probably cues initial ovarian development in black ducks because reproductive tissue (Fig. 4) and follicle sizes were similar among groups of females in March. However, supplemental cues of feeding frequency and perhaps temperature modulate further commitments to reproduction as suggested for opportunistically breeding songbirds (Hahn 1995, 1998; Hahn et al. 1997). This suggestion of inducible development in reproductive tissues is supported by increased ovarian development in domestic chickens following dietary restriction during the growth phase (Hocking 1987). Supplemental cues from dietary changes are also used to modulate egg production and molt in domestic chickens (National Research Council 1994; Johnson 2000). Neuroendocrine links between feeding frequency, body composition and reproduction

Table 2. Mass (g, mean ± SD) of whole body and tissues in captive male and female black ducks during winter. Birds were fed each day before they were killed in January (pre-treatment, $n = 9$). Birds were killed in March after 8 weeks of the following treatments: unfasted (daily feeding, $n = 3$); fasted 2 days.week^{-1} (short fast, $n = 3$); fasted 4 days.week^{-1} (long fast, $n = 3$)

Measure	Male				Female			
	January Pretreatment	March			January Pretreatment	March		
		Daily feeding	Short fast	Long fast		Daily feeding	Short fast	Long fast
Body mass	1401 ± 49	1260 ± 12	1417 ± 110	1255 ± 156	1298 ± 158	979 ± 54	1052 ± 117	1143 ± 138
Feathers	91 ± 3	101 ± 12	94 ± 6	96 ± 4	83 ± 6	91 ± 3	87 ± 10	88 ± 8
Skin	308 ± 35	220 ± 22	317 ± 96	232 ± 93	325 ± 94	99 ± 24	164 ± 66	202 ± 77
Musculoskeleton	610 ± 23	596 ± 19	621 ± 23	582 ± 35	537 ± 32	483 ± 44	489 ± 20	514 ± 29
Breast muscle	262 ± 8	255 ± 7	258 ± 10	245 ± 20	235 ± 14	231 ± 17	231 ± 19	233 ± 13
Omental adipose	66 ± 13	27 ± 4	53 ± 24	29 ± 19	66 ± 30	1 ± 1	13 ± 11	20 ± 14
Heart	11.2 ± 1.5	9.6 ± 0.4	11.3 ± 1.0	10.1 ± 1.6	10.7 ± 1.5	8.7 ± 0.3	9.3 ± 0.5	8.8 ± 1.7
Liver	16 ± 3	18 ± 2	19 ± 1	22 ± 2	14 ± 1	16 ± 2	22 ± 2	28 ± 3
Kidney	5.3 ± 0.6	6.1 ± 0.6	6.1 ± 1.2	5.5 ± 0.4	5.1 ± 0.6	5.3 ± 0.9	6.1 ± 0.4	6.1 ± 1.2
Reproductive tract	0.3 ± 0.1	0.9 ± 0.1	2.2 ± 0.6	1.3 ± 0.1	0.2 ± 0.1	3.6 ± 1.3	6.0 ± 3.7	3.6 ± 1.9
Pancreas and spleen	4.7 ± 1.0	3.3 ± 0.7	3.2 ± 0.7	3.3 ± 0.2	4.2 ± 1.3	1.9 ± 0.3	3.3 ± 0.6	3.6 ± 0.1

Table 3. Mass (g) and nominal surface area (cm^2) of digestive tract segments (mean ± SD) in captive male and female black ducks during winter. Birds were fed each day before they were killed in January (pre-treatment, $n = 9$). Birds were killed in March after 8 weeks of the following treatments: unfasted (daily feeding, $n = 3$); fasted 2 days.week^{-1} (short fast, $n = 3$); fasted 4 days.week^{-1} (long fast, $n = 3$). (*SI* small intestine, *hindgut* is the ceca and colon)

Measure	Male				Female			
	January Pretreatment	March			January Pretreatment	March		
		Daily feeding	Short fast	Long fast		Daily feeding	Short fast	Long fast
Full tract	56 ± 9	48 ± 6	50 ± 6	50 ± 5	42 ± 3	40 ± 7	44 ± 2	55 ± 2
Gizzard tissue	29 ± 5	24 ± 3	25 ± 3	24 ± 2	21 ± 1	17 ± 3	19 ± 3	24 ± 3
Gizzard content	6.3 ± 3.6	5.9 ± 1.1	6.5 ± 1.2	5.0 ± 0.7	4.0 ± 1.4	5.9 ± 3.1	4.4 ± 0.5	6.3 ± 1.8
SI tissue	12.1 ± 1.0	9.4 ± 0.2	11.1 ± 1.8	12.3 ± 1.4	9.7 ± 1.1	10.2 ± 1.3	12.7 ± 1.4	13.8 ± 2.1
SI content	3.5 ± 1.2	4.3 ± 1.0	3.7 ± 1.0	4.6 ± 2.2	2.6 ± 1.0	2.8 ± 0.9	3.8 ± 1.3	5.8 ± 0.9
Hindgut tissue	2.8 ± 0.3	2.6 ± 0.3	2.4 ± 0.5	2.7 ± 0.3	2.3 ± 0.3	2.4 ± 0.5	2.4 ± 0.4	2.4 ± 1.0
Hindgut content	1.5 ± 0.9	1.7 ± 1.1	1.1 ± 0.5	1.5 ± 0.3	1.1 ± 0.4	1.2 ± 0.4	1.7 ± 0.4	2.4 ± 0.9
SI area	128 ± 11	115 ± 18	116 ± 3	107 ± 4	116 ± 16	112 ± 7	124 ± 8	113 ± 3
Cecal area	31 ± 5	23 ± 6	24 ± 2	19 ± 6	24 ± 8	25 ± 1	29 ± 10	22 ± 3
Colon area	14 ± 3	12 ± 1	11 ± 4	12 ± 3	13 ± 4	11 ± 2	12 ± 4	12 ± 1

await further studies of waterfowl during winter and spring.

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Appendix

This appendix comprises Tables 2 and 3.

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