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THE ROLE OF NUTRIENT RESERVES IN MALLARD REPRODUCTION

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ABSTRACT.—Mallard (*Anas platyrhynchos*) populations breeding in temperate North America obtain a significant part of the energy and lipid requirements of reproduction at sites occupied prior to arrival on the breeding grounds. Protein for egg formation, however, is obtained principally from the diet during the nesting period. Both sexes arrive heavy and fat in North Dakota but experience substantial weight loss and lipid depletion during the nesting cycle. Weight loss is most pronounced among females and averages 25% from prelaying to late incubation. Body weights of both sexes are positively correlated with carcass lipid content. The paired male draws upon lipids early in the nesting season when an activity center is being established and defended and when females are preparing to nest. The female's lipid reserves are utilized primarily during laying and early incubation. The significance of lipid reserves diminishes as the nesting season progresses, and females do not acquire substantial lipid stores prior to renesting when the initial clutch is destroyed. The magnitude of lipid reserves carried in female carcasses is positively correlated with clutch size from mid-April to early June. Protein transfer for egg formation from flight and leg muscle and body organs can account for only a small part of the protein requirement for the clutch. By utilizing lipid reserves to meet energy requirements, the female can acquire sufficient protein from the diet to produce a large initial clutch even when foods are relatively scarce, whereas the renesting female must rely entirely upon food resources available at the breeding site for its nutrient and energy requirements. *Received 3 January 1980, accepted 18 July 1980.*

REPRODUCTION by waterfowl requires a substantial allocation of nutrients, especially lipids and protein, to form eggs. Egg and yolk size are proportionately large in comparison to body size in Anatidae (Lack 1968), and the daily maximum cost of egg production has been estimated to be 52–70% of daily energy intake at constant body weight (King 1973). Nutrients for reproduction must be either drawn from body reserves or obtained from food resources at the time of breeding, or both. Among arctic-nesting geese that breed in environments where food is scarce at the time of nesting, it has been shown that stored nutrient reserves contribute substantially to reproduction (Hanson 1962, Barry 1962, Ankney and MacInnes 1978, Raveling 1979).

Although the Mallard is one of the most extensively studied waterfowl species in the world and many aspects of its biology are well known, nutrient dynamics during reproduction remain poorly understood. This paper, based upon findings from studies conducted during 1974–1977, describes the magnitude of lipid reserves carried to the breeding grounds, identifies their utilization patterns during the breeding cycle, and considers the significance of lipid and other nutrient reserves to clutch size and the life cycle of the species.

METHODS

Dispersed pairs of breeding Mallards formed the sample for weight and lipid measurements. These birds were captured or collected in prairie pothole habitat within a radius of 160 km of Jamestown, North Dakota, from spring arrival to termination of nesting. Body weights were obtained for 95 males and 151 females from individuals either collected for nutrient analyses, captured by rocket netting for telemetry research, or live-trapped at nest sites using a remote-controlled capture technique described by Shaiffer and Krapu (1978). Lipid and other measurements were taken of 43 males and 71 females collected

during 1974–77. Stage of incubation was determined for 27 females by backdating from hatching date; two eggs were removed from each clutch and placed in a mechanical incubator on the same date a female was captured and weighed. Total body weight (wet) of collected specimens was measured on a Pennsylvania scale to the nearest gram (g). Live-trapped specimens were weighed in the field using a Salter suspended scale calibrated to the nearest 5 g.

Collected males and females were plucked in the laboratory in preparation for lipid extraction. The ovary and oviduct of each female were removed, weighed to the nearest 0.1 g on a triple-beam balance, and examined to determine reproductive status. Criteria used to classify reproductive status are as follows: prelaying—from arrival to ovulation, laying—from ovulation of the first ovum to oviposition of the last egg of the clutch, and incubation—female brooding clutch. The prelaying stage includes two phases, i.e. prenesting and rapid follicular development. A prenesting status was assigned to dispersed pairs in early spring with ovary weights <3.0 g and rapid follicular development to pre-ovulating females with ovary weights ≥ 3.0 g. Renesting females in rapid follicular development were identified by the presence of a brood patch acquired during a previous nesting attempt. The gizzard, heart, liver, flight muscle (pectoralis and supracoracoideus), and leg muscle were removed from the carcasses of both sexes and weighed separately wet to the nearest 0.1 g on a triple-beam balance. Fat adhering to the viscera was removed and included in the lipid analyses. Body components were stored in sealed plastic bags in airtight containers at -20°C . Preceding lipid extraction, samples were dried for 6 h at a temperature of 105°C . Lipid extraction was performed on homogenized and dried samples by the Soxhlet process using petroleum ether and following procedures recommended by Horwitz (1975).

The level of feeding activity by female Mallards during reproduction was measured using radio-telemetry and time-budget techniques as described by Dwyer et al. (1979). Clutch-size measurements are from completed clutches laid by wild females in south central North Dakota during 1974–1976. Clutch sizes were segregated and averaged for each 10-day period by date of nest initiation; these periods were 11–20 April, 21–30 April, 1–10 May, 11–20 May, 21–30 May, and 31 May–9 June. Date of nest initiation was determined by identifying stage of incubation using the field candling technique described by Weller (1956) and backdating to date the first egg was laid.

RESULTS

Breeding phenology.—Widespread dispersal of Mallard pairs into prairie pothole habitat of south-central and eastern North Dakota typically begins during late March and early April. Timing of dispersal and establishment of activity centers differs between years in response to unstable and variable weather conditions during late March and April. Significant nesting activity is underway by mid-April during years when weather conditions are favorable, but when daytime maximum temperatures remain below 10°C and snow cover is present, the onset of laying is delayed accordingly (Krapu and Doty 1979).

Laying was in progress by 16 April, 26 April, 10 April, and 17 April during 1974–1977, respectively. Five monitored nests hatched 25 days following deposition of the last egg of the clutch in the nest. First sightings of broods during 1974–1977 occurred on 28 May, 1 June, 22 May, and 19 May.

Body weight.—Both sexes are heavy at arrival on the breeding grounds but undergo a marked decline in weight during the course of the nesting season, with females experiencing a greater weight loss (Fig. 1). Average weight losses among paired males and females were 94 g and 217 g, respectively, from mid-April to late May.

Female body weight changed with reproductive stage (Table 1); a significant increase occurred from prelaying to laying ($P < 0.01$), followed by a highly significant decline during incubation ($P < 0.001$). The 101-g increase in mean body weight of females from prelaying to laying reflects the added weight of a mature or fully developed ovary and oviduct (Table 1) and the presence of an egg in the oviduct of most laying females. The female body weight curve during incubation (Fig. 2)

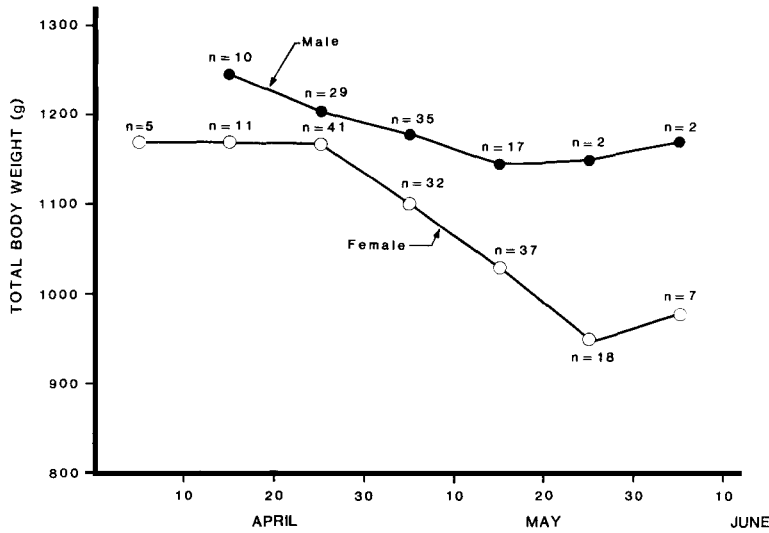


Fig. 1. Mean body weights of breeding male and female Mallards in North Dakota by 10-day intervals during the nesting season.

reflects atrophy of reproductive organs during the first week (Table 1), followed by a gradual leveling off as lipid reserves are depleted. By late incubation, females are highly emaciated; 11 live-trapped females weighed during the last 5 days of incubation averaged 900.3 ± 30.1 g (mean \pm SD), or 25% less than during prelaying. Reduced female feeding activity during incubation probably contributes to weight loss. Observations from five radio-marked incubating females indicated that all regularly left the nest to forage during incubation. Two radio-marked females monitored closely during incubation fed an estimated 1 h daily, whereas layers fed approximately 8 h. The loss of body weight that occurred between the laying and incubation periods was statistically significant ($P < 0.001$) and due primarily to the diminished size of lipid reserves and reproductive organs (Table 1). The general trend of decreasing body weight observed during May among sampled specimens (Fig. 1) reflects the rising proportion of females either in an advanced stage of nesting (laying or incubation) or having previously made one or more unsuccessful nesting attempts.

TABLE 1. Changes in body, tissue, and organ weights and total lipids of females in relation to breeding status. Sample sizes are in parentheses.

Weight (g)	Prelaying (mean \pm SD)	P^b	Laying (mean \pm SD)	P	Incubation ^a (mean \pm SD)
Body	1,199.8 \pm 78.0 (19)	**	1,300.6 \pm 114.6 (10)	***	967.3 \pm 44.5 (3)
Flight muscle ^c	65.1 \pm 5.6 (19)	NS	65.1 \pm 5.5 (11)	NS	58.3 \pm 1.9 (3)
Leg muscle ^c	27.4 \pm 3.1 (14)	NS	27.2 \pm 5.4 (5)	NS	24.8 \pm 5.9 (3)
Total lipids	109.6 \pm 33.7 (17)	*	79.6 \pm 37.2 (11)	*	17.1 \pm 14.7 (3)
Gizzard	33.7 \pm 6.9 (18)	NS	28.6 \pm 4.3 (7)	*	21.7 \pm 1.1 (3)
Heart	13.4 \pm 2.3 (18)	NS	14.2 \pm 2.7 (11)	NS	11.1 \pm 1.3 (3)
Liver	30.4 \pm 6.4 (19)	NS	31.3 \pm 5.7 (11)	NS	27.1 \pm 4.6 (3)
Ovary	6.3 \pm 8.7 (17)	***	31.9 \pm 8.0 (8)	***	1.8 \pm 0.8 (3)
Oviduct	13.5 \pm 9.5 (19)	***	32.1 \pm 5.0 (10)	***	7.2 \pm 1.3 (3)

^a Females were collected on day 6 of incubation.

^b P = significance level of t -test between means in adjacent columns. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; NS indicates $P > 0.05$.

^c Lipid-free dry weight; other measurements are on a wet weight basis.

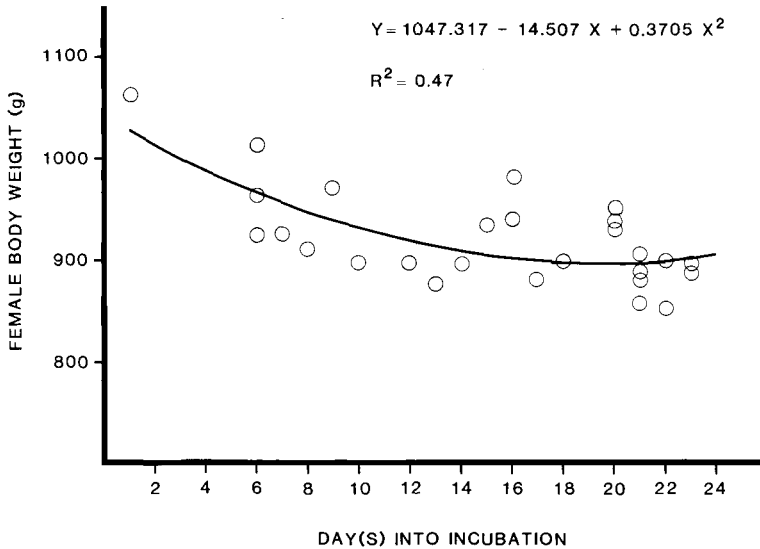


Fig. 2. Body weight curve of female Mallards in relation to stage of incubation.

The correlation coefficients of female and male body weights with total carcass lipids were highly significant ($r = 0.60$, 69 df, $P < 0.001$) and significant ($r = 0.48$, 41 df, $P < 0.01$), respectively.

Lipid reserves.—Both sexes arrive on the breeding grounds with substantial lipid reserves. Lipid levels of 4 paired males and 6 paired females collected during the 1–15 April period averaged 85.7 ± 58.3 g and 108.9 ± 36.5 g lipids, respectively. Lipid content among pair members declined rapidly as the breeding season progressed; lipids were largely exhausted by late May (Fig. 3). Lipid reserves of the male were utilized rapidly during the period in which activity centers were being established, whereas female utilization of lipids tended to lag behind the male, although ultimately falling to a lower level. The higher lipid levels of paired female 8 (Fig. 3) reflects that this bird was about to begin laying, and lipid reserves remained largely intact.

Lipid reserves change with reproductive status (Table 1). Seven prenesting females collected shortly after arrival carried lipid depots that averaged 109.2 ± 42.5 g. Lipid content in female carcasses did not decline significantly with growing ovary weight during the rapid follicular development phase (Fig. 4A). Substantial lipid utilization, however, occurred during the laying stage, and body lipid content was negatively correlated with number of ruptured ovarian follicles (Fig. 4B). Loss of lipids from laying (an average of 4 eggs had been laid by females in the sample) to day 6 of incubation averaged 63 g, or 57% of the lipid reserves present during prenesting (Table 1). Body weights and total lipid content of incubating females suggest that lipid reserves typically are exhausted by hatching date. Females rely upon lipids for only part of the energy requirements during incubation. Two radio-marked individuals monitored intensively throughout incubation averaged 2.6 h off the nest daily of which an estimated 38% was spent feeding.

Female lipid reserves and clutch size exhibited similar trends from mid-April to early June (Table 2). The magnitude of lipid reserves in female carcasses was pos-

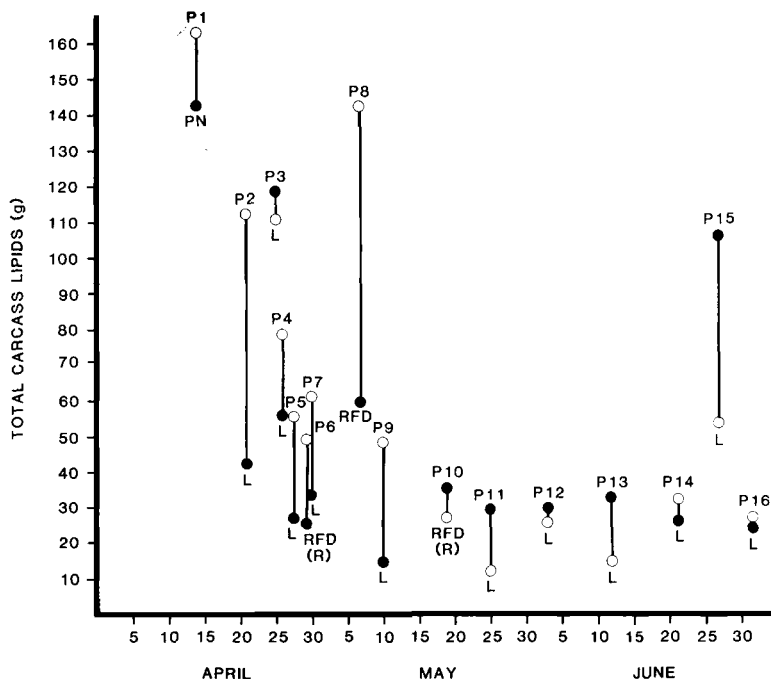


Fig. 3. Lipid reserves of individual Mallard pairs are compared by date and reproductive status. Females are denoted by open circles and males by solid circles. Reproductive categories are as follows: prenesting (PN), rapid follicular development (RFD), and laying (L). (R) denotes females known to be initiating renesting attempts.

itively correlated with clutch size when analyzed by 10-day interval during the nesting season ($r = 0.98$, 4 df, $P < 0.01$).

Labile protein reserves.—Female Mallards apparently obtain only a small part of the protein required to produce a clutch and for growth of reproductive organs from stored reserves. Lipid-free dry weight of flight muscle did not decline significantly during rapid follicular development (Fig. 4C) or during laying (Fig. 4D), and most change occurred during incubation. The lipid-free dry weight of leg muscle exhibited a pattern similar to flight muscle (Table 1).

Some additional protein may be available for ovarian and oviduct growth from other body tissues. The gizzard is the most probable source of significant protein for egg production from among body organs; the weight of this organ declined significantly ($P < 0.05$) from laying to incubation, while other organs exhibited only minor weight loss (Table 1). Gizzards of males and females were of comparable weight at arrival, but those of paired females collected from late April to early July weighed significantly less than did those of their mates, i.e. 36.1 ± 4.2 g versus 28.5 ± 7.4 g, respectively ($P < 0.01$). Why gizzards of females undergo greater muscle atrophy during the nesting season is uncertain. It may be caused by a higher proportion of animal matter in the diet, reduced feeding during incubation, protein mobilization for egg formation, or a combination of these factors. A decline in gizzard weight during nesting has been reported previously in female Lesser Snow Geese (*Chen caerulescens*) (Ankney 1977), Canada Geese (Raveling 1979), Common Eider (*So-*

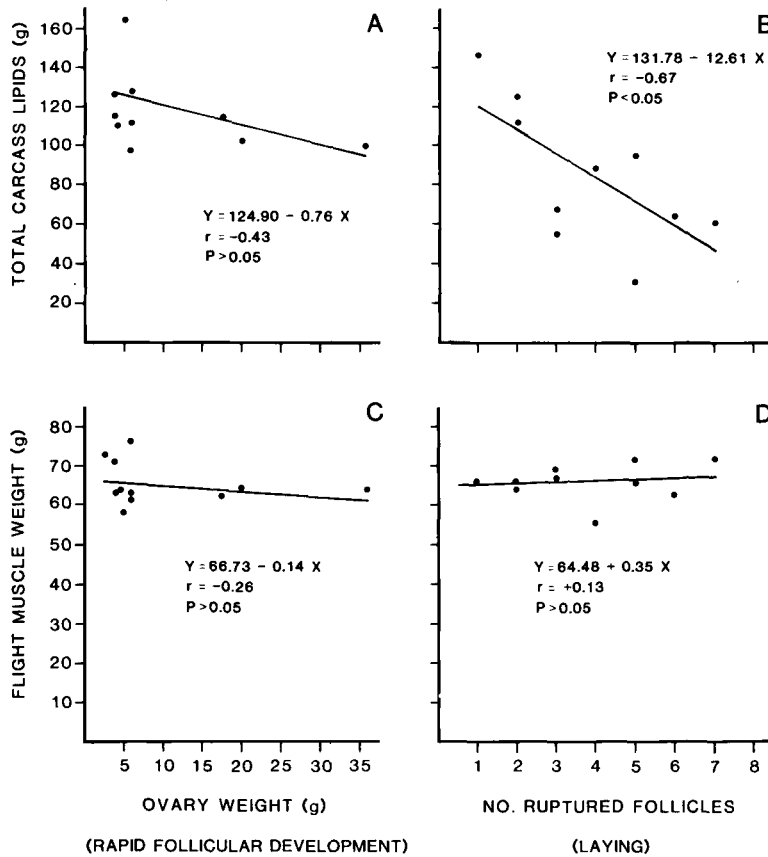


Fig. 4. Total carcass lipid content and lipid-free dry weight of flight muscle of female Mallards are plotted in relation to ovary weight (A,C) and number of ovulated follicles (B,D) during rapid follicular development and laying, respectively.

materia mollissima) (Korschgen 1977), Black Duck (*Anas rubripes*) (Reinecke 1977), and Wood Duck (*Aix sponsa*) (Drobney 1977).

The protein content of the gizzard increases linearly with wet weight in the Common Eider (Korschgen 1977). Applying his findings to Mallards, I found that approximately 4 g of gizzard protein is expended during the prenesting to incubation interval and may be available for egg formation. A wild Mallard clutch laid during 11–20 April averages 11 eggs (Table 2) and contains approximately 69 g of protein

TABLE 2. Clutch size (mean \pm SD) and carcass lipid reserves of female Mallards are compared during six 10-day intervals from 11 April–9 June. Sample sizes are in parentheses.

Trait	Time interval					
	1	2	3	4	5	6
Clutch size	11.1 \pm 0.9 (35)	10.4 \pm 1.7 (67)	9.1 \pm 1.2 (66)	9.4 \pm 2.0 (35)	8.6 \pm 1.3 (25)	7.8 \pm 1.1 (13)
Total lipids ^a	115.5 \pm 42.1 (6)	96.0 \pm 38.1 (22)	57.9 \pm 33.3 (10)	55.4 \pm 27.0 (13)	20.7 \pm 13.7 (6)	12.0 \pm 4.8 (6)

^a Measurements are expressed in g.

TABLE 3. A comparison of body, tissue, certain organ weights, and total carcass lipids of female Mallards in the rapid follicular development phase of initial and renesting attempts.

Weight	Nesting attempt				<i>t</i>	<i>P</i>
	Initial		Renest			
	$\bar{x} \pm \text{SD}$	<i>n</i>	$\bar{x} \pm \text{SD}$	<i>n</i>		
Body	1,217.8 \pm 79.4 ^a	11	1,065.4 \pm 54.6	7	4.43	<0.001
Flight muscle ^b	65.3 \pm 5.6	11	60.0 \pm 1.9	7	2.35	<0.05
Total lipids	116.4 \pm 18.9	10	29.9 \pm 17.4	7	9.59	<0.001
Gizzard	32.5 \pm 6.3	10	21.8 \pm 1.1	2	2.31	<0.05
Heart	14.3 \pm 2.1	11	12.8 \pm 1.9	7	1.51	>0.10
Liver	32.4 \pm 7.4	11	31.8 \pm 6.8	7	0.17	>0.10

^a All weight measurements are expressed in g.^b These data are expressed as lipid-free dry weight; other measurements are wet weight values.

(Krapu unpubl. data). If it is assumed that some labile protein is drawn from the body musculature and gizzard to supply egg protein, a reasonable assumption based on the findings in other species (Jones and Ward 1976, Ankney and MacInnes 1978, Raveling 1979), then a major part of the protein needs of female Mallards must still be met from food sources available at the time of breeding.

Status of nutrient reserves during renesting.—Body, tissue, and certain organ weights of females changed markedly from initial to later nesting attempts. Body weight loss between initial and renesting attempts was highly significant ($P < 0.001$) and averaged 152 g (Table 3); approximately 57% of the decrease came from the depletion of lipid reserves. Lipid content in carcasses of females about to renest averaged 74% less than among females initiating the first nest; this change was highly significant ($P < 0.001$). These data indicate that females do not store substantial amounts of lipids prior to renesting but rather that energy requirements are acquired largely from the diet at the time the clutch is produced. Lipid reserves of the male are also depleted by the time of renesting (Fig. 3). Lipid-free dry weight of flight muscle averaged 5.3 g less among renesting females, probably reflecting weight loss associated with incubation of the previous clutch. Gizzard weight was reduced by 33% among renesters, but the sample size was small (Table 3); neither the heart nor liver weight changed significantly ($P > 0.10$).

DISCUSSION

Body-weight trends of male and female Mallards breeding in North Dakota compare favorably with spring weights reported by Folk et al. (1966) in Czechoslovakia. Females in both areas are heavy at the onset of the nesting season and experience a marked decline in body weight between April and June. In the case of males, some decline in body weight was evident at both locations from April to May. In Czechoslovakia, a marked rise in body weight of males occurred between May and June. My data are scant for the late May–June period but suggest a similar trend. At both sites, lipid utilization presumably is responsible for a major part of the observed declines in body weight.

Lipid reserves carried to the breeding grounds contribute substantially to the needs of Mallard pairs during reproduction. Lipid depots reduce the food intake necessary to satisfy male energy requirements, thus permitting increased attentiveness to the female during a period of intensive foraging to meet nutrient requirements for egg formation. Using time-budget analyses, Dwyer et al. (1979) reported that

male and female Mallards spent 20 and 55% of the daylight hours, respectively, foraging during the laying period. The energy requirement of a male is particularly high during the establishment of an activity center early in the nesting period when food resources are being partitioned among pairs. Flight is the most energy-intensive activity (Owen and Reinecke 1979), and the frequency of pursuit flights by males is highest during the prenesting period, with the duration of flights increasing slightly during laying (Titman 1973). Pursuit flights and other aggressive behaviors associated with defense of the pair's activity center probably account for the utilization of a significant part of the male's lipid reserves during late April and early May, particularly when high population densities lead to intense intraspecific competition. Male attentiveness to the female during the period of egg formation increases the amount of time she can actively forage and lowers the probability of her falling victim to a predator; both factors enhance recruitment. Findings presented in this paper suggest that a major part of the lipid reserves of the female are utilized during the laying stage, presumably to form yolk in developing follicles and as an energy source for securing protein-rich foods. On a daily energy-intake basis early in the nesting season, the energy cost for egg formation in free-living populations of Mallards is less than the maximum rate of 52–70% estimated by King (1973) for females at constant weight because of the substantial contribution of stored lipids.

The initiation of nesting by Mallards appears to be timed to coincide with access to adequate protein-rich food resources to meet needs for egg formation. Food resources apparently must reach a certain threshold level on the breeding grounds before nesting will occur given the need for significant intake of dietary protein. My data suggest that mobilization of labile protein reserves from the sarcoplasm of flight muscle, as described for the Red-billed Quelea (*Quelea quelea*) by Kendall et al. (1973) and Jones and Ward (1976), or from other tissues can account for only part of the protein required by female Mallards to form the initial clutch of eggs. Protein utilized in egg formation by Mallards apparently is obtained principally from the diet. It has been shown that female Mallards forage principally on invertebrates during the laying period (Swanson et al. 1979). Female Pintails and Wood Ducks similarly obtain protein needs for egg formation primarily through dietary intake rather than endogenous reserves (Krapu 1974, Drobney 1977).

An adaptive advantage of endogenous lipid reserves in early spring is that females can forage for scarce aquatic invertebrates of high protein content for long periods, even though searching for these foods is energetically inefficient in comparison to foraging on waste grains available on agricultural lands. Female Mallards experimentally confronted with low protein plant diets of the type now available on agricultural lands in early spring continued to lay, but at reduced rates, and produced eggs with lower hatchability rates than did females feeding on a protein-rich diet (Krapu 1979). This relationship implies that access to animal matter during the nesting season favors higher recruitment rates both by increasing the probability of a female continuing to renest until successful and by producing more offspring when successful because of a larger clutch size and higher hatch rate. Invertebrate intake by females provides a more balanced ration of calcium and the essential amino acids that form egg constituents (Krapu and Swanson 1975).

When compared by 10-day interval, the positive correlation between the magnitude of female lipid reserves and the number of eggs laid by females suggests that clutch size is moderated by the magnitude of stored lipids. A positive correlation

between potential clutch size and nutrient reserves available at the onset of laying has been reported for the female Lesser Snow Goose (Ankney and MacInnes 1978). In this species, feeding declines to a low level during laying (Ankney 1977), in contrast to the Mallard, which forages actively during the laying period (Dwyer et al. 1979). Clutch size and laying date in the Mallard presumably are under significant genetic control, as suggested by Batt and Prince (1979), with lipid reserves being an adaptive mechanism that allows the female to acquire adequate nutrient resources to produce a clutch of optimum size. The decline in clutch size that occurs as the nesting season progresses appears to be related to the exhaustion of lipid reserves. Ricklefs (1974) indicated that when energy deprivation to the female does occur, the size and quality of the eggs are not altered appreciably, only the number.

Age influences the magnitude of lipid reserves carried by Mallards during the nesting season. This difference may result because inexperienced yearlings are less efficient at capturing invertebrate prey, which leads to more rapid lipid utilization. Subtle differences in physical condition, timing of nesting, and clutch size that have been detected between yearling and adult female Mallards suggest that adults can better cope with unfavorable environmental conditions existing at the breeding site. Compared to yearlings, adult wild female Mallards tend to carry more lipids, to lay larger clutches, and to initiate laying earlier (Krapu and Doty 1979).

Stored lipids appear to moderate clutch size through their influence on female capacity to secure protein needs. When lipid reserves are expended, the energy costs associated with female foraging efforts to secure protein are no longer met from fat depots, which increases the energy requirement that must be met from the diet during the period of egg formation and presumably intensifies the impact of protein on clutch size. Drobney (1977), working with Wood Ducks, concluded that the availability of protein was most likely to limit clutch size. His conclusion was based upon the facts that protein requirements were high, the foraging effort needed to acquire protein was extensive, and protein is stored in only limited quantities. In the case of the Mallard, protein intake presumably limits clutch size, with lipid reserves providing the energy resources necessary for the female to acquire the invertebrate foods and protein needs for the initial clutch under all but the most severe environmental conditions. Clutches laid by renesting females, however, are largely the product of the food-resource base available on the breeding grounds. Therefore, while most females lay a clutch during most years, the level of renesting activity can be expected to vary widely among years in response to the status of food resources available in wetlands at the breeding site.

ACKNOWLEDGMENTS

I thank D. G. Jorde and S. Stewart for assistance in processing the carcasses of collected specimens, C. W. Shaiffer for support in live-trapping birds, L. M. Cowardin and D. S. Gilmer for making available data on body weights, G. A. Swanson for providing additional specimens for carcass lipid analysis, V. A. Adomaitis and J. A. Shoesmith for conducting lipid analyses, and D. H. Johnson for aid in statistical analyses. I am grateful to C. D. Ankney, R. D. Drobney, W. R. Goforth, D. H. Johnson, D. G. Raveling, K. J. Reinecke, and M. W. Weller for critically reviewing earlier drafts of this manuscript.

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