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UNIVERSITY OF ALBERTA

**THE USE OF FEED RESTRICTION FOR IMPROVING REPRODUCTIVE
TRAITS IN MALE-LINE LARGE WHITE TURKEY HENS**

BY

ROBERT A. RENEMA



A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

IN

ANIMAL PRODUCTION

DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA

FALL 1993



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ISBN 0-315-88414-2

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REPRODUCTIVE TRAITS IN MALE-LINE
LARGE WHITE TURKEY HENS
DEGREE: MASTER OF SCIENCE
YEAR THIS DEGREE GRANTED: FALL 1993

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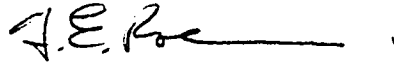
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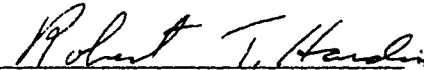
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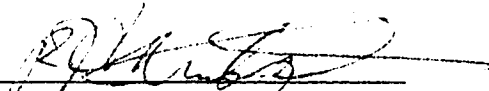
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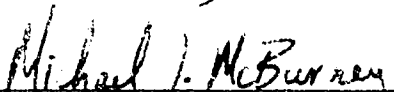
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ABSTRACT

Turkey breeding stock consists of male-lines, which contribute the growth and carcass traits, and female lines, which contribute the reproductive traits. A negative relationship exists between increased body size and reproductive efficiency in turkeys. The influence of feed allowance to male-line Large White breeder hens during rearing was investigated in terms of effects on growth curves, body composition, reproductive morphology and egg production. A flock of 200 poults was reared under four treatments based on qualitative or quantitative feed restriction from 4 to 28 wk of age as follows: full-fed controls (FF), low protein diet (12% C.P. from 12 to 28 wk; LP), and reduced BW (10 or 20% lower BW than FF; R10 and R20). At photo-stimulation (28 wk), all birds were fed a commercial breeder diet *ad libitum* for the remainder of the study (48 wk of age). Statistical significance was based on testing at the .05 level.

BW differed between treatments during most of rearing. LP birds were similar in BW to the R10 birds at 28 wk of age. By 40 wk of age in the breeder period, growth curves of all treatments became similar, with the R20 group having lower BW. Frame size was reduced by feed restriction. Feed restriction reduced breast muscle and abdominal fatpad weight early in lay, except for the LP group, which had heavier fatpads. Liver lipid content increased throughout the breeder period. Changes in liver weight followed the pattern of BW changes. Total carcass protein content changes in time reflected breast muscle mass changes. In R20 treatment birds, carcass lipid content was reduced, and ash content increased.

Sexual maturity was delayed in the R20 treatment. Settable egg production values (eggs per hen) to 48 wk for all hens, and those in lay were: FF, 9.4 (48.6); LP, 42.7 (51.7); R10, 41.4 (52.8); R20 40.7 (55.4). At first egg there were an average of 4.9 unreconciled post-ovulatory follicles per hen in all treatments. Differences in egg number within a treatment reflect a reduced persistency of lay in the R10 and R20 treatments. Feed restriction treatments demonstrated a trend towards reduced large follicle numbers on the ovary, proportion of multiple ovulations, and incidence of double yolked eggs. The proportion of yolk and shell in the egg, and egg specific gravity were

improved with feed restriction. Sequence length was longer in the R20 treatment, and pause length was shortened in the R10 and R20 treatments. The proportion of multiple follicle sets was reduced in the R10 and R20 treatments, and the R20 treatment had the highest egg production rate in early lay. These results indicate that feed restriction can alter body composition in a way that is beneficial to reproductive traits. Quantitative restriction during rearing reduced body weight, altered body composition, and improved reproductive traits most effectively. The R20 treatment had the most positive results, and would be the recommended feed restriction treatment for male-line turkey breeder hen candidates during the rearing period.

ACKNOWLEDGMENTS

This thesis would not have been completed without the love and support of many. I would like to thank God for giving me the abilities needed to handle this program. Stephanie, my wife, is deserving of a lot of praise for the work she has done. This thesis could not have been written without Stephanie taking over the bulk of my responsibilities so that I could concentrate on what had to be done. Her encouragement for my progress, and patience with my busyness kept me going. I really appreciated her pride in me. Jeremy, our son, also deserves thanks for his distractions, and joy that I was home, even if I was a fixture in the office. I am grateful to my parents for teaching me to work hard at what I do, and to take pride in it. Dr. Frank Robinson is a good friend and supervisor. He was always enthusiastic, and knew the perfect balance between encouragement and expectation to make me work well. I would like to thank Dr. R. T. Hardin for the productive hours in his office working through my statistical problems. I thank Dr. F. X. Ahern and Dr. R. J. Christopherson for serving on my M. Sc. committee, and for being available for me. Dr. L. Bagley and R. Walker of Hybrid Turkeys Inc. were always good to talk to because of their enthusiasm for the project and seemingly endless knowledge of the turkey.

The laboratory work was completed with the training and assistance of Ms. P. Marceau, and Ms. R. Niskala. I am indebted to Ms. F. Dennis and the staff of the University of Alberta Poultry Research Center for the hours they spent preparing for these birds, and keeping them weighed and well.

This work was supported in part by the Natural Sciences and Engineering Research Council of Canada (NSERC), Hybrid Turkeys Inc., Central Soya of Canada, the Alberta Agricultural Research Institute, the Canadian Turkey Marketing Agency, and the University of Alberta Poultry Research Center.

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I. INTRODUCTION

The domestication of the turkey (*Meleagris gallopavo*) is believed to have occurred very recently. Current evidence points to domesticated birds existing in Mexico between 200 B.C. and A.D. 700 (Crawford, 1990). In the early 1500's the turkey had been introduced to Europe by the Spanish Conquistadors to be bred for meat production. In the 1600's, European settlers to eastern North America brought turkeys with them as a food source. They discovered that their domestic hens would occasionally be bred by eastern wild turkey toms, giving rise to a bird that was much larger than either parent. These crossbred turkeys, with their superior size and vigor, became the foundation of the domestic turkey stock, and eventually evolved into the modern broad-breasted type (Crawford, 1990).

During the 1930's, the poultry breeding industry developed a planned approach to poultry development. Turkey breeders began to consider genetic traits such as body weight, vigor, breast muscle size, egg production and parenting abilities in their selection programs (Cline, 1936; Singh, 1993). Although the primary selection pressure in the 1930's was geared towards keeping the birds small (Cline, 1936), the emphasis began to shift towards increased body weight. Figure I-1 demonstrates the increase that has been accomplished in 18 week body weight of toms from 1982 to 1990 (Sell, 1990). These values were compiled from production records from all flocks processed in North America in those years. The increase in the incremental gains in the late 1980's is due to the introduction of several larger turkey strains (Nixey, 1989). The rate of genetic change has been estimated at 3 percent per year in broilers (McCarthy and Siegel, 1983), and slightly lower for turkeys. In the late 1980's, turkey body weight changes became even more pronounced, with change near 4 percent each year (Sell, 1990).

Genetic selection has vastly improved growth rate and feed conversion. Broiler chickens can now reach a market weight of 1800-2000 g at one half the age possible 35 years ago (Siegel and Dunnington, 1985). In turkeys, the feed conversion ratio has dropped from 6:1 to as low as 2:1 in the same time period (Singh, 1993). As well, market age has decreased and body weights have

increased dramatically. In meat-type chickens, these improvements in growth parameters have been found to be most directly related to increased feed and water intake (Marks, 1980). Birds eat near gut capacity (Barbato *et al.*, 1984), resulting in growth selected birds being fatter than non-selected strains (Chambers *et al.*, 1981). Excess fat deposition in fast growing birds has been observed to be detrimental to feed efficiency (Brody, 1935), due to the high energy density of fat.

Turkey hens are very similar to broilers with their large appetites and potential to store excess fat. Obesity in broiler breeders is generally associated with reduced egg production, fertility and hatchability (Wilson and Harms, 1986). In a similar fashion, increased body size and growth rates in turkey breeders have detrimental effects on reproductive traits. A negative correlation has been observed between body weight and egg production in broiler breeders (Siegel and Dunnington, 1985), Japanese quail (Marks, 1979, 1985) and turkeys (Nestor, 1971). McCartney *et al.* (1968) found the genetic correlation between 24 week body weight and egg production of turkeys to be $-.14$ after four generations of body weight selection from a random bred population. Heritabilities for egg production are low, ranging from $.10$ to $.21$ (Nestor *et al.*, 1987), while body weight heritabilities are approximately $.40$ (McCartney *et al.*, 1968).

The presence of excess ova on the ovaries of growth selected birds play a role in their lower egg production. When comparing heavy to light weight lines, the heavy lines consistently have a greater number of ovarian follicles in both turkeys (Nestor *et al.*, 1970, 1980, 1981; Bacon *et al.*, 1972; Hocking, 1992a) and broiler breeders (Udale *et al.*, 1972; Reddy and Siegel, 1976). Further increases are seen with early photostimulation (Hocking *et al.*, 1988). With increased follicle numbers, the production of two or more ovulable follicles is more likely to occur (Hocking, 1992a, 1992b; Nestor *et al.*, 1980), which results in lowered egg numbers through the production of defective or shell-less eggs (Jaap and Muir, 1968; van Middelkoop, 1971; Bacon *et al.*, 1972; Nestor and Bacon, 1972;). Growth selected lines of chickens have also been observed to have a decreased gonadotrophin secretion capacity and a decreased gonadal sensitivity to pituitary extracts as compared to low body weight lines (Van Krey and Siegel, 1968). Decreased progesterone production capacity in large ovarian follicles has been observed in chickens selected for growth rate

as compared to birds selected for improved feed efficiency and decreased fat content (Decuypere *et al.*, 1993).

Increased follicle numbers and decreased hormone secretions are a perplexing side effect of genetic selection for body size. An understanding of the function of the reproductive system and control of the ovulatory cycle in the turkey can contribute to the understanding of the mechanisms of abnormal reproductive events.

The Ovulatory Cycle and Egg Production

Ovary Morphology and Follicular Growth

The single functional ovary of the turkey lies in the left, cranial region of the abdominal cavity just anterior to the left kidney and caudal to the left lung (Burke, 1984; Gilbert and Wells, 1984). The cortex of the ovary contains the follicles, while the medulla beneath it contains the rich vasculature and nervous tissue associated with the ovary (King and McLelland, 1984). Preovulatory follicles are arranged in a hierarchy of size, and represent the majority of the ovary weight. The ovary of an egg-type chicken contains 6-8 large follicles of 10 mm or greater in diameter (Gilbert, 1971). A turkey in peak production has 9-10 large yellow follicles (LYF) (Sharp, 1989). These follicles are usually identified according to size and proximity to ovulation (F1-F7) with the largest follicle being called F1. The ovary also contains many small follicles, with up to 2,500 visible to the naked eye (Gilbert, 1971), and 12,000 with a light microscope. The small follicles on the ovary were classified by Robinson and Etches (1986) as small white (SWF, <1 mm), large white (LWF, 2-3 mm), and small yellow (SYF, 5-10 mm). In the domestic hen, there are several thousand SWF, 10-20 LWF and about 5-10 SYF (Robinson, 1986). Follicles are thought to be recruited from the slow growing phase of the small follicles into the rapid growth phase of the large follicles soon after the largest follicle has been ovulated. It is likely, however, that the hierarchy exists functionally down to the level of follicles 1-3 mm in diameter, as demonstrated by their orderly system of growth, so recruitment must be occurring at this level (Gilbert and Wells, 1984). The mechanism for

follicular recruitment is not known, but has been shown to occur within a restricted period of the day (Zakaria *et al.*, 1984), which suggests the regulatory mechanisms of the ovulatory cycle are involved. The majority of follicles undergoing atresia will do so in the slow growing phases (Gilbert *et al.*, 1983). Once part of the LYF hierarchy, they will likely ovulate if standard ovarian conditions prevail.

The preovulatory follicle consists of an oocyte and its' surrounding layers. Immediately surrounding the oocyte is the perivitelline layer, whose fibrous mesh contains the mass of yolk material upon ovulation (Gilbert and Wells, 1984). A layer of granulosa cells surround the perivitelline layer, and have contact with the underlying yolk through cellular processes (Burke, 1984; Gilbert and Wells, 1984). The theca interna and theca externa are the next layers encountered. Large numbers of terminal capillaries are situated in the theca interna from which the yolk precursors are obtained (Moran, 1987). The theca externa is well vascularized and innervated, and contains many collagen fibers (Gilbert and Wells, 1984; King and McLelland, 1984). The granulosa and thecal layers are the primary regions of steroidogenesis. An outer tunic of connective tissue containing the major blood vessels covers everything except the stigma, an avascular area where follicular rupture occurs during ovulation (Burke, 1984).

The vast majority of follicular growth occurs when the yellow yolky material is being added to the oocyte. The majority of the yolk components are synthesized in the liver (Leveille *et al.*, 1975), and transported to theca interna cells in the blood plasma. A filtering process occurs as the smaller materials are allowed to pass on to the granulosa cells. Once in contact with the surface of the oocyte, components are incorporated through receptor-mediated endocytosis (Gilbert and Wells, 1984; King and McLelland, 1984). Very low density lipoproteins (VLDL) are the major precursor of yellow yolk, making up about 45% of turkey egg yolks (Bacon, 1986). Due to the yolk lipoprotein being metabolized differently than normal VLDL, it is target specific for ovarian uptake rather than for fat deposition (Bacon, 1981; Burley *et al.*, 1993). The increased number of follicles in meat-type turkeys is not the result of increased plasma VLDL levels (Bacon *et al.*, 1973). The combined growth rate of SWF and LWF has been estimated at 1 mm per day (Gilbert and Wells,

1984). The size of the follicle upon transfer into the rapid growth phase is between .6 g (Bacon *et al.*, 1972) and .7 g (Zakaria *et al.*, 1984). The time required for a follicle to go through the yellow-yolky stage has been estimated at 11-13 days in the turkey (Bacon and Chermis, 1968; Bacon *et al.*, 1972; Hocking *et al.*, 1987b), and 7-11 days for chickens (Gilbert, 1971; Grau, 1976).

Ovulation of the mature F1 follicle occurs as a result of a response to hormonal interactions. The ovum enters the oviduct through the infundibulum, whose thin, lightly muscularized tissue acts as a funnel to direct the ova into the oviduct. It is very motile near the time of ovulation, and it engulfs a follicle even before its release (Burke, 1984). Fertilization occurs in the infundibulum. Secretion of albumen takes place in the second portion of the oviduct, the magnum. Previously formed egg albumen is released as the ovum passes. Compression of the magnum wall helps release the albumen material directly in front of the moving ovum (Burke, 1984; Moran, 1987). After 3-4 hours of peristaltic movement through the magnum, the ovum moves into the isthmus, where two shell membranes are added in the next 1.5 hours. In the uterus, or shell gland, plumping occurs as fluid is added to the albumen, and a calcium carbonate and glycoprotein matrix is secreted to form the hard shell. A chicken egg normally spends 20 hours in the shell gland. The egg travels through the vagina in a matter of seconds in the chicken, while it can take 1-2 hours in the turkey before oviposition (King and McLelland, 1984). The overall length of egg formation in the turkey can take up to 3-4 hours longer than in the chicken (Sharp, 1989), although the average difference is 2 hours.

Physiological Control of Egg Production

Most of what is known about neuroendocrine and ovarian hormonal interactions related to development of the ovary and control of ovulation comes from research on the domestic fowl. This body of research can for the most part be applied to the turkey, and is complemented by fragmented literature on turkey ovarian function.

The ovulatory cycle of the chicken averages about 25 hours, with a range of 21 to 28 hours (Etches *et al.*, 1984; Etches, 1990). The turkey's cycle averages 27 hours (Pyrzak and Siopes,

1989), with a 25 to 28 hour range (Sharp, 1989). This results in a sequence of eggs being laid, each egg coming slightly later in the day than the previous one. Ovulation and oviposition are restricted to an 8-10 hour period of the day in the domestic hen, and 10-11 hour period in the turkey (Sharp *et al.*, 1981). This range, referred to as the 'open period for LH release', is regulated by the photoperiod (Wilson and Cunningham, 1984). The open period results in a periodic termination of the sequence and 'resetting of the clock' before commencement of the following ordered sequence (Bahr and Johnson, 1984). Sequences are separated by one or more pause days on which no eggs are produced. The interaction of two physiological systems gives the ovulatory cycle its asynchronous nature. They are the circadian rhythm that restricts the range of ovulation times, and the rate of follicular maturation (Fraps, 1965). Ovulation will only occur if a follicle becomes mature in the open period, thereby meeting the requirements of both cycles. It is generally understood that the onset of darkness is the environmental cue that sets the circadian rhythm (Etches, 1990).

Photostimulation is the increase in daylength that acts as the signal for the onset of reproduction. In birds, the photoreceptor is in or near the hypothalamus, with the suprachiasmatic nucleus being the likely mediator (Moore, 1983), as this is the key component of mammalian biological clocks. The light signal ultimately triggers the release of gonadotrophin-releasing hormone (GnRH-I) to be released from the anterior hypothalamus. GnRH-I is released into the anterior pituitary, where it stimulates gonadotrophin secretion (Sharp, 1993). In turkeys, a minimum of 13 hours of light is needed to stimulate peak egg production (Sharp, 1989). Growth and function of the ovary are associated with the increased levels of these hormones observed within 2-3 days of photostimulation (Burke and Dennison, 1980; El Halawani *et al.*, 1984).

Rapid follicular growth takes 4-12 days to begin, and first egg can arrive between 19 and 31 days (Bacon and Chermis, 1968). Both follicle stimulating hormone (FSH) and luteinizing hormone (LH) are released from the anterior pituitary. LH acts on the thecal layer, stimulating the production of dehydroepiandrosterone (DHEA), which likely acts as a substrate for the elevated androstenedione and estradiol levels observed in SWF and LWF (Robinson, 1986). These small follicles are the

hen's major source of androgens and estrogens (Robinson and Etches, 1986). LH is also involved in the formation of the preovulatory peak of progesterone (Etches, 1990). A small, daily surge of LH at the onset of darkness exists, which may be the physiological result of the night signal in setting the open period for LH release (Johnson and van Tienhoven, 1980). It may also be initiating maturational changes in receptor numbers and steroidogenic capacity of the new F1 follicle (Cunningham *et al.*, 1984). FSH stimulates granulosa cell development in small follicles and promotes progesterone production in these cells in follicles 9-12 mm in diameter (Tilly *et al.*, 1991; Johnson, 1993). The acquisition of the ability to generate progesterone signifies a change from the Δ^5 to the Δ^4 steroidogenic pathway in the thecal tissue. Thecal tissue converts the progesterone produced in the granulosa cells into androstenedione and estrogen (Robinson and Etches, 1986). This process is continued until 12 hours before ovulation, when the thecal tissue loses its ability to further metabolize progesterone. The granulosa tissue of the F1 follicle releases the highest volume of progesterone into circulation (Etches *et al.*, 1981), with the majority of the progesterone in the lesser developed follicles being metabolized into other steroids (Robinson and Etches, 1986). The production of estrogens in the thecal tissue declines as the follicle matures (Bahr *et al.*, 1983). It has been theorized that as the follicle matures, it has a decreased capacity to bind FSH, resulting in reduced conversion of androgens to estrogen (Etches, 1984), due to a decrease in the number of FSH receptors (Ritzhaupt and Bahr, 1987). Robinson *et al.* (1988) concluded that FSH may play a very limited role in steroidogenesis compared to LH, however, and that it is possible that multiple forms of LH may be involved in regulating steroid production. Increased ovarian steroid levels, particularly estrogens, are associated with increased plasma concentrations of calcium and fatty acids associated with impending egg production (Bajajee and Brown, 1972), and trigger the formation of yolk and albumen proteins (Moran, 1987).

Prostaglandins are involved in oviposition. The primary source is the post-ovulatory follicle (Shimada and Saito, 1989), where prostaglandin levels have been found to increase dramatically in the hour preceding oviposition (Burke, 1984). The ovulation of a new oocyte stimulates the oviposition of the previous one, through the stimulation of contraction in the shell gland (Shimada

and Saito, 1989). Prostaglandins of the E and F series can both stimulate contraction of the uterine muscle, enabling oviposition (Burke, 1984). They are not crucial to oviposition, however, as their elimination does not alter time of oviposition.

Control of Ovulation

The follicle is considered to be mature when it can respond to an LH signal by ovulating. Ability to ovulate is not related to the size of the follicle, as it will continue to sequester yolk until ovulation (Etches *et al.*, 1983). The acquisition of the ability to ovulate is also not related to the actual time of ovulation, as follicles can wait from 10 to 28 hours in an ovulable state, depending on when they mature in relation to the open period (Etches, 1984). The F1 follicle will cause an increase in serum progesterone levels with its' lost ability to convert progesterone to androstenedione (Robinson and Etches, 1986). The progesterone acts on the hypothalamus, which releases GnRH into the hypothalamic-pituitary portal system, followed by increased LH production from the anterior pituitary. The LH acts on the granulosa cells of the F1 follicle, triggering an even greater progesterone release (Etches, 1990). This positive feedback mechanism results in the LH peak that occurs 4-6 hours before ovulation in the domestic hen (Johnson and van Tienhoven, 1980), and 6-8 hours prior to ovulation in the turkey (Sharp *et al.*, 1981). The initiation of the progesterone and LH peaks appear simultaneous (van Tienhoven, 1981). More recently, however, Johnson and van Tienhoven (1984) have shown with the use of the steroid synthesis inhibitor, aminoglutethimide, that the preovulatory surge of progesterone appears to both precede and initiate the LH surge. The dependence of the ovulatory cycle on the presence of a mature follicle to initiate the ovulation process demonstrates the regulatory capacity of follicular maturation on the ovulatory cycle and sequence length (Bahr and Johnson, 1984). The LH peak cannot occur if the hypothalamus has not first been primed by estrogens, which increase the number of progesterone receptors a few hours before the LH surge (Wilson and Sharp, 1976). The failure of a follicle to ovulate can result in atresia (Gilbert *et al.*, 1983) due to too great a delay beyond acquisition of maturity.

Egg Production Disorders

A negative correlation has been observed between body weight and egg production in broiler breeders (Siegel and Dunnington, 1985; Robinson *et al.*, 1993a), Japanese quail (Marks, 1979, 1985) and turkeys (Nestor, 1971). The production of excess ova in growth selected birds play a role in their lower egg production. When comparing heavy to light weight lines, the heavy lines consistently have a greater number of ovarian follicles in both turkeys (Nestor *et al.*, 1970, 1980, 1981; Bacon *et al.*, 1972; Hocking, 1992a) and broiler breeders (Udale *et al.*, 1972; Reddy and Siegel, 1976). Further increases are expressed with early photostimulation (Hocking *et al.*, 1988, 1992). With increased follicle numbers, the production of two or more ovulable follicles (multiple follicle sets) is more likely to occur (Nestor *et al.*, 1980; Hocking, 1987a, 1989, 1992a, 1992b). Rather than having a single set of large to small follicles, there can be two or more follicles at the same stage at maturity, contributing to a double or triple hierarchy arrangement. Multiple follicle sets result in lowered egg numbers through the production of defective or shell-less eggs (Jaap and Muir, 1968; van Middelkoop, 1971, 1972; Bacon *et al.*, 1972; Nestor and Bacon, 1972; Hocking, 1992b; Yu *et al.*, 1992b). Experiments have shown that both growth selected turkeys and chickens produce more yolks than eggs (Jaap and Mohammadian, 1969; Nestor *et al.*, 1970), and defective eggs at levels up to ten times greater than egg or non-selected lines. Jaap (1969) theorized that the inheritance which favors rapid protein anabolism (rapid body growth) may also favor rapid formation of lipoprotein in the liver, and therefore increased yolk production. Defective eggs were believed to be caused by a lack of synchronization between ovarian and oviductal functions.

Erratic oviposition can be a common characteristic of growth selected lines (Jaap and Muir, 1968; Nestor and Bacon, 1972; Yu *et al.*, 1992b). Erratic laying is considered to be the laying of eggs outside the normal 8-10 hour period related to the open period. Often erratic laying is due to multiple ovulations resulting in premature oviposition and/or multiple oviposition. The incidence of defective shells is high, which is detrimental to fertility (Cherms and Wolff, 1968; van Middelkoop, 1971, 1972; Stephenson and Krause, 1988). This phenomenon has been called erratic oviposition

and defective egg syndrome (EODES). Jaap and Mohammadian (1969), believed that a reduction in the apparent overproduction of yolks in the ovary might partially alleviate these problems.

A multiple ovulation resulting in simultaneous release of ova can result in the formation of a multiple yolked egg. These eggs are larger than single yolked eggs, and typically have poor shell quality. Although two or more viable embryos may exist early in incubation, they do not survive incubation, and do not hatch two or more chicks (Robinson, unpublished data). Bacon and Chermis (1968) observed that each ovum had identical ovum growth and maturation sequences, up to and including ovulation. Multiple ovulations that do not occur simultaneously can have varied results. There can be the production of several membranous eggs (no shell formation), or a membranous egg with a normal or thin-shelled (soft-shelled) egg. Thin-shelled eggs are eggs ejected from the shell gland before shell formation has been completed. They are not usually hatchable eggs because their porous nature leads to excessive water loss during incubation. Hester *et al.* (1991) suspect certain prostaglandins play a role in the premature oviposition of membranous and possibly of thin-shelled eggs, especially when the eggs occur individually. Compressed-sided eggs (flat eggs) are thought to occur when ovulation of the first egg is delayed, and the second egg is early (van Middelkoop, 1971). This results in two eggs bumping in the shell gland, and the membranous second egg having the dent that forms upon contact harden. The second egg has a shortened time in the shell gland, and poor shell quality (van Middelkoop, 1971). Internal ovulation occurs when the ovum is not captured by the infundibulum, and remains free in the body cavity (van Middelkoop, 1972). This can occur more easily later in life, when the reproductive structures are less responsive to hormonal stimulation, or in fat birds whose infundibular motility is hampered by the presence of fat. The ovum is usually reabsorbed within a few days, but evidence for its occurrence can be found upon dissection by the presence of small pieces of cheesy material lying loose near the ovary. Internal ovulation can lead to yolk peritonitis, which can have potentially damaging effects to the well-being of the hen. The effects of the ovulated ovum not forming an egg on the preceding and following ovulations are not known (van Middelkoop, 1972). A rare disorder is internal laying. This occurs when a partially or fully formed egg is sent back up the oviduct by reverse peristalsis and deposited

in the body cavity. Bacon *et al.* (1972) believed that meat-type turkeys lose potential eggs primarily through a combination of double yolked eggs and multiple ovulations, atrophy of follicles in the fast growing stage, and through loss of ova in the body cavity.

Effect of Age on Laying Traits

Reproductive aging in turkeys and broiler breeders is the cumulative result of functional changes in the ovary and its' control mechanisms. There is a decline in reproductive efficiency as the bird ages. Once the peak rate of egg production has been reached early in lay, there is a gradual, linear decline in performance (Robel, 1981). The average sequence length declines with age, while the inter sequence pauses increase in duration (Robinson *et al.*, 1990; Lerner *et al.*, 1993). There is a reduced rate of follicular recruitment and maturation in older turkey hens (Hocking *et al.*, 1988), broiler-breeders (Yu *et al.*, 1992b), and egg-type hens (Williams and Sharp, 1978a; Robinson, unpublished data), as shown by fewer large follicles existing in older hens. Eggs from older hens are less likely to be fertilized, and usually exhibit poorer hatchability. In older turkeys, decreased rates of fertilization are related to fewer storage glands containing spermatozoa in the oviduct (Christensen, 1981). Hatchability problems are related in part to delays in ovulation caused by the inter sequence pause. First-of-sequence eggs have been found to be less fertile, less hatchable, and more likely to undergo embryonic loss in both turkeys (Bacon and Nestor, 1979; Lerner *et al.*, 1993), and in broiler breeders (Robinson *et al.*, 1991b; Fasenko *et al.*, 1992). Although this is thought to be due to aging of the oocyte during the inter sequence pause (Bacon and Nester, 1979; Robinson *et al.*, 1991b), Lerner *et al.* (1993) found that decreased fertility and hatchability in first of sequence eggs were also very closely related to egg grade. First of sequence eggs tend to have poor shell quality. The combination of oocyte aging and shell quality problems suggest a more active selection in parent stock for increased sequence length, as this will reduce the number of first of sequence eggs. An increase in average sequence length would also have a positive effect on chick production.

A reduced capacity to respond to hormone signals is involved in decreasing egg production rates with time. Johnson *et al.* (1986) found that the response of the largest follicles to LH declined with age. Williams and Sharp (1978b) found that the hypothalamus was not as responsive to progesterone feedback in older hens. Decreased estrogen production observed in old hens may be responsible for decreases in follicular recruitment and growth (Bahr and Palmer, 1989), as yolk and albumen precursors would be negatively affected (Gruber, 1972).

The weight of the ovum at ovulation increases steadily throughout the laying cycle, which is a reflection of the increased time needed to reach maturity (Bacon and Chermis, 1968; Sharp, 1989). The increase in yolk size directly relates to an increase in egg size (Bacon *et al.*, 1972), which results in a larger poult size (Shanaway, 1984). The yolk:albumen ratio increases in broiler-breeder eggs with age (O'Sullivan *et al.*, 1991). Despite the increase in albumen weight, it does not match the increases in yolk weight. Shell weight increases with time (Rahn *et al.*, 1981), but shell quality declines slightly late in lay, as reflected in lower levels of plasma calcium and phosphorous at this time (Strong and Nestor, 1978).

Termination of Egg Production

Photorefractoriness

Photorefractoriness is an event that negatively impacts egg production later in the laying cycle, and appears to lead to broody behavior in the wild bird. Under natural light while the turkey hen is in production, GnRH-I is at sufficient levels to stimulate egg production. At the same time, however, GnRH-II is being produced and is slowly building up in the system. GnRH-II is known to have negative effects on egg production. The inhibitory effects of GnRH-II are enabled when decreasing daylength can no longer sustain a stimulatory signal for GnRH-I production (Sharp, 1993). GnRH-II triggers a series of events that result in the gradual shut down the ovary. There is a reduction in LYF on the ovary (Hocking *et al.*, 1988), and a gradual drop in progesterone throughout the laying period (Mashaly and Wentworth, 1974), although gonadotrophin levels are not affected

(El Halawani *et al.*, 1984). Plasma estrogen levels decline, which contributes to the shutdown of the ovary as yolk and albumen precursors decline in availability (Gruber, 1972; Cogger *et al.*, 1979). Plasma prolactin levels, which are known to have anti-gonadal qualities (Opel and Proudman, 1980), slowly increase. Photorefractoriness can be disrupted with novel lighting programs, including increasing daylength throughout the production cycle (Sharp, 1989).

Broodiness

The development of broodiness, or incubation behavior, is disruptive to turkey egg production. Broodiness is a natural parental behavior, intended to allow the development and hatch of each brood of chicks (Sharp, 1989). Broodiness is characterized by high prolactin levels (Burke and Dennison, 1980; Proudman and Opel, 1981; Etches and Cheng, 1982), and would appear to continue from where photorefractoriness ends, as it would in the wild. Broody behavior is, however, described independently of photorefractoriness. High prolactin levels in the broody bird are soon accompanied by strong nesting behavior and decreased LH and gonadal steroid levels (Lea *et al.*, 1981; Harvey and Bedrak, 1984), and the ovary is shut down due to a lack of yolk precursors. Broodiness is most likely to occur 4-8 weeks into egg production (Nestor *et al.*, 1986), which coincides with the highest plasma prolactin levels of the production cycle (Etches and Cheng, 1982). It is possible that prolactin levels have passed a threshold level and are predisposing the bird to broodiness rather than directly initiating it (Sharp, 1989). As only certain birds are affected, it is possible to genetically select against the expression of incubation behavior (Bacon *et al.*, 1983). High temperature has been linked with sudden elevation of prolactin and elevated levels of broodiness (Thomason *et al.*, 1972; El Halawani *et al.*, 1984). For this reason temperature control is very important, particularly with large turkey lines, which are more susceptible to broodiness. This relationship may help explain the expected 15% drop in summer egg production levels as compared to any other part of the year (Hulet *et al.*, 1993).

Control of Broodiness

Broody behavior can be controlled in a variety of ways, but to be effective the treatment has to begin immediately after nesting behavior is observed. Nestor *et al.* (1986) found that establishing a full broody control program resulted in an extra 22 and 25 eggs per hen for medium and large turkey lines respectively. The key to any broody control program is the removal of the hen from the nest, which disrupts the stimulus to prolactin levels created by the nest (El Halawani *et al.*, 1980). The first signs of incubation behavior are nesting without a hard shelled egg in the shell gland or without laying that day. Hens can physically be checked for the presence of an egg, and broody control initiated. Broodiness is discouraged by the placement of the hen in an altered environment. Treatments exist such as cages (Burrows and Byerly, 1938), altered floor materials that discourage squatting, continuous or bright light (Nestor *et al.*, 1971), and hormones or chemicals (Haller and Chermis, 1961). These procedures could be reducing prolactin through a stress response, which has been found to depress prolactin levels in incubating hens (El Halawani *et al.*, 1988). Recent work by El Halawani's group has found the neuropeptide, Vasoactive Intestinal Peptide (VIP), to be the primary prolactin-releasing factor in incubating Bantam hens (Macnamee *et al.*, 1986), and in the turkey (El Halawani *et al.*, 1990a, 1990b). Active immunization against VIP in turkeys led to a 20-30 egg increase in egg production through decreased prolactin levels resulting in a reduced expression of incubation behavior (El Halawani *et al.*, 1993).

The Use of Feed Restriction for the Improvement of Reproductive Traits

There are strong similarities between broiler breeders and turkeys with regard to reduced reproductive performance associated with genetic increases in body size. A negative correlation has been observed between body weight and egg production in broiler breeders (Siegel and Dunnington, 1985), Japanese quail (Marks, 1979, 1985) and turkeys (Nestor, 1971). Obesity in broiler breeders is generally associated with reduced egg production, fertility and hatchability (Wilson and Harms, 1986). In turkeys, fat content is highly correlated with body weight (Robel, 1984). Abdominal

fatpad content has risen with selection for increased body weights on both an actual and percentage basis (Nestor, 1982). Reducing fat content and body size in turkeys often results in improved egg production through a decrease in follicle and defective egg numbers, and possibly an increase in overall egg production (Miles and Leeson, 1990a; Hocking, 1992b).

It is common practice to feed restrict broiler breeder hen candidates beginning at an early age (Costa, 1981), to circumvent reproductive problems brought about by selection for growth (Siegel and Dunnington, 1985). Restriction of body size in turkey breeders has been attempted with similar intent, but the results have not been as promising or effective. The problem is becoming more critical as body weights continue to increase in commercial turkeys, and problems associated with low egg production, multiple ovulation, and poor shell quality are likely to increase (Hocking *et al.*, 1988). Expected rates of lay for a male-line hen, where growth characteristics are almost exclusively selected for, are less than half that of the smaller female-line birds (Hocking, 1992a). A male-line hen may provide a good picture of what turkeys may be like in the future if current selection practices continue. The presence of high numbers of follicles and multiple follicle sets in these large birds (Hocking, 1992a) supports the need to understand what may be gained reproductively from feed restriction.

Broiler breeder restricted feeding research is more extensive and thorough than turkey research, and thus can act as a model for the turkey. Care must be taken, however, not to take broiler breeder research at face value. Despite similarities in growth characteristics during rearing, the turkey is a very different bird than the broiler breeder during the laying cycle. In a typical turkey breeder, there is a sudden drop in feed intake as the first eggs are laid just after 30 weeks of age. This results in a body weight decline that does not level off until 41 weeks of age (Whitehead, 1989). In the wild turkey, this is the result of a natural process that allows the hen to stay near the nest without ranging far for feed (Hulet *et al.*, 1993). During this time of reduced feed intake, egg mass is increasing, resulting in a negative energy balance, which is compensated for by a loss of body mass (Leeson and Summers, 1991). Turkeys will not increase feed consumption in this period, even if allowed to. In contrast, body weights of broiler breeder hens continue to gradually rise throughout

most of the laying period. Robinson *et al.* (1993b) found that allowing restricted-fed hens *ad libitum* access to feed in the middle of the breeder period resulted in substantial increases in feed intake, and rapid body weight gains. There were also increases in follicle number within seven days of full-feeding which resulted in an ovary appearance characteristic of full-fed hens. For these reasons, feed restriction programs in turkeys only involve the rearing period, while broiler breeders are restricted throughout the breeder period.

Feed Restriction in Turkeys

There has been renewed interest in the use of feed restriction for turkey breeder hen candidates. The interest is rooted in the continued success with broiler breeder restriction programs, and because primary breeders are shifting selection emphasis more towards growth to their female lines (Miles and Leeson, 1990a). In 1983, selection pressure in female pedigree lines switched from a program focusing heavily on reproductive traits to a program emphasizing growth. By 1986, larger breeder hens were being utilized to service the further processing industry. Body weights of these "new" hens increased by 25% between 1985 and 1989 (Hester and Stevens, 1990). For most of the turkey industry, the interest in feed restriction has been based on how to generate more product with less cost, *i.e.* how to produce a bird with maximum reproductive potential as economically as possible (Whitehead, 1989). For this reason, the vast majority of research on turkey feed restriction in the last 25 years is limited to analyzing body weights, feed consumption, feed per egg, egg numbers, hatchability and perhaps day of sexual maturity. Restriction programs of the past have involved: 1) skip-a-day feeding; 2) high fiber or low energy diets; 3) distasteful chemicals in the feed; 4) use of low protein or amino acid deficient diets; 5) limited daily access to feed (quantitative feed restriction). The general findings are that feed restricted turkeys exhibit a reduction in body weight and a delay in sexual maturity, while egg weight, fertility and hatchability are not affected. Results for feed efficiency and egg production appear to be more variable, however (Hester and Stevens, 1990). Feed restriction has been implemented almost exclusively during the rearing period, with the most promising results coming from experiments that managed to restrict

body size during rearing, and have some of these differences last throughout the egg production cycle (Hester and Stevens, 1990).

Role of Original Body Size in Feed Restriction Programs

Experimental feed restriction programs in turkeys usually utilize the Broad Breasted Large White turkey. Occasionally the Medium White has been used, or the Broad-Breasted Bronze turkey in some of the older studies. Whitehead (1989) observed that body weight restrictions of up to 20% in the larger birds would not impair reproduction, whereas similar degrees of restriction in lighter hens could have damaging effects on reproduction. In experiments using heavier birds (full-fed hen weight 9.0 to 12.5 kg), no effects on egg production were observed (Borron *et al.*, 1974; Cherms *et al.*, 1976; McCartney *et al.*, 1977; Potter *et al.*, 1978; Nestor *et al.*, 1981; Ferket and Moran, 1986; Miles and Leeson, 1990a, 1990b), with the exception of Krueger *et al.* (1978). The experiment of Krueger *et al.* (1978) consisted of a skip-a-day restriction program with a 25% feed reduction beginning at 22 weeks of age until photostimulation. Other experiments with the same restriction method and levels (Voitle and Harms, 1972; Voitle *et al.*, 1973, 1978; Balloun, 1974) did not negatively affect egg production. Balloun (1974), used lighter birds under similar conditions and reported an increase in egg production. For larger birds, 22 weeks of age may be too late to begin feed restriction because growth patterns and carcass traits may be too established to be able to adjust to feed restriction conditions before egg production begins. Touchburn *et al.* (1968), restricted birds at 70% of *ad libitum* feed intake beginning at 12 and 18 weeks of age. Egg production was depressed by 11% when restriction began at 12 weeks of age, and 29% when there was an 18 week of age commencement. A relatively early age of commencement for feed restriction programs during rearing appears to generate more positive results.

Feed restriction programs found to be detrimental to egg production were: Touchburn *et al.* (1968), Jones *et al.* (1976), Andrews and Morrow (1978), Krueger *et al.* (1978), Voitle and Harms (1978), and Meyer *et al.* (1980). Except for Touchburn *et al.* (1968), whose birds weighed 7.0 kg, all of these experiments involved turkeys with a maximum body weight of 8.2 to 9.3 kg, with the

average being 8.6 kg. Whitehead (1989), noted that in birds of this size, there appears to be a threshold value for tolerance of feed restriction. For example, Touchburn *et al.* (1968) found that a 20% restriction of feed from full-fed levels only reduced egg production slightly, whereas a 30% restriction resulted in a significant decline in production values. As well, Voitle and Harms (1978) found that restricting body weight to 11% below control weight did not negatively affect egg production, whereas a 30% difference did. In this experiment, the two restriction groups were both protein restricted to 10% protein in the diet (half of control value), but one restriction period ended at 25 weeks of age, while the other went on to 30 weeks of age (photostimulation). It appears that the effects of a substantial restriction on reproductive function can be decreased if it is terminated some time before photostimulation (Whitehead, 1989). Owings and Sell (1980) generated a restricted turkey body weight 40% lower than that of the control birds by 20 weeks of age, when the restriction treatment ended. By photostimulation at 32 weeks of age, a 16% difference still existed between body weights of the two treatments, but there were no adverse effects on reproduction. A delayed age of photostimulation will also offset effects of severe feed restriction (Whitehead, 1989) by allowing the bird more time to mature.

Restriction Programs Improving Egg Production

Feed restriction programs that had a positive effect on egg production were those initiated by Balloun (1974), McCartney *et al.* (1977), Miles and Leeson (1990a), and Hocking (1992b). It is difficult to speculate why these treatments improved reproductive traits, as no unique features are apparent. McCartney *et al.* (1977) fed a high fiber diet with limited availability, as did Borron *et al.* (1974), who reported no differences. The length of the laying cycle varied by nearly 10 weeks between these experiments, which may affect final production values if a treatment produces more heavily early or late in the cycle. The experiment of Balloun (1974), using skip-a-day feeding of a reduced amount of feed, was very similar to the work of Voitle *et al.* (1973), where the differences were smaller. These projects are of little interpretive value, however, as the production parameters reported are general production means. Miles and Leeson (1990a) examined the carcass

composition and laying parameters of hens reared under full-feeding, a skip-1-day (per week) program, and a 5% quantitative feed restriction program. The daily feed restriction proved to be much more effective, eliciting a 34% increase in egg production over full-fed control values as compared to an 8% increase for the skip-1-day program. Miles and Leeson (1990a, 1990b) reported that only minor differences in feed consumption (daily restriction group consumed 7% less than controls) can have large repercussions on reproductive performance. Hocking (1992b) observed a substantial reduction in unsettable eggs when birds were restricted to 60% of full-fed BW during rearing.

Methods of Feed Restriction

Concern about nutrient shortages during the period of weight loss following the onset of egg production gives cause for the turkey industry to use caution in feed restricting hens. To improve the energy density of breeder diets, work has been done with various dietary fat types and inclusion rates. A positive effect on reproductive performance has been observed by adding fat to the breeder diet at levels between 5 and 10% (Harms and Wilson, 1983; Robel, 1985). Adding fat in the grower diet also has a positive influence (Harms *et al.*, 1984), probably through the increase in fat stores of the growing turkey (Leeson and Summers, 1991). According to Whitehead (1989), response to dietary fat can be variable, but because of an average 2 to 3% increase in egg numbers, a fat level of at least 5% is recommended.

During the weight loss seen in early lay, the hen is obtaining energy from carcass fat stores, and protein from muscle. In hens with minimal fat content and body size, such as is the case with feed restricted birds, there will be minimal weight loss, and greater feed intake during this period to compensate for the lack of available stores and to meet energy demands (Whitehead, 1989). From an economic standpoint, this makes feed restriction a viable option if the turkey can be held small enough to reduce overall feed consumption, or is close enough to full-fed body size to reduce over-consumption of the expensive breeder ration.

Diet dilution is a form of qualitative feed restriction, and is the simplest method of restricting energy intake. This method involves adding a substance to the diet with negligible nutritive qualities to increase bulk, such as ground oat hulls or cellulose, and allowing *ad libitum* access. In order for these low energy diets to be effective, they may also need to be physically restricted as turkeys will consume extra feed to meet their metabolizable energy need (Roachrough *et al.*, 1983; Whitehead, 1989). Potter and Leighton (1973) fed a high fiber diet (44% oat hulls) *ad libitum* and observed the energy restricted birds increased their feed intake by 50%, although final body weights were very similar. Nestor *et al.* (1981) observed a 150-157% increase in feed consumption when oat hulls were used to replace corn in the diet at a 69% level during the rearing and breeding period, and observed a transient increase in egg production. Nestor included fiber at a level that could not be compensated for through increased feed intake, resulting in significant differences in body weight. In broiler breeders, *ad libitum* fed low energy diets during rearing are considered uneconomical (Lee *et al.*, 1971). Low energy diets in turkeys have resulted in differences in body weight between treatments, and minor increases in egg production have involved an energy reduction along with physically limiting feed intake to full-fed control levels (Borron *et al.*, 1974; McCartney *et al.*, 1977).

Protein restriction is another form of qualitative feed restriction. It is not commonly used in broiler breeder stocks, as birds fed low protein during rearing tend to be heavier and fatter at photostimulation than quantitatively restricted birds (Leeson and Summers, 1991). There are a limited number of reports of projects using protein restriction during rearing in turkeys. Of the experiments performed, there was either a decrease in egg production (Mitchell *et al.*, 1962; Voitle and Harms, 1978; Meyer *et al.*, 1980; Noll *et al.*, 1993), or no differences observed (Voitle *et al.*, 1973; Cherms *et al.*, 1976). Noll *et al.* (1993) observed a 13% drop in egg production with a diet restricting protein by just 3%, and including 2% feather meal. Feeding a low plane of nutrition, with the energy level also reduced (Ferket and Moran, 1986), likely has fewer detrimental effects than restricting protein alone.

Limited daily access and skip-a-day feeding are both forms of quantitative feed restriction. They can be administered with or without diet dilution, and usually are calculated as a percentage of *ad libitum* feed intake levels. As with the other types of restriction, quantitative feed restriction produces mixed results. Early studies either reduced egg production (Touchburn *et al.*, 1968), or had no discernible effect (Anderson *et al.*, 1963; Voitle and Harms, 1972). Recent studies show limited daily access to have more beneficial effects on reducing fat levels and maintaining or improving egg production over full-fed levels (Miles and Leeson, 1990a, 1990b; Noll, *et al.*, 1991). Although daily feed restriction can be difficult to administer without the proper equipment, it appears to generate the greatest differences in turkey body size, composition, and reproductive traits, with the lowest feed intake and cost.

Carcass Composition

Until recently, turkey feed restriction research has dealt very little with the effects of restriction on carcass traits. Fat content is of primary interest because of its implications for reproductive efficiency and its variability under different feeding regimes. In overweight broiler breeders, an infiltration of fat in the sperm storage glands at the uterovaginal junction can reduce sperm storage efficiency (McDaniel *et al.*, 1981). Infundibular motility is reduced with excess fat deposition, which can also lead to the production of fewer settable, fertile eggs. With the trend towards further processing in turkeys, any excess fat is wasteful, and selection against fat content will likely increase in the future (Whitehead and Griffin, 1985). Body weight selection in turkeys has been demonstrated to increase the amount of abdominal fat both on an actual and a percentage basis (Nestor, 1982). Large turkey strains typically contain more fat on a whole carcass basis (Emmans, 1989), and the fat content of the largest lines is the least responsive to feed restriction programs (Hocking, 1992a). Hocking restricted male-line female body weight by 40% and observed only a 7% drop in carcass fat, compared to a 25% decrease in female-line hens reared under the same conditions. The large turkey strains of today appear able to tolerate high levels of feed restriction without limiting effects on their carcass composition.

Under normal rearing conditions, the percentage of fat in a turkey hen will steadily decline from photostimulation to the end of the laying cycle. Moisture content increases gradually, following an inverse path to fat levels (Robel, 1984). Protein content tends to follow the body weight curve, declining gradually to 40–45 weeks, and then slowly increasing until the end of the breeder period (Robel, 1984; Whitehead, 1989). Borron *et al.* (1974) found that high energy diets did not alter carcass fat or protein levels at photostimulation, while low energy diets generated lower fat levels and slightly increased protein levels. Rosebrough *et al.* (1983) assessed liver lipid levels in turkeys on diets varying in protein and energy level. The turkeys altered their feed intake to meet their energy requirement, resulting in lipid levels being the highest in hens on all diets high in protein. Liver lipid levels reflect the energy state of the bird, with higher lipid levels reflecting a more positive energy balance. It has been found that plasma low density lipoprotein concentrations in broiler chickens are closely related to body fat (Whitehead and Griffin., 1984). Studies done in the turkey also have shown VLDL concentrations to be a good indicator of fatness (Griffin and Whitehead, 1985).

Miles and Leeson (1990b) compared the effectiveness of skip-a-day feeding during rearing to limited daily feeding programs in altering body composition. They observed that restriction programs limiting daily access to feed reduced carcass fat levels and increased carcass protein levels more effectively than skip-a-day programs. Most recently, Hocking (1992b) examined the effects of age of photostimulation and quantitatively restricting birds to 60% of full-fed size during rearing. Abdominal fatpad size and total fat were substantially reduced in the restricted birds at photostimulation. Within 6 weeks of photostimulation, the fat was not distinguishably different between restricted and control hens. Protein and ash content were lower in the restricted group when photostimulated at 30 weeks of age.

Shank length measurements are an indicator of frame size. In broiler breeders, the standard restriction program can limit shank by 15% during rearing (Yu *et al.*, 1992a). Feed restriction in turkeys can also limit shank length (Borron *et al.*, 1974). Owings and Sell (1980) concluded that

restricting feed intake to less than 80% limited turkey growth, which may be indicated by reduced shank lengths.

Egg Characteristics

As mentioned previously, the weight of the ovum at time of ovulation steadily increases throughout the laying period, and this increased yolk size directly relates to increased egg size (Bacon and Chermis, 1968; Sharp, 1989). Broiler breeder eggs show increased shell, yolk, and albumen weights as hens age (O'Sullivan *et al.*, 1991). Increased yolk size is a reflection of the increased time required to reach maturity (Bacon and Chermis, 1968; Sharp, 1989). Higher shell weights are due to extra calcification, as larger eggs spend more time in the oviduct (Melek *et al.*, 1973). The first few eggs laid by a turkey may be fairly small. Hatcheries have a lower cut-off for eggweight to ensure poults of good body size and vigor. Early photostimulation has been shown to cause an increase in the incidence of small eggs (Woodard *et al.*, 1974; Hocking, 1992b), and when in combination with feed restriction during rearing, they can be even smaller (Hocking, 1992b).

Ferket and Moran (1986) examined the proportion of shell, yolk, and albumen through time from birds reared on a high or low plane of nutrition. The percentage of yolk was found to significantly increase through time. This was at the expense of albumen, although shell values also declined. Although similar, yolk proportion was significantly lower in the low energy treatment birds. Smaller yolks could potentially decrease poult size.

In most experiments with feed restriction in turkeys, fertility and hatchability are not affected by the restriction programs (Hester and Stevens, 1990). In the situation where hatchability does decline, it has been found to be primarily due to increased late embryonic death, which is related to a poor blood glucose level late in incubation (Christensen and Krueger, 1993). Hatchability may not be affected by feed restriction until the bird is forced below a required threshold of nutrient supply and body stores for proper egg composition.

Specific gravity, an indicator of shell quality, is a measure of shell density. Eggs with higher specific gravities have improved hatchability (McDaniel *et al.*, 1981), and defective eggs have

low hatchabilities due to shell quality problems (Stephenson and Krause, 1988). It has been demonstrated in broiler breeders that heavier birds lay eggs with lower specific gravity values, and that these eggs have poorer hatchability (Wilson and Harms, 1986), presumably due to increased moisture loss during incubation.

Ovary Morphology and Laying Patterns

Very little research has been done with the effects of feed restriction of turkeys on ovarian characteristics, and laying patterns. The intended effect of feed restriction on the reproductive system is a reduction in the number of defective eggs, and an improvement in laying patterns (such as sequence length). This can be done primarily through the reduction of developing large follicles on the ovary, which will decrease the frequency of multiple follicle set formation. Multiple follicle sets are the major cause of lower egg numbers through the production of defective eggs (Jaap and Muir, 1968; van Middelkoop, 1971, 1972; Bacon *et al.*, 1972; Nestor and Bacon, 1972; Hocking, 1992b; Yu, 1992b).

Hocking (1992a) found that quantitatively restricting body size by 20 or 40% during rearing resulted in decreased follicle numbers in female-line birds at 30 weeks of age, while male-line birds were not affected. The larger strains were more resistant to the restriction programs. As a result, female-line birds had a reduced incidence of follicles occurring in pairs, and a smaller stroma (remainder of ovary when large follicles removed) weight. The male-line hens had no differences in the occurrence of multiple follicle sets, although stromal weight was reduced in restricted birds. Reduced stromal weight could have long term effects on egg production through decreased development of the small follicle pool. Besides reduction in follicle numbers and multiple follicle sets, a reduction in follicular atresia of the yellow follicles and the LWF has been observed (Hocking *et al.*, 1992). Decreased atresia could indicate that excess follicle production is under more control. Feed restriction decreased atresia to a 13% incidence, which is similar to levels in turkey egg-lines (Bacon *et al.*, 1972). Meat-type turkey hens have been observed to have about a 35% incidence of follicular atresia (Bacon *et al.*, 1972; Hocking *et al.*, 1992). Bacon *et al.* (1972)

observed evidence of internal ovulation to be lower in the smaller turkey strain (13% vs. 23%), which may be an achievable level using feed restriction today.

With reduced follicle losses and multiple sets in restriction treatments, the incidence of defective eggs would be expected to decline. Andrews and Morrow (1978) found a significant reduction in both misshapen (flat) and soft shelled eggs in hens that were restricted during rearing and subsequently full-fed compared to levels in birds exclusively full-fed. Hocking (1992b) had similar results, with a significant reduction in double yolk and soft shelled eggs in hens restricted until photostimulation at 30 weeks of age. Part of these differences could be due to altered steroid production in the largest follicles. In broiler breeders, it has been reported that in full-fed hens, some F2 follicles produce large amounts of progesterone, and very little androstenedione, making them functionally the same as the F1 follicle (Yu *et al.*, 1992c). With the ovulatory signal, both follicles would be able to ovulate. This situation did not exist in any hens under restriction conditions, which would explain the reduced defective egg production in restricted birds.

Anthony *et al.* (1991), in comparing a line of turkeys selected for egg production to a randombred control population, found that the primary way eggs were added was through increases in egg sequence length. In broiler breeders it has been observed that as rate of lay increases, average sequence length increases (Lerner *et al.*, 1993). The length of the prime sequence (a characteristically long sequence early in production) is correlated with total egg production for the bird (Lerner *et al.*, 1993). *Ad libitum* fed hens have shorter prime sequences than restricted fed hens (Robinson *et al.*, 1991b). Bacon and Chermis (1968) found that pause length in turkeys increased with age, and that for sequences of four eggs or greater, the time interval between ovipositions was the same. This is supported by Pyrzak and Siopes (1989), who found the average interval between eggs in a sequence to be 27 hours, regardless of sequence length. These results differ from previous reports on turkey sequence analysis (Woodard *et al.*, 1963), and sequences of the domestic fowl (Etches, 1990), where the egg interval was reported to decrease in longer sequences of eggs. Bacon and Chermis (1968) also observed that first of sequence ova were not any heavier than ova from later in the sequence. This is contrary to what Etches *et al.* (1983) report. Etches and co-workers found

that the follicle sequesters yolk material up to the time of ovulation, which should make first of sequence eggs heavier. Robinson *et al.* (1991a) found the first egg in a sequence to be heavier, which was presumably due to increased yolk size.

Pyrzak and Siopes (1989) examined different aspects of laying patterns. Of all of the eggs laid in a 23 week laying cycle, they report that 15% of them were laid during the dark period. Since the open period for LH release is only 8 to 10 hours, it would be expected that the laying sequence would be restricted to a similar range. In broiler breeders, this type of erratic oviposition has been correlated with production of defective eggs, and low settable egg production (Yu *et al.*, 1992b). Although they only report total egg production, Pyrzak and Siopes (1989) found the laying patterns of the high egg producers varied highly. A hen could lay either within a narrow range of time, or it could lay erratically throughout the 24 hour day. No laying range was preferred over another, but each hen was highly specific to its particular oviposition range throughout the entire laying cycle. It was concluded that some hens do not have their oviposition times synchronized by the daily photoperiod. It is unfortunate that settable and cull egg data were not available, as this may have revealed more about the reproductive fitness of the erratic layers. It would be useful to study how feed restriction in the growing phase affects both sequence length and the daily time range of laying patterns and their relatedness to defective egg production.

Concerns With Feed Restriction

Delayed Sexual Maturity

It is well documented that feed restriction during rearing will delay the onset of sexual maturity (day of first egg) (Hester and Stevens, 1990). However, this delay typically has no effect on final egg production levels. The period of delay also does not appear to be linked to total egg numbers. Borron *et al.* (1974) found their low energy diet to delay sexual maturity by up to a week, with either no effect or a slight improvement in production. Krueger *et al.* (1978) observed a 4 day delay in maturity in birds restricted to 75% of full-fed levels, and ultimately lower egg numbers for these birds. More extreme delays were recorded by Voitle *et al.* (1973), with low protein and skip-a-

day treatment birds lagging in maturity by 40 to 50 days, with no effect on egg production. They reported that the lack of difference was due in part to high levels of unsettable eggs produced by the full-fed controls. Reduced production of unsettable eggs likely contributes to the lack of difference in final egg numbers observed in feed restriction treatments of the rearing phase, as has been observed in broiler breeder feed restriction programs (Katanbaf *et al.*, 1989). Hocking (1992a) observed a two week increase in the time required from photostimulation to sexual maturity in large male-line hens compared to hens of several female-lines photostimulated at the same time. It was hypothesized that this was due to a decreased sensitivity to photostimulation in the larger turkey strains. Excessive defective egg production in fast-growing chickens is thought to be related to reduced sensitivity to circadian rhythms (Jaap and Muir, 1968). Perhaps poor light sensitivity contributed to the highly erratic laying patterns observed in some turkeys by Pyrzak and Siopes (1989). Studies on the effects of substantially increasing light intensity on egg production have either shown minimal improvements in egg production (El Halawani *et al.*, 1981), or no observable differences (Siopes, 1992).

Early photostimulation can lead to depressed egg production when administered in conjunction with feed restriction during rearing. Hocking (1992b) found that onset of lay was delayed by 50 days in birds restricted to 60% of control bird body weight and photostimulated at 18 weeks of age, and no delay when photostimulated at 30 weeks of age. Egg production in birds photostimulated at 30 weeks of age was not affected, while it was significantly depressed in restricted birds photostimulated at 18 weeks of age. A high proportion of turkeys in the 60% of control body weight restriction group photostimulated at 18 (Hocking, 1992b) or 24 weeks of age (Woodard *et al.*, 1974; Hocking, 1992a, 1992b; Hocking *et al.*, 1992) either fail to come into production, or have difficulties maintaining production. It can be hypothesized from these results that if long delays in the onset of lay or depressed egg production are being observed in restriction treatments, photostimulation may be occurring too early. The turkeys may need to reach some level of physical maturity in order to properly maintain lay that is not met under feed restriction conditions. The base percentage of carcass fat may be the crucial element. Hocking (1992b) found

the proportion of carcass fat in both full-fed and restricted birds to double between 18 and 30 weeks of age. With higher base levels of fat (>17.5%) in similarly restricted birds of another experiment, sexual maturity was not delayed (Hocking, 1992a). The threshold value for carcass fat appears to be about 10 to 11% with photostimulation at 30 weeks of age, and potentially higher when photostimulating earlier. In broiler breeders, it has been found that full-fed birds depend on reaching a critical age for the onset of egg production, while feed restricted birds with delayed maturity are dependent on reaching critical body weight and carcass fat levels (Brody *et al.*, 1984; Katanbaf *et al.*, 1989). Restricting broiler breeders at levels well below recommended standards can result in increased persistence of lay with no effect on egg production (Fattori *et al.*, 1991), or in reduced egg numbers, particularly in early lay (Wilson and Harms, 1986), which suggests the birds are having some difficulty in attaining sexual maturity.

Unintentional Nutrient Restriction

With broiler breeders, there has been some concern that limited daily access to feed will inadvertently restrict crucial nutrients during portions of the laying cycle. Summers and Leeson (1978) used dietary self-selection techniques to show that growing pullets and broiler breeders have a greater energy requirement during the first 10 weeks of rearing, and a greater energy requirement during the next 10 weeks. Harms and Wilson (1987) proposed the use of eight different diets to accommodate nutrient needs at various growth stages, and avoid unintentional excess protein or energy restriction. Research on self-selection diets in turkeys focuses on the breeder period, where some studies found increased protein intake late in lay (Emmerson *et al.*, 1990, 1991), and others find elevated protein intake occurs early in lay (Hulet *et al.*, 1993). Differences were thought to be seasonally and perhaps strain related (Hulet *et al.*, 1993). This type of work shows that nutrient requirements vary, and that care must be taken when designing feed restriction programs. It also supports the possibility of protein restriction during the laying cycle, as self-selecting hens consumed 35-40% less protein than control birds (Emmerson *et al.*, 1990, 1991).

Flock Uniformity and Feed Restriction

Flock uniformity is a measure of the extent of variability in the weight range of a flock. It has traditionally been measured by calculating the percentage of the flock weighing in the range of either 10 or 15% above and below the mean group weight. The use of daily feed restriction is detrimental to flock uniformity in that the aggressive birds get a disproportionate amount of a limited feed source. This has been demonstrated in broiler breeders, where aggressive birds are found to grow larger more quickly while passive birds remain smaller and are under more severe restriction conditions due to lack of feed access (Petitte *et al.*, 1981). Skip-a-day feeding programs have been found to maintain uniformity at a higher level. This is a result of increased feed availability on feeding days, which allows all birds to eat their fill (Bartov *et al.*, 1988). In female turkey breeding stock, however, daily feed restriction has been shown to have much more positive effects on reproductive performance and carcass composition than skip-a-day programs (Miles and Leeson, 1990a, 1990b). This result could be due to less of a metabolic stress on the bird brought about by more uniform feed availability.

Flock uniformity is not considered a serious problem in turkey operations. To date, the majority of feed restriction is on breeder toms, with restriction of feed intake representing about half of this (Kuhl, 1993). The majority of birds are either *ad libitum* fed, or allowed *ad libitum* access to a qualitative restriction diet. The quantitatively restricted birds will often be on skip-a-day programs, or at levels relatively close to full feeding. The result is that access to feeder space is not a serious problem, and uniformity should not be seriously affected. With changes in feeder design for daily restriction in broiler breeder operations, the equipment is now available for daily feed restriction, although it is not readily utilized as it is viewed as too complex (Noll *et al.*, 1993). As research continues with daily restriction programs, especially where target weights are near half that of control birds (Hocking, 1992a, 1992b; Hocking *et al.*, 1992; Christensen and Krueger, 1993), flock uniformity will have to be addressed. Current techniques using broiler breeders include increasing feeder space to improve feed access, and sorting birds into body weight groups and differing their feeding programs (Petitte *et al.*, 1981; Kling *et al.*, 1985). Zuidhof *et al.* (1993) had

perhaps the most promising method, using a combination of daily feed restriction and nutrient dilution with ground oat hulls. They found the flock uniformity improved over time in dilution treatments compared to the quantitatively restricted control group.

Research Projects

Objectives

The purpose of this research was to examine the composition and reproductive fitness of male-line breeder hens under full-fed conditions or various levels of nutrient restriction during the rearing period. The effects of nutrient level during rearing on growth and carcass characteristics, ovarian morphology, and egg production and laying patterns were examined.

The low protein and limited daily access feed restriction programs have both been demonstrated to reduce final body size during rearing. The hypothesis of this study was that the feed restriction programs will reduce body size and feed consumption, and alter carcass composition. These changes will have a positive effect on reproductive traits.

Project Descriptions

- Project 1.** This project was designed to examine the effects of nutritional intake during the rearing period on growth, feed intake, selected organ weights, and carcass composition. The effectiveness of various feed restriction programs in decreasing feed intake and altering carcass traits was determined.
- Project 2.** This project was designed to examine the effects of nutritional intake during the rearing period on ovarian morphology, egg production, laying patterns, and egg traits. The occurrence of multiple follicle sets and defective egg production was of particular interest.

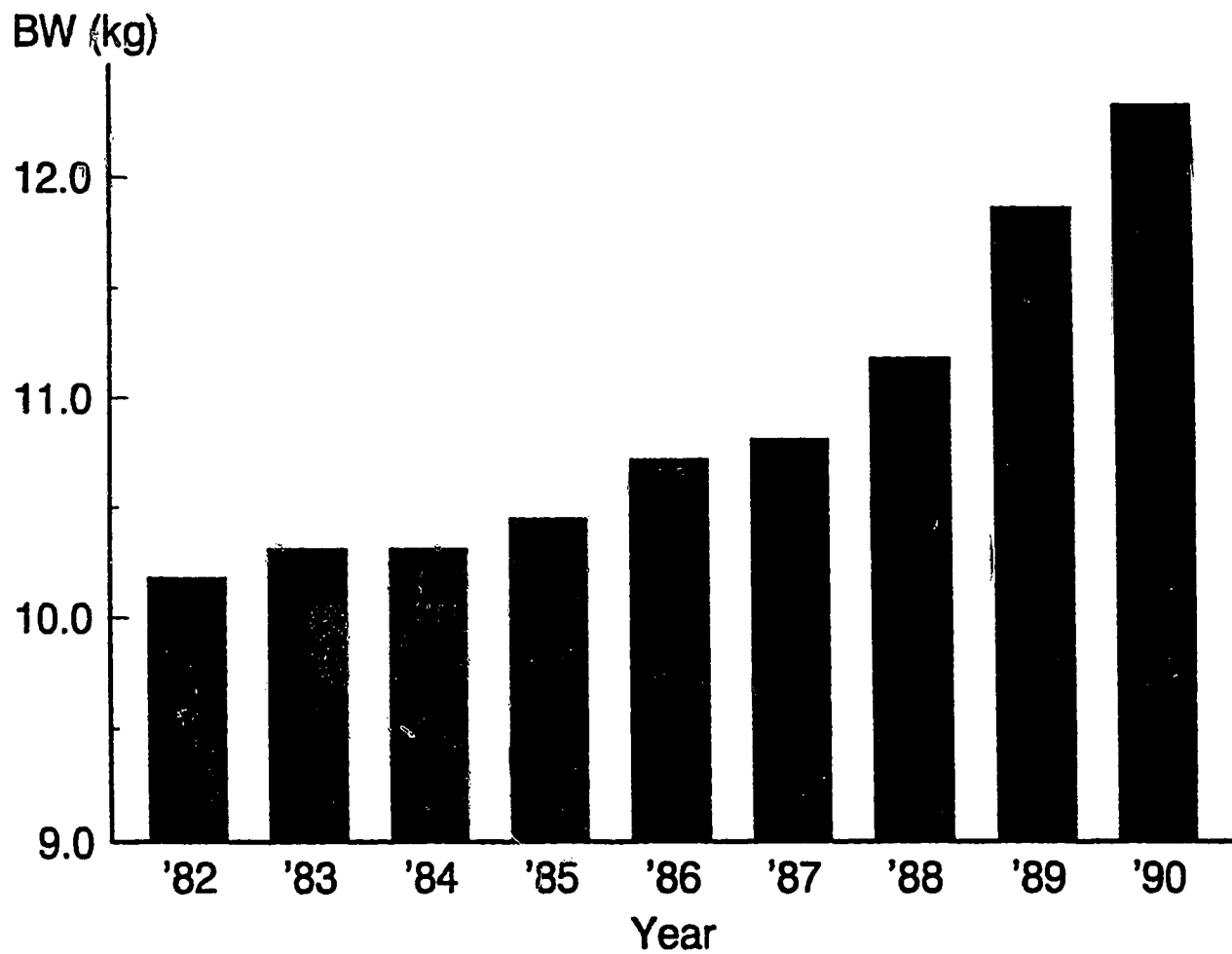


FIGURE I-1 Average 18 wk body weights of tom turkeys marketed between 1982 and 1990.
Data from Sell, 1990.

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II. THE USE OF FEED RESTRICTION FOR IMPROVING REPRODUCTIVE TRAITS IN MALE-LINE LARGE WHITE TURKEY HENS: 1. GROWTH AND CARCASS CHARACTERISTICS¹

Introduction

Broiler breeder hen candidates are routinely feed restricted beginning at an early age (Costa, 1981), to circumvent reproductive problems brought about by selection for growth (Siegel and Dunnington, 1985). Restriction of body size in turkey breeders has been attempted with similar intent, but the results have not been as effective or conclusive. The problem is becoming more critical as body weights continue to increase in commercial turkeys, and hence the associated problems of low egg production, multiple ovulation, and poor shell quality are likely to increase (Hocking *et al.*, 1988). Primary breeders are placing more selection emphasis for growth on their female lines (Miles and Laeson, 1990a), and have begun to utilize larger size lines to meet the demand for turkeys for the further processing industry. Body weights of breeder parent stock have increased by 25% between 1985 and 1989 (Hester and Stevens, 1990).

A negative correlation has been observed between body weight and egg production in turkeys (Nestor, 1971; Nestor *et al.*, 1980). In broiler breeders, obesity is generally associated with reduced egg production, fertility and hatchability (Wilson and Harms, 1986). The fat content of turkeys is highly correlated with body weight (Robel, 1984). Abdominal fat content has increased with selection for increased body weight on both an actual weight and percentage basis (Nestor, 1982), and carcass fat levels are greater in large turkey strains (Emmans, 1989). Selection for rapid growth rate increases the potential for multiple ovulations (Nestor *et al.*, 1980), thereby increasing defective egg production (Jaap and Muir, 1968; van Middelkoop, 1971; Nestor and Bacon, 1972; Hocking, 1992b). Reducing fat content and body size in turkeys can result in

¹The content of this chapter was presented at the 82nd annual meeting of the Poultry Science Association, held in East Lansing, Michigan; July 26-29, 1993. Poultry Sci. 72(Suppl 1):44. (Abstr.)

improved egg production through a decrease in the number of follicles and the incidence of defective eggs (Miles and Leeson, 1990a; Hocking, 1992b).

The expected rate of lay for a male-line hen, which has been almost exclusively selected for growth characteristics, is less than half that of smaller female-line birds (Hocking, 1992a). A male-line hen may give a good indication of what turkeys may be like in the future if current selection practices continue. The presence of high numbers of follicles and multiple follicle sets in such large birds (Hocking, 1992a) is reason to examine what may be gained from feed restriction.

Turkey feed restriction programs of the past have examined the effects of various forms of nutrient restriction, including high fiber or low energy diets, low protein diets, and quantitative feed restriction, which includes skip-a-day and limited daily access feeding. Restriction programs occur almost exclusively during rearing. In general, feed restricted turkeys exhibit reduced body weight and delayed sexual maturity, while egg weight, fertility and hatchability are not affected (Hester and Stevens, 1990). Egg production results are more variable, with some programs improving egg production (Balloun, 1974; McCartney *et al.*, 1977; Miles and Leeson, 1990a; and Hocking, 1992b), and others decreasing egg production (Touchburn *et al.*, 1968; Andrews and Morrow, 1978; Krueger *et al.*, 1978; Voitle and Harms, 1978; and Meyer *et al.*, 1980). Negative effects have tended to be associated with smaller birds, which appear to be more sensitive to the effects of restriction than the larger turkey strains (Whitehead, 1989; Hocking, 1992a). Improvements in egg production due to feed restriction are usually due to a reduction in the production of defective eggs. The most promising results come from experiments that have managed to restrict body size during rearing (Hester and Stevens, 1990).

There is little information reported on the effects of feed restriction on body composition in modern strains. Published data on carcass composition of male-line hens is almost nonexistent. The purpose of this experiment was to determine the effects of low protein and limited daily access forms of feed restriction during rearing on growth rates and selected organ weights and carcass composition of male-line Large White turkey breeder hens throughout the breeder period.

Materials and Methods

Stocks and Management

Two hundred day-old female poult of a male parent line were acquired from Hybrid Turkeys². The poult were divided, 50 per pen, into four floor pens (4.75 m X 5.85 m) and fed *ad libitum*. At four weeks of age poult were wing-banded and randomly assigned to one of two pens designated to each of four treatments. Treatments consisted of a full-fed control (FF), and three feed restricted groups. The low protein restriction treatment (LP) was a qualitatively restricted group, receiving a 12% C.P. diet *ad libitum* in the period from 12 to 20 weeks of age, rather than the 18% and 15% C.P. diet in this time period. The remaining restriction treatments, Restricted -10% BW (R10) and Restricted -20% BW (R20), were quantitatively restricted groups with feed withheld at a level that would result in birds either 10% or 20% lighter than the FF controls. Restriction treatments continued until photostimulation at 28 wk of age, when the turkeys were placed on an *ad libitum* breeder diet and the nest-boxes were installed. The sequence of diets fed to each treatment is presented in Table II-1. Except for the pre-starter diet (0-4 weeks), all diets were corn-soy based and formulated following breeder guidelines. The ingredients, composition and period fed for each diet is presented in Table II-2. All diets were fed in a mash form. Water was available *ad libitum* during the light period from suspended bell drinkers. Bedding was removed periodically from around drinkers and fresh straw added to pens periodically.

The poult received 24 hours of light on day 1 (24L:0D). The photoperiod was set at 23L:1D from 2 to 5 d, and 14L:10D between 5 d and 14 wk of age. Daylength was reduced to 8L:16D at 14 wk, 7L:17D at 18 wk, 6L:18D at 22 wk and 5L:19D at 26 wk of age. Photoperiod for the breeder period, beginning at 28 wk of age, was 14L:10D. Daylength was increased by 1 h at 34, 38 and 42 wk of age to a maximum photoperiod of 17L:7D

²Hybrid Turkeys Inc., 9 Centennial Drive, Kitchener ON. N2B-3E9

Post mortem analysis was performed on all birds that died or were culled throughout the experiment³.

Feed Intake, BW, and Body Composition

Feed intake was calculated on a weekly basis for all treatments, and total feed intake calculated for selected periods. Individual BW was recorded on a bi-weekly basis to 28 wk of age and weekly thereafter. Total gain for the rearing period (0 to 28 wk) and selected periods during the rearing period (29 to 48 wk) were calculated. A sample of birds was weighed weekly during the rearing period to determine feed allowance for the R10 and R20 treatments. BW at sexual maturity (first egg) was recorded for all birds. Shank length was used as an indicator of frame size. Shank length (measured from the top of the hock joint to the spur) was recorded at 4 wk intervals between 4 and 28 wk of age for all birds. After photostimulation, shank length was recorded every 8 wk, with a final measurement performed at 48 wk of age.

At 28 wk of age, eight randomly selected birds were removed from each of the four treatment for carcass analysis. The turkeys were deprived of feed and water for 12 h, and killed by lethal injection using T-61⁴ (3 cc dosage). Carcasses were weighed and shank length was recorded. The breast muscles were excised and weighed. The weight of the heart, liver, and abdominal fat pad were recorded. The abdominal fat pad included fat surrounding the proventriculus and gizzard. The liver was frozen separately for future analysis of total liver lipids, and the remaining organs returned to the carcass, which was then frozen. The frozen carcasses were cut into pieces (approximately 12 cm diameter) and passed through a large meat grinder (25 cm diam. bore; 1 cm diam. screen openings) until homogenous. A 2 kg sub-sample taken from each carcass was autoclaved for 6 h, sub-sampled after blending with an industrial blender, and freeze-dried, as described by Yu *et al.* (1990). Chemical analyses following standard procedures (Association of Official Analytical Chemists, 1980) were performed on the freeze-dried samples for determination of total dry matter,

³Animal Health Division, Veterinary Laboratory, Alberta Agriculture, 6909-116 St., Edmonton, AB T6H-4P2

⁴Hoechst Canada Inc., 295 Henderson Dr., Regina, Sask. S4N-6C2

total protein, total lipid, and total ash. Total liver lipid content was determined with petroleum ether extraction.

At sexual maturity, ten pre-selected birds from each treatment were processed as described above. A further eight birds per treatment were removed midway through the cycle (40 wk), which corresponded with the lowest BW of the breeder period. At the end of the experiment (48 wk), hens remaining in lay were processed, to a maximum of eight randomly selected birds per treatment. Hens that were not in production were also processed at this time for comparison with birds in lay at 48 wk of age.

Statistical Analysis

Data were evaluated by analysis of variance using the General Linear Models (GLM) procedures (SAS Institute, 1985). Preliminary analyses indicated the variation among pens was essentially the same as the variation among birds within pens. On this basis the pen variation was combined with the bird variation to form the error variation. Feeding regimens (treatments) were compared within periods of interest and / or times in the growth and production cycle. For specific body weights and shank length, sources of variation were treatments and birds within treatments. Feed data and flock uniformity data were analyzed at the pen level, as this was the lowest level of variability for these factors. Body composition traits were analyzed across both treatment and time. Sources of variation were treatment, time, and treatment * time interaction. Differences between treatments in a time period were examined, as well as differences in time within a treatment. Differences between means were evaluated with the TTEST procedure (SAS Institute, 1985). Pearson correlation coefficients (Steel and Torrie, 1980) were computed as a measure of relationships among several body components and production parameters. The Pearson correlation coefficients were computed across all treatments. The correlations of body weights and age at sexual maturity were computed as partial correlations adjusted for treatment differences using GLM. Stepwise regression (SAS Institute, 1985) was used to determine the relative contribution of BW at selected times during the breeder cycle on settable egg production. Simple regression of day of

sexual maturity or settable egg production on BW at first egg was computed within treatments. Unless otherwise stated, all statements of significance were based on testing at the .05 level.

Results and Discussion

Rearing Period

During the rearing period (0-28 wk), FF control birds consumed 65.8 kg of feed each, consisting of 188,462 kcal ME, and 10.9 kg of protein. The LP, R10, and R20 treatments consumed 95.5%, 84%, and 74% of FF feed levels in this period (Table II-3). Weekly feed consumption values are presented in Table V-1 (Appendix 1). Protein intake in the feed restricted treatments was 9.5, 9.1 and 8.1 kg for the LP, R10, and R20 groups respectively. The LP birds consumed 13% less protein and 8% less energy than FF birds despite only a 4.5% lower feed intake. Total protein intake in LP birds was very similar to that of the R10 group. All restricted birds consumed significantly less protein, and R10 and R20 birds significantly less feed than FF controls.

Complete BW data for the grower period are presented in Table II-4. BW of the quantitatively restricted groups (R10 and R20) were significantly lower than FF BW by 6 wk of age. The BW of the LP birds was significantly different than FF BW by 14 wk of age, 2 wk after the onset on restriction in these birds. The target BW for the R10 and R20 treatments of 10% and 20% below FF BW was achieved between 16 and 18 wk, and maintained until the end of the restriction period at 28 wk (Figure II-1). At this time the FF birds weighed significantly more than all restricted treatment birds. The LP birds had a similar BW to the R10 birds, likely a reflection of their similar protein intakes. The total BW gain for the grower period was significantly different, with restricted birds gaining less than FF birds, and R20 birds gaining the least amount (Table II-3). Feed efficiency during this period, although not significantly different, was numerically superior in the R10 and R20 treatments. Shank lengths in the restriction treatments were affected in a similar manner to BW during the rearing period (Table II-5). At 28 wk, the shanks of quantitatively

restricted birds were significantly shorter than FF shanks, and the shanks of LP and R10 birds were similar in length.

The average flock uniformity (% within $\pm 10\%$ of mean BW) improved throughout the grower period in all treatments except R20, which did not change between the period from 4-12 wk to 13-28 wk (Table II-6). From 13-28 wk, the uniformity in the R10 and R20 treatments was significantly worse than that of the FF and LP treatments, which were being *ad libitum* fed. When examining uniformity on a weekly basis (Figure V-2, Appendix 1), quantitative restriction did not have a negative effect on uniformity until 14 weeks of age, from which time the uniformity was reduced to a plateau at 20 wk. Uniformity was significantly worse in the R20 treatment than the R10 treatment in this period (Table II-6). It may be of benefit to consider using nutrient dilution in combination with the quantitative restriction programs during rearing to counteract the negative effects on flock uniformity. Zuidhof *et al.* (1993) diluted daily feed allotments for broiler breeders with 15% oat hulls to slow feed disappearance, and found flock uniformity to improve over time compared to birds on the undiluted control diet.

At 28 wk of age, The FF group had the largest breast muscle weight at 4.1 kg, and the LP, R10, and R20 treatments were 9, 8, and 20% less than this respectively (Table II-7). The abdominal fatpad was the heaviest in the LP treatment (267 g), followed by the FF, R10, and R20 treatments at 3, 16 and 39% smaller respectively (Table II-8). The R20 birds had the smallest breast muscles and fatpads. As a percentage of BW, there were no differences between treatments for either breast muscle or fatpad weight, although the fatpad of the R20 treatment was numerically smaller. Liver size and liver lipid content followed a similar pattern, with the FF group having the highest weights, and the R20 group the lowest (Table II-9, II-10). Total carcass protein, lipid, and water weights were the greatest in the FF treatment, with consistently significantly low values for the R20 group (Table II-11, II-12, II-14). On a percentage basis, there were no significant differences, although the R20 group had the highest protein and lowest lipid content, while the LP group had the highest lipid content. Weight of ash was not affected by feed restriction (Table II-13). As an indicator of bone

mineralization, this suggests that bone growth was less influenced by nutrient deprivation than muscle and adipose tissue were.

The percentage of carcass fat and abdominal fatpad in the current study were both less than expected. Previous work with smaller strains by Miles and Leeson (1990b), and Hocking (1992a, 1992b) show the fat content of full-fed birds at photostimulation varies between 19 and 24%. Lipid levels of male-line females were found to be 24.6% (Hocking, 1992a) compared to a 14% level in the current study (Table II-12). Abdominal fatpads represented 2.5 to 4% of BW in various turkey strains (Hocking, 1992a, 1992b), compared to a 2% peak in this study (Table II-8). Strain differences could contribute to these differences as well.

In the only other reported study using male-line breeder hens, Hocking (1992a) did not observe any differences between *ad libitum* fed and minus 20% BW birds in carcass lipid content (24.6 vs. 24.6%) or fatpad weight as a percentage of BW (3.7 vs. 4.2%). In the current study there was a numerical difference in FF compared to R20 treatment levels of carcass fat (13.7 vs. 12.3%), and in fatpad as a percentage of BW (1.9 vs. 1.6%). These birds were slightly more sensitive to the effects of feed restriction, which may be partly due to their body weight at photostimulation (28 to 30 wk) being 20% less than that of the birds of Hocking (1992a).

Breeder Period

Feed consumption during the breeder period was not significantly different between treatments, with feed intake ranging from 54.4 kg (FF) to 50.7 kg (R20) per bird (Table II-3). Feed intake to sexual maturity was significantly lower in the FF treatment compared to the restriction treatments, with 9.3 kg consumed per bird compared to levels 13, 14, and 24% higher in the LP, R10, and R20 treatments respectively. Differences were due both to differences in days to sexual maturity, and to differences in feed intake per day. The protein intake in this period in the FF, LP, R10, and R20 treatments was 1.4, 1.5, 1.5, and 1.7 kg per bird respectively. Protein intake accounts in part for the significant difference in BW gain from 28 wk to sexual maturity (Table II-3). The FF treatment gained .4 kg, the LP and R10 treatments gained .76 and .67 kg respectively, and the R20

treatment gained 1.13 kg. Despite the BW gains in restricted treatments, BW was still significantly different at sexual maturity, with birds in the FF, LP, R10, and R20 treatments weighing 14.6, 13.9, 13.5, and 12.2 kg respectively⁵. The gain in the R20 treatment appears to be compensatory growth as a result of *ad libitum* access to feed. The R20 treatment gained the most abdominal fat, liver, liver lipids (Table II-8, II-9, II-10), and high amounts of breast tissue, carcass protein, ash and water (Table II-7, II-11, II-13, II-14). There were significant increases in liver weight and lipids, and in ash and water content in this treatment. The LP treatment had increased breast muscle size and protein content in this period (Table II-7, II-11), possibly also a compensatory response due to increased access to protein. The significant increase in liver lipid levels and substantial gains in liver size in the restricted treatments signify a positive energy balance in these birds.

Carcass fat content increased by 250 g in FF treatment, and 200 g in the restriction treatments between 28 wk and first egg (Table II-12). Of this fat, 10, 20, 20, and 50 g is accounted for by increased fatpad size in the FF, LP, R10, and R20 treatments respectively (Table II-8). The remainder of the fat is presumably predominantly for ovary growth (240, 180, 180, and 150 g for FF, LP, R10, and R20 respectively). Ovary weight was found to be highly correlated with BW ($r = .49$, $P \leq .0001$), breast muscle weight ($r = .37$, $P \leq .0004$), and fatpad size ($r = .37$, $P \leq .0004$). Reducing fat content and body size in turkeys can result in improved egg production through a decrease in the number of follicles and defective eggs, and possibly an increase in overall egg production (Miles and Leeson, 1990a; Hocking, 1992b). Considering the strong relationship between ovary size and follicle numbers and arrangement (Section III), it would appear that the effects of feed restriction on body composition at first egg are advantageous to ovary morphology.

The mean day of sexual maturity (days past photostimulation) was 25.8, 26.9, 27.2, and 28.5 days for birds of the FF, LP, R10, and R20 treatments respectively. Although only a 2.7 day difference, R20 birds were significantly slower than FF birds in reaching sexual maturity. It is well known that feed restriction during rearing can cause a delay in sexual maturity (Hester and Stevens,

⁵Values significantly different at $P < .05$ level, with the superscripts, a, b, b, and c assigned to the FF, LP, R10 and R20 treatment groups respectively. SEM = 0.2 kg

1990), although there is usually no effect on egg production. The length of the delay does not appear to be linked to egg production either, as delays of 40 to 50 days have been shown to have no influence on settable egg production (Voitle *et al.*, 1973). In broiler breeders, it has been found that full-fed birds depend on reaching a critical age for the onset of egg production, while feed restricted birds with delayed maturity are dependent on reaching critical body weight and carcass fat levels (Brody *et al.*, 1984; Katanbaf *et al.*, 1989). In turkeys, the proportion of carcass fat has been demonstrated to double between 18 and 30 wk of age (Hocking, 1992b), with substantial delays in sexual maturity in the feed restricted birds with lower fat content. The carcass fat levels of 12 to 14% in the current study (Table II-12) appear adequate for age being the signal for sexual maturity. The small delay observed in the maturation of the R20 birds could be due to a delay in the maturation of the hypothalamic-adenohypophyseal axis, which would slow the production of hormones crucial to the development of the reproductive tract. BW at first egg was found to have an influence on day of sexual maturity. The correlation between BW and age of sexual maturity was positive ($r = .22$, $P \leq .011$) when treatment differences in BW were removed. Regression analysis within treatments of day of sexual maturity on BW at first egg indicated a significant difference within the LP treatment, where an increase of 1 kg BW was predicted to delay maturity by 2.2 days ($P \leq .005$). Graphical examination of the data showed this to be a relationship of the values at the extremes, as the average birds were all fairly clumped.

In turkey breeders there is a sudden drop in feed intake as the first eggs are laid, just after 30 wk of age (Whitehead, 1989). In the current study, this resulted in a BW decline that did not level off until 40 to 41 wk (Table II-4). At this time the growth curves of the FF, LP, and R10 treatments were indistinguishable from each other, while the R20 treatment BW was significantly less than the other treatments (Figure II-3). With regard to BW, the effect of feed restriction in the LP and R10 treatments was to flatten the growth curve through the onset of production and early lay. The growth curve of the R20 treatment was permanently lower, indicating stunted growth. Shank length, which is an indicator of frame size, was significantly lower throughout the breeder period in the R20 treatment (Table II-5). Borron *et al.*, (1974) also observed reduced shank length in turkeys under

feed restriction conditions. Owings and Sell (1980), concluded that restricting feed intake to less than 80% of full-fed levels limits growth. Whitehead (1989) stated that BW restrictions of up to 20% in the larger turkey strains does not impair reproduction. Turkeys in the R20 group were restricted to 74% of full-fed values during rearing (Table II-3), and restricted to 80% of full-fed BW.

Weight loss between sexual maturity and 40 wk was significantly greater in the FF treatment than in the restricted treatments, with a loss of 1.9 kg compared to 1.2, .9, and .8 kg for the LP, R10, and R20 treatments respectively (Table II-3). On average, there was a significant loss of 240 g of carcass protein in all hens (Table II-11). Protein loss was predominately breast muscle, for which the FF, LP, R10, and R20 treatments there was a loss of 700, 1100, 700, and 400 g respectively (Table II-7). Breast muscle as a percentage of BW declined by 4% between 28 and 40 wk, while carcass protein declined only 1%. This difference in utilization demonstrates that breast muscle is preferentially catabolized over other carcass protein sources. The loss of abdominal fat between first egg and 40 wk was not significant, although greater in the FF and LP treatments (Table II-8). The decline in total lipids was substantially greater, and significantly different on average, with a 350, 350, 130, and 90 g loss for the FF, LP, R10, and R20 treatments respectively (Table II-12). While the liver weights of the R10 and R20 treatments dropped significantly in this period (Table II-9), liver lipid levels increased, and kept pace with the levels of the FF and LP treatments (Table II-10). The composition of the hens of all treatments was very similar at 40 wk of age. There were no significant or numerical differences between treatments for breast muscle, fatpad or liver lipid weights (Table II-7, II-8, II-10), and no differences for the percentage of carcass protein, lipid, ash, or water (Table II-11, II-12, II-13, II-14). This is similar to what Hocking (1992b) found in hens restricted to 60% of full-fed BW during rearing. By 6 wk after photostimulation, restricted birds had similar proportions of fat and protein to full-fed controls.

During the period of weight loss in early lay, the hen presumably used fat stores. In hens with minimal fat, such as a feed restricted bird, a minimal weight loss, and a greater feed intake are expected to meet energy demands (Whitehead, 1989). The pattern of protein and fat loss in the R10 and R20 treatments demonstrate the pattern of a bird deficient of nutrient stores, while the LP

treatment was found to act more like the FF treatment group. The excess feed intake of the quantitatively restricted birds was not apparent in the breeder period (29 to 48 wk), as the basal metabolic requirement was lower in the smaller bodied R10 and R20 hens.

In the final portion of the laying period (41 to 48 wk), the nutrient demands for egg production are in decline as egg production drops, and the turkeys are beginning to gain weight again. The BW gains in this period were not significantly different (Table II-3). The FF treatment behaved differently than the restricted treatments in this period, with a significant loss in carcass protein and fat, while all other treatments gained protein and fat (Table II-11, II-12). Liver size and lipid content reflected this altered metabolic state, with a substantially lower liver size, and significantly lower lipid content than the restricted treatments (Table II-9, II-10). The LP and R10 treatments had substantial gains in fatpad weight, and percentage of carcass fat (Table II-8, II-12). There was a significant increase in liver size in the R10 and R20 treatment groups (Table II-9), although liver lipids in the R20 group remained the same, while they increased significantly in the R10 group (Table II-10). The increases in liver lipid levels appeared closely related to gains in carcass lipids and fatpad size, as it was the greatest in the LP and R10 treatments. The increase in liver size in the R10 and R20 treatments was associated with increases in ovary size at this time (Section III). Liver lipid weight was correlated more strongly with fatpad size than liver weight was ($r = .60$ rather than $.37$, $P \leq .0001$). While ovary weight correlated with liver weight ($r = .27$, $P \leq .01$), there was no relationship to liver lipids.

The average flock uniformity early in the breeder period did not change from late grower period mean (Table II-6). However, there was a significant drop in the uniformity of the LP treatment, and a significant increase in the R20 group value. The improvement in R20 uniformity was due to *ad libitum* access to the breeder diet. Full-feeding removes the advantage of the aggressive birds in feed access, and keeps them from growing disproportionately larger (Petitte, *et al.*, 1981). Uniformity was good until 40 wk, at which time values became more variable due to low bird numbers, and the presence of non-laying birds following alternate growth curves (Figure V-2, Appendix 1).

Throughout the breeder period, the proportion of the breast muscle fluctuated in the same pattern as BW (Table II-7), declining through most of the period, and increasing near the end. Breast weight was found to be highly correlated to BW ($r = .84$, $P \leq .0001$). The weight of liver lipids, and the proportion of abdominal fatpad increased steadily throughout the laying cycle (Table II-8, II-10), although the weight of the fatpad was highly correlated with BW ($r = .50$, $P \leq .0001$). On average, the R20 treatment had the greatest carcass protein and ash content (Table II-11, II-13) and the lowest carcass lipid levels (Table II-12). The LP treatment had the highest lipid content (Table II-12), and significantly the highest fatpad weight. It is suspected that the extra fat is due to over consumption of the low protein diet during rearing to compensate for deficient protein levels, resulting in excess energy intake. Excess fat production could also result from an amino acid deficiency, as the carbon skeletons of unused amino acids can be utilized for fat formation. The increased fat in LP treatment birds may also be responsible for the poor feed efficiency in this treatment compared to the other restriction treatments (Table II-3). Excess fat deposition in fast growing birds has been observed to be detrimental to feed efficiency (Brody, 1935), due to the high energy density of fat. Besides its influence on ovary size and defective egg production, excess fat can also be detrimental to reproduction through a reduction in sperm storage efficiency due to an infiltration of fat in the sperm storage glands at the uterovaginal junction (McDaniel *et al.*, 1981), and through reduced motility of the infundibulum.

The effects of the restriction programs on egg production, ovary morphology, and laying patterns are reported in Section III. Treatment had no significant effect on egg production, although individual hens in the restriction treatments laid numerically more eggs on average than FF treatment hens did. Stepwise regression analysis showed BW at first egg to be the weight that had the most effect on settable egg production ($r^2 = .14$, $P \leq .0012$). BW at first egg was negatively correlated to settable egg production ($r = -.37$, $P \leq .0015$). Regression analysis within treatments of settable egg production on BW at first egg indicated a significant difference within the LP ($P \leq .034$) and R20 ($P \leq .018$) treatments, where for every kg increase in body weight, a loss of 4.7 and 3.0 eggs was predicted respectively.

Total feed consumption (0-48 wk) was significantly different between the FF and R20 treatment group, with the FF group birds each consuming 120 kg, and the LP, R10, and R20 birds consuming 97%, 89%, and 83% of this level respectively (Table II-3). Total protein intake in the LP, R10, and R20 treatments was 92%, 88%, and 82% respectively of the FF treatment intake of 18.9 kg. These results demonstrate the potential for substantial feed saving, particularly in the grower period, with negative effects on egg production.

Throughout the breeder period, particularly toward the end, a number of hens in each treatment went out of production. This phenomenon was more pronounced in the R10 and R20 treatments. There was no relationship between body size and poor persistence of lay within a treatment. Although the non-laying hens in all treatments were lighter than their laying counterparts at 48 wk, much of this effect likely came after laying ceased, where broody behavior would cause weight loss in a portion of these birds. Fatpad proportions were significantly lower in non-laying birds in most treatments (Table II-8). Breast muscle weight was similar in restriction treatment groups, and significantly increased in FF non-layers (Table II-7). The amount of carcass protein and percentage of lipid followed a similar pattern, although total fat increased in FF non-layers (Table II-11, II-12). Liver weight and lipid levels were significantly lower in the non-layers of the restriction treatments and numerically lower in the FF treatment (Table II-9, II-10). The reduced liver weights and fat levels seen in non-laying turkeys is partly due to reduced circulating levels of estrogen. The release of estrogens into the blood of a bird nearing sexual maturity will cause an increase in plasma concentrations of fatty acids associated with impending egg production from the liver (Bajpayee and Brown, 1972), along with increased yolk proteins (Moran, 1987). The major source of estrogens is the small ovarian follicles (Robinson and Etches, 1986), which depend on a functioning reproductive hormone network in order to generate estrogen.

Mortality throughout the experiment was not found to be treatment related. There were, however, treatment differences for birds culled. For prolapsed uterus, which tends to be BW related, there was one cull for each of the FF, LP, and R10 treatments. There were four birds culled for bad legs during the breeder period, all of them in the FF treatment. There were hens with poor legs and

swollen hock joints still in the experiment, with the majority of them being large birds. Figure II-3 shows the weight of the shank (leg from the hock joint down, including the foot) throughout the breeder period. Unlike BW and carcass traits, which became more similar as time went on, significant differences remain in shank weight for the entire breeder period. Apart from differences accounted for by shank length, it is possible that the weight difference reflects an increased size of the hock joint from swelling and infection brought on by the bird's extreme weight.

The three rearing restricted feeding regimens all had an effect on carcass traits during the breeder period, particularly prior to 40 wk of age. The R10 and R20 treatments, however, were more effective than the LP treatment at reducing fat levels and BW at photostimulation and at sexual maturity. Feed consumption was reduced, and feed efficiency improved to a greater degree in the quantitative restriction treatments. These results concur with those of Miles and Leeson (1990a, 1990b), who found that limited daily access to feed during rearing most effectively reduced the proportion of fat while increasing protein content. It was concluded that quantitative feed restriction may be the only effective method of reducing obesity in turkey breeders. Noll *et al.* (1991) also found limited daily access to feed to be the most effective method of reducing BW. Hocking (1992b) found quantitative feed restriction to be effective in reducing body size, feed intake, and fat content, with no effect on the proportion of protein. Daily feed restriction methods appear to generate the greatest differences in turkey body size, composition, with lower feed costs.

TABLE II-1. Age of feeding of experimental diets.

Age (wk)	Feeding Regimen ¹			
	FF	LP	R10	R20
	Diet fed			
0 - 4	S1	S1	S1	S1
4 - 8	S2	S2	S2	S2
8 - 12	G1	G1	G1	G1
12 - 16	D1	D3	D1	D1
16 - 20	D2	D3	D2	D2
20 - 28	D3	D3	D3	D3
28 - 48	BR	BR	BR	BR

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

TABLE II-2. Percentage composition and analysis of experimental diets

Ingredients	Diets							
	SI ¹	S2	G1	D1	D2	D3	BR	
Ground yellow corn	---	37.37	50.04	53.98	38.74	37.47	45.78	
Ground wheat	41.90	15.00	13.40	17.90	35.00	35.00	25.00	
Ground barley	---	---	---	---	10.00	20.00	10.00	
Soybean meal (47%)	48.00	32.30	24.00	18.80	5.10	1.30	8.30	
Corn gluten meal	2.00	2.00	3.60	2.00	2.00	---	2.00	
Canola meal	---	6.00	2.00	2.00	4.90	2.00	---	
Canola oil	---	1.50	2.00	1.20	---	---	0.50	
Animal fat	2.00	---	---	---	---	---	---	
Ground limestone	2.50	1.90	1.70	1.40	1.40	1.50	5.70	
Biofos	2.00	2.60	2.00	1.50	1.60	1.60	1.60	
Microingredients	0.50 ²	0.50 ¹	0.50 ⁴	0.50 ⁴	0.50 ⁴	0.50 ⁴	0.50 ³	
Iodized salt	0.35	0.34	0.32	0.29	0.28	0.28	0.31	
NF 180	0.10	---	---	---	---	---	---	
L-Lysine	---	0.20	0.20	0.20	0.25	0.20	0.09	
DL-Methionine	0.10	0.19	0.14	0.13	0.13	0.05	0.05	
Choline chloride	0.50 ⁵	0.10	0.10	0.10	0.10	0.10	0.15	
Vitamin C	---	---	---	---	---	---	0.20	
Amprol	0.05	---	---	---	---	---	---	
Calculated analysis								
ME (kcal/kg)	2703	2798	3000	3002	2859	2860	2833	
CP (%)	28.90	24.25	21.28	17.40	15.32	12.46	14.69	
Calcium (%)	1.35	1.30	1.09	0.89	0.89	0.90	2.50	
Available P (%)	0.54	0.70	0.55	0.44	0.46	0.45	0.45	
Lysine (%)	1.61	1.45	1.15	1.00	0.75	0.55	0.60	
Methionine (%)	0.54	0.60	0.51	0.45	0.39	0.25	0.30	

¹SI diet is a University of Alberta diet. All other diets formulated by Dr. J. R. Blackman of Central Soya Canada Ltd.

²Provided per kg of diet: vitamin A, 12,000 IU; vitamin D, 3,000 IU; vitamin E, 40 IU; vitamin K, 2.0 mg; pantothenic acid 20 mg; riboflavin, 6.0 mg; folacin, 1.2 mg; niacin, 90 mg; thiamine, 3.0 mg; pyridoxine, 5.5 mg; vitamin B12, .02 mg; biotin, .25 mg; Fe, 100 mg; Mn, 75 mg; Cu, 15 mg; Zn, 80 mg; and Se, .3 mg.

³Provided per kg of diet: vitamin A, 12,000 IU; vitamin D, 4,500 IU; vitamin E, 45 mg; vitamin K, 2.5 mg; pantothenic acid 25 mg; riboflavin, 15 mg; folacin, 2.5 mg; niacin, 100 mg; thiamine, 3.0 mg; pyridoxine, 5.0 mg; vitamin B12, .04 mg; biotin, .30 mg; Fe, 80 mg; Mn, 120 mg; Cu, 10 mg; Zn, 120 mg; and Se, .3 mg.

⁴Provided per kg of diet: vitamin A, 9,000 IU; vitamin D, 3,000 IU; vitamin E, 25 IU; vitamin K, 2.0 mg; pantothenic acid 20 mg; riboflavin, 10 mg; folacin, 2.0 mg; niacin, 80 mg; thiamine, 2.0 mg; pyridoxine, 3.5 mg; vitamin B12, .02 mg; biotin, .15 mg; Fe, 60 mg; Mn, 90 mg; Cu, 8 mg; Zn, 90 mg; and Se, .3 mg.

⁵Choline chloride premix in the S1 diet supplies choline chloride at level of 100 mg/kg.

TABLE II-3. Feed intake, major body weight changes, and feed efficiency of turkey breeder hens reared under different feeding regimens.

Variable	Feeding Regimen ¹				SEM
	FF	LP	R10	R20	
	-----Feed per bird (kg)-----				
<u>Feed Intake (per bird):</u>					
Grower period (4-28 wk)	65.8 ^a	62.9 ^{ab}	55.7 ^{bc}	48.9 ^c	2.1
Breeder period					
28 wk to first egg	9.3 ^b	10.5 ^a	10.6 ^a	11.5 ^a	.3
First egg to 48 wk	45.1	43.2	40.4	39.2	2.1
Total (28-48 wk)	54.4	53.6	50.9	50.7	2.4
Total feed consumed	120.2 ^a	116.5 ^a	106.6 ^{ab}	99.6 ^b	4.0
	-----BW change (kg)-----				
<u>Body weight gains</u>					
Grower period (4-28 wk)	14.5 ^a	13.8 ^b	13.4 ^b	12.1 ^c	.2
Breeder period					
28 wk to first egg	.38 ^c	.76 ^b	.67 ^b	1.13 ^a	.09
First egg to LBW ²	-1.94 ^a	-1.15 ^b	-.90 ^b	-.80 ^b	.19
LBW to 48 wk	.80	.42	.17	.51	.33
Feed efficiency (0-28 wk) (feed:gain ratio)	4.53	4.56	4.16	4.04	.14

^{a-c}Means within a row with no common superscripts differ significantly ($P < .05$).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²LBW = Lowest body weight of the breeder period, occurring between 40 and 41 weeks of age.

TABLE II-4. Body weights of turkey breeder hens during the grower period (0 to 28 wk), and the breeder period (29-48 wk)¹.

Age (wk)	n ³	Feeding Regimen ²			
		FF	LP	R10	R20
		----- (Body weight (kg) ± SEM) -----			
4	45	.83 ± .02	.83 ± .02	.83 ± .02	.83 ± .02
6	45	1.81 ± .03 ^a	1.83 ± .03 ^a	1.51 ± .03 ^b	1.47 ± .03 ^b
8	45	3.44 ± .05 ^a	3.44 ± .05 ^a	2.72 ± .05 ^b	2.56 ± .05 ^c
10	45	4.77 ± .07 ^a	4.82 ± .07 ^a	4.35 ± .07 ^b	4.04 ± .07 ^c
12	44	6.52 ± .08 ^a	6.71 ± .09 ^a	6.11 ± .09 ^b	5.35 ± .08 ^c
14	44	8.13 ± .10 ^a	7.65 ± .10 ^b	7.19 ± .10 ^c	6.54 ± .10 ^d
16	44	9.47 ± .11 ^a	8.90 ± .11 ^b	8.71 ± .11 ^b	7.75 ± .11 ^c
18	44	10.76 ± .14 ^a	10.06 ± .14 ^b	9.35 ± .14 ^c	8.67 ± .13 ^d
20	43	11.66 ± .15 ^a	10.74 ± .15 ^b	10.28 ± .15 ^c	9.13 ± .14 ^d
22	43	12.79 ± .16 ^a	11.67 ± .16 ^b	11.28 ± .16 ^b	9.92 ± .16 ^c
24	43	13.57 ± .17 ^a	12.68 ± .17 ^b	11.95 ± .17 ^c	10.90 ± .17 ^d
26	43	14.13 ± .18 ^a	13.54 ± .18 ^b	12.61 ± .18 ^c	11.46 ± .18 ^d
28	35	14.59 ± .20 ^a	13.87 ± .21 ^b	13.45 ± .20 ^b	12.16 ± .19 ^c
29	35	15.06 ± .20 ^a	14.28 ± .20 ^b	13.92 ± .20 ^b	12.64 ± .19 ^c
30	35	15.17 ± .20 ^a	14.54 ± .20 ^b	14.14 ± .19 ^b	13.01 ± .19 ^c
31	35	15.25 ± .20 ^a	14.61 ± .20 ^b	14.24 ± .19 ^b	13.26 ± .18 ^c
32	27	14.77 ± .25 ^a	14.29 ± .25 ^{ab}	14.00 ± .22 ^b	13.34 ± .22 ^c
33	25	14.96 ± .25 ^a	14.32 ± .25 ^{ab}	14.12 ± .24 ^b	13.22 ± .23 ^c
34	25	14.65 ± .24 ^a	14.06 ± .25 ^{ab}	13.92 ± .23 ^b	13.02 ± .22 ^c
35	24	14.27 ± .25 ^a	13.84 ± .26 ^a	13.61 ± .25 ^a	12.94 ± .24 ^b
36	24	14.31 ± .27 ^a	13.82 ± .28 ^a	13.62 ± .26 ^a	12.87 ± .25 ^b
37	24	13.83 ± .27 ^a	13.40 ± .28 ^a	13.40 ± .26 ^a	12.53 ± .26 ^b
38	24	13.70 ± .28 ^a	13.34 ± .29 ^a	13.33 ± .28 ^a	12.50 ± .27 ^b
39	24	13.73 ± .28 ^a	13.45 ± .29 ^a	13.43 ± .27 ^a	12.58 ± .27 ^b
40	16	13.63 ± .33 ^a	13.56 ± .34 ^a	13.62 ± .32 ^a	12.44 ± .31 ^b
41	16	13.29 ± .33 ^a	13.41 ± .34 ^a	13.45 ± .32 ^a	12.19 ± .31 ^b
42	16	13.44 ± .34 ^a	13.46 ± .35 ^a	13.41 ± .33 ^a	12.25 ± .32 ^b
43	15	13.65 ± .33 ^a	13.51 ± .33 ^a	13.53 ± .31 ^a	12.41 ± .30 ^b
44	15	13.47 ± .37 ^a	13.49 ± .36 ^a	13.55 ± .33 ^a	12.38 ± .32 ^b
45	15	13.74 ± .41 ^a	13.59 ± .40 ^{ab}	13.46 ± .37 ^{ab}	12.57 ± .37 ^b
46	15	13.71 ± .43 ^a	13.75 ± .40 ^a	13.47 ± .37 ^{ab}	12.54 ± .37 ^b
47	15	13.91 ± .44 ^a	13.83 ± .40 ^a	13.62 ± .38 ^{ab}	12.70 ± .38 ^b

^{a-d}Means within a row with no common superscripts differ significantly ($P < .05$).

¹Weight data for week 48 was not available.

²Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

³n = Average number of birds in each treatment.

TABLE II-5. Shank length of turkey breeder hens reared under different feeding regimens.

Age (wk)	n ²	Feeding Regimen ¹			
		FF	LP	R10	R20
(Shank length ³ (mm) ± SEM)					
4	45	50.5 ± .4	50.6 ± .4	50.5 ± .4	50.6 ± .4
8	45	81.7 ± .6 ^a	81.5 ± .6 ^a	77.0 ± .6 ^b	75.8 ± .5 ^b
12	44	96.2 ± .5 ^{ab}	96.9 ± .5 ^a	95.4 ± .5 ^b	93.0 ± .5 ^c
16	44	100.8 ± .5 ^a	100.7 ± .5 ^a	100.0 ± .5 ^a	98.6 ± .5 ^b
20	43	100.8 ± .5	99.9 ± .5	99.6 ± .5	99.6 ± .5
24	43	101.7 ± .5 ^a	100.8 ± .5 ^{ab}	100.7 ± .5 ^{ab}	99.7 ± .5 ^b
28	35	102.8 ± .5 ^a	101.6 ± .5 ^{ab}	101.2 ± .5 ^b	100.6 ± .5 ^b
36	24	102.1 ± .8 ^a	100.9 ± .8 ^{ab}	101.1 ± .7 ^{ab}	99.7 ± .7 ^b
44	15	102.6 ± .9 ^a	100.2 ± .8 ^{ab}	101.3 ± .8 ^a	99.1 ± .8 ^b
48	15	102.7 ± .9 ^a	101.4 ± .9 ^{ab}	101.7 ± .8 ^a	99.5 ± .8 ^b

^{a-c}Means within a row with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²n = Average number of birds in each treatment.

³Shanks were measured from under the spur to the top of the hock joint.

TABLE II-6. Flock uniformity of turkey breeder hens reared under different feeding regimens.

Age (wk)	Feeding Regimen ¹				Mean
	FF	LP	R10	R20	
(Percentage (within $\pm 10\%$ of mean BW) \pm SEM)					
4 to 12	73.8 \pm 3.0 ^{a, x}	70.6 \pm 3.0 ^{ab, y}	66.1 \pm 3.0 ^{ab, x}	65.7 \pm 3.0 ^{b, x}	69.1 \pm 1.5 ^x
13 to 28	83.7 \pm 2.3 ^{a, w}	85.0 \pm 2.3 ^{a, w}	76.2 \pm 2.3 ^{b, w}	65.9 \pm 2.3 ^{c, x}	77.7 \pm 1.2 ^w
29 to 40	82.5 \pm 1.9 ^{a, w}	78.1 \pm 1.9 ^{ab, x}	76.2 \pm 1.9 ^{b, w}	74.6 \pm 1.9 ^{b, w}	77.9 \pm 1.0 ^w
41 to 47	78.0 \pm 2.5 ^{a, wx}	75.5 \pm 2.5 ^{a, xy}	76.3 \pm 2.5 ^{a, w}	60.0 \pm 2.5 ^{b, x}	72.5 \pm 1.3 ^x
Mean	79.5 \pm 1.2 ^a	77.3 \pm 1.2 ^a	73.7 \pm 1.2 ^b	66.6 \pm 1.2 ^c	

^{a-c}Means within a row with no common superscripts differ significantly ($P < .05$).

^{w-y}Means within a column with no common superscripts differ significantly ($P < .05$).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

TABLE II-7. Effect of feed allowance during rearing (0-28 wk) on breast muscle weight and weight as a percentage of body weight at photostimulation and selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
----- (Breast muscle weight (kg) ± SEM) -----						
Photostim.	8	4.08 ± .17 ^{a, w}	3.70 ± .17 ^{ab, wx}	3.76 ± .17 ^{a, w}	3.26 ± .17 ^{b, wx}	3.70 ± .08 ^{wx}
Sex. Mat.	10	3.93 ± .15 ^{a, w}	4.01 ± .14 ^{a, w}	3.73 ± .16 ^{ab, wx}	3.41 ± .15 ^{b, wx}	3.77 ± .08 ^w
40 wk	8	3.24 ± .17 ^x	2.92 ± .18 ^z	3.00 ± .17 ^y	3.03 ± .18 ^x	3.05 ± .09 ^z
48 wk-L	6	3.15 ± .21 ^x	3.42 ± .18 ^{xy}	3.37 ± .18 ^{wxy}	3.43 ± .24 ^{wx}	3.34 ± .10 ^y
48 wk-NL	8	3.80 ± .18 ^{a, w}	3.20 ± .19 ^{b, yz}	3.31 ± .16 ^{b, xy}	3.58 ± .14 ^{ab, w}	3.47 ± .07 ^{xy}
Mean		3.64 ± .08 ^a	3.45 ± .08 ^{ab}	3.43 ± .05 ^{ab}	3.34 ± .08 ^b	
----- (Breast muscle weight (% of BW) ± SEM) -----						
Photostim.	8	29.3 ± .8 ^w	27.7 ± .8 ^w	29.3 ± .8 ^w	27.7 ± .8 ^{wx}	28.5 ± .4 ^w
Sex. Mat.	10	27.0 ± .7 ^x	27.4 ± .7 ^w	26.7 ± .7 ^x	26.1 ± .7 ^{xy}	26.8 ± .3 ^x
40 wk	8	25.0 ± .8 ^y	22.9 ± .8 ^y	24.4 ± .8 ^y	24.4 ± .8 ^y	24.2 ± .4 ^y
48 wk-L	6	23.5 ± 1.0 ^{b, y}	24.6 ± .8 ^{ab, xy}	25.0 ± .8 ^{ab, xy}	26.6 ± 1.1 ^{a, wxy}	24.9 ± .5 ^y
48 wk-NL	8	28.7 ± .8 ^{a, wx}	25.8 ± .9 ^{b, wx}	25.9 ± .7 ^{b, xy}	28.7 ± .7 ^{a, w}	27.3 ± .4 ^x
Mean		26.7 ± .4 ^a	25.7 ± .4 ^b	26.3 ± .3 ^{ab}	26.7 ± .4 ^a	

^{a-b}Means within a row with no common superscripts differ significantly (P<.05).

^{w-z}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Photostim. = photostimulation (28 wk); Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment; L = laying birds; NL = non-laying birds.

³n = Average number of birds in each treatment.

TABLE II-8. Effect of feed allowance during rearing (0-28 wk) on abdominal fatpad weight and weight as a percentage of body weight at photostimulation and selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
----- (Abdominal fatpad weight (g) ± SEM) -----						
Photostim.	8	258 ± 27 ^{ab, w}	267 ± 27 ^a	224 ± 27 ^{ab, x}	190 ± 27 ^{b, wx}	234 ± 14 ^w
Sex. Mat.	10	269 ± 24 ^w	284 ± 24	245 ± 25 ^{wx}	240 ± 24 ^w	260 ± 12 ^w
40 wk	8	229 ± 27 ^{wx}	247 ± 29	235 ± 27 ^{wx}	244 ± 29 ^w	239 ± 14 ^w
48 wk-L	6	217 ± 24 ^{b, wx}	324 ± 29 ^a	308 ± 29 ^{a, w}	241 ± 38 ^{ab, w}	273 ± 16 ^w
48 wk-NL	8	157 ± 31 ^{b, x}	260 ± 38 ^a	182 ± 25 ^{ab, x}	138 ± 24 ^{b, w}	184 ± 15 ^x
Mean		226 ± 13 ^b	278 ± 13 ^a	239 ± 12 ^b	210 ± 13 ^b	
----- (Abdominal fatpad weight (% of BW) ± SEM) -----						
Photostim.	8	1.86 ± .19 ^w	1.98 ± .19	1.74 ± .19 ^{wx}	1.60 ± .19 ^w	1.80 ± .09 ^w
Sex. Mat.	10	1.86 ± .17 ^w	1.94 ± .17	1.76 ± .17 ^{wx}	1.85 ± .17 ^w	1.85 ± .08 ^w
40 wk	8	1.73 ± .19 ^w	1.92 ± .20	1.89 ± .19 ^{wx}	1.94 ± .20 ^w	1.87 ± .10 ^w
48 wk-L	6	1.61 ± .23 ^{b, wx}	2.33 ± .20 ^a	2.27 ± .20 ^{a, w}	1.87 ± .26 ^{ab, w}	2.02 ± .11 ^w
48 wk-NL	8	1.17 ± .21 ^{b, x}	1.95 ± .26 ^a	1.42 ± .17 ^{ab, x}	1.07 ± .17 ^{b, x}	1.41 ± .10 ^x
Mean		1.65 ± .09 ^b	2.02 ± .09 ^a	1.82 ± .08 ^{ab}	1.67 ± .09 ^b	

^{a-b}Means within a row with no common superscripts differ significantly (P<.05).

^{w-x}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Photostim. = photostimulation (28 wk); Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment; L = laying birds; NL = non-laying birds.

³n = Average number of birds in each treatment.

TABLE II-9. Effect of feed allowance during rearing (0-28 wk) on liver weight and weight as a percentage of body weight at photostimulation and selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
------(Liver weight (g) ± SEM)-----						
Photostim.	8	173 ± 10 ^a	151 ± 10 ^{a, xy}	132 ± 10 ^{b, y}	140 ± 10 ^{b, x}	149 ± 5 ^{yz}
Sex. Mat.	10	163 ± 9 ^b	193 ± 8 ^{a, w}	167 ± 9 ^{b, x}	178 ± 9 ^{ab, w}	175 ± 5 ^x
40 wk	8	175 ± 12 ^a	174 ± 11 ^{a, wx}	135 ± 10 ^{b, y}	141 ± 11 ^{b, x}	156 ± 5 ^y
48 wk-L	6	178 ± 13	196 ± 11 ^w	200 ± 11 ^w	192 ± 14 ^w	191 ± 6 ^w
48 wk-NL	8	155 ± 11 ^a	133 ± 13 ^{ab, y}	126 ± 9 ^{b, y}	130 ± 9 ^{ab, x}	136 ± 5 ^z
Mean		169 ± 5 ^{ab}	170 ± 5 ^a	152 ± 4 ^c	156 ± 5 ^{bc}	
------(Liver weight (% of BW) ± SEM)-----						
Photostim.	8	1.24 ± .07 ^{a, wx}	1.13 ± .07 ^{a, x}	1.02 ± .07 ^{b, xy}	1.19 ± .07 ^{a, x}	1.15 ± .04 ^{yz}
Sex. Mat.	10	1.12 ± .06 ^{b, x}	1.32 ± .06 ^{a, w}	1.21 ± .07 ^{ab, x}	1.38 ± .06 ^{a, w}	1.26 ± .03 ^x
40 wk	8	1.31 ± .08 ^{a, wx}	1.36 ± .08 ^{a, w}	1.09 ± .07 ^{b, xy}	1.13 ± .08 ^{ab, x}	1.22 ± .04 ^{xy}
48 wk-L	6	1.35 ± .09 ^w	1.41 ± .08 ^w	1.48 ± .08 ^w	1.50 ± .10 ^w	1.43 ± .04 ^w
48 wk-NL	8	1.18 ± .08 ^{wx}	1.04 ± .09 ^x	1.01 ± .07 ^y	1.01 ± .06 ^x	1.06 ± .04 ^z
Mean		1.24 ± .03 ^{ab}	1.25 ± .03 ^a	1.16 ± .03 ^b	1.24 ± .03 ^{ab}	

^{a-b}Means within a row with no common superscripts differ significantly ($P < .05$).

^{w-z}Means within a column with no common superscripts differ significantly ($P < .05$).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Photostim. = photostimulation (28 wk); Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment; L = laying birds; NL = non-laying birds.

³n = Average number of birds in each treatment.

TABLE II-10. Effect of feed allowance during rearing (0-28 wk) on total liver lipid weight and on lipid weight as a percentage of liver weight at photostimulation and selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
----- (Total liver lipids (g) ± SEM) -----						
Photostim.	8	4.21 ± .38 ^{xy}	3.86 ± .38 ^y	3.37 ± .38 ^y	3.03 ± .38 ^x	3.61 ± .19 ^y
Sex. Mat.	10	4.78 ± .34 ^{wx}	5.23 ± .33 ^x	4.63 ± .36 ^x	5.04 ± .34 ^w	4.92 ± .17 ^x
40 wk	8	5.43 ± .41 ^w	5.97 ± .41 ^{wx}	5.10 ± .38 ^x	5.42 ± .41 ^w	5.48 ± .20 ^w
48 wk-L	6	4.85 ± .48 ^{c, wxy}	6.83 ± .41 ^{a, w}	6.25 ± .41 ^{ab, w}	5.18 ± .54 ^{bc, w}	5.78 ± .23 ^w
48 wk-NL	8	3.67 ± .41 ^y	3.59 ± .44 ^y	3.58 ± .36 ^y	2.90 ± .32 ^x	3.43 ± .19 ^y
Mean		4.59 ± .18 ^b	5.10 ± .18 ^a	4.59 ± .17 ^b	4.31 ± .18 ^b	
----- (Total liver lipids (% of liver weight) ± SEM) -----						
Photostim.	8	2.54 ± .24 ^x	2.68 ± .24 ^y	2.80 ± .24 ^x	2.41 ± .24 ^{xy}	2.61 ± .12 ^y
Sex. Mat.	10	3.02 ± .22 ^{wx}	2.78 ± .21 ^y	2.88 ± .23 ^x	2.96 ± .22 ^{wx}	2.91 ± .11 ^{xy}
40 wk	8	3.43 ± .24 ^w	3.68 ± .26 ^y	3.95 ± .24 ^w	3.87 ± .26 ^w	3.74 ± .13 ^w
48 wk-L	6	2.90 ± .31 ^{wx}	3.56 ± .26 ^y	3.25 ± .26 ^x	2.77 ± .35 ^{wxy}	3.12 ± .15 ^x
48 wk-NL	8	2.41 ± .26 ^x	2.99 ± .28 ^{wx}	2.88 ± .23 ^x	2.45 ± .21 ^y	2.68 ± .12 ^y
Mean		2.86 ± .11	3.13 ± .11	3.15 ± .11	2.89 ± .12	

^{a-c}Means within a row with no common superscripts differ significantly (P<.05).

^{w-y}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Photostim. = photostimulation (28 wk); Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment; L = laying birds; NL = non-laying birds.

³n = Average number of birds in each treatment.

TABLE II-11. Effect of feed allowance during rearing (0-28 wk) on total carcass protein weight and weight as a percentage of body weight at photostimulation and selected times during the breeder period (29-48 wk).

Time ³	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
----- (Total carcass protein (kg) ± SEM) -----						
Photostim.	8	2.28 ± .10 ^{a, w}	2.17 ± .10 ^{ab, wx}	2.14 ± .10 ^{ab}	2.01 ± .10 ^{b, wx}	2.15 ± .05 ^w
Sex. Mat.	10	2.27 ± .09 ^w	2.26 ± .09 ^w	2.17 ± .09	2.10 ± .09 ^{wx}	2.20 ± .04 ^w
40 wk	8	2.04 ± .10 ^w	1.98 ± .10 ^x	1.92 ± .10	1.91 ± .10 ^x	1.96 ± .05 ^x
48 wk-L	6	1.64 ± .12 ^{b, x}	2.11 ± .10 ^{a, wx}	2.05 ± .10 ^a	1.98 ± .14 ^{ab, wx}	1.95 ± .06 ^x
48 wk-NL	8	2.21 ± .11 ^w	2.08 ± .12 ^{wx}	2.12 ± .09	2.16 ± .08 ^{a, w}	2.14 ± .05 ^w
Mean		2.09 ± .05	2.12 ± .05	2.08 ± .04	2.04 ± .05	
----- (Total carcass protein (% of BW) ± SEM) -----						
Photostim.	8	16.7 ± .6 ^w	16.5 ± .6	16.9 ± .6	17.5 ± .6	16.9 ± .3 ^w
Sex. Mat.	10	15.9 ± .5 ^w	15.9 ± .5	15.9 ± .6	16.5 ± .5	16.1 ± .3 ^x
40 wk	8	16.2 ± .6 ^w	16.2 ± .6	15.9 ± .6	16.2 ± .6	16.1 ± .3 ^{wx}
48 wk-L	6	12.5 ± .7 ^{b, x}	15.5 ± .6 ^a	15.6 ± .6 ^a	16.0 ± .8 ^a	14.9 ± .4 ^y
48 wk-NL	8	16.5 ± .7 ^w	16.6 ± .7	16.7 ± .6	17.4 ± .5	16.8 ± .3 ^{wx}
Mean		15.5 ± .3 ^b	16.1 ± .3 ^{ab}	16.2 ± .3 ^{ab}	16.7 ± .3 ^a	

^{a-b}Means within a row with no common superscripts differ significantly (P<.05).

^{w-y}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Photostim. = photostimulation (28 wk); Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment; L = laying birds; NL = non-laying birds.

³n = Average number of birds in each treatment.

TABLE II-12. Effect of feed allowance during rearing (0-28 wk) on total carcass lipid weight and weight as a percentage of body weight at photostimulation and selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
------(Total carcass lipid weight (kg) ± SEM)-----						
Photostim.	8	1.88 ± .14 ^{a, w}	1.87 ± .14 ^{a, wx}	1.59 ± .14 ^{ab, x}	1.44 ± .14 ^{b, wx}	1.69 ± .07 ^{xy}
Sex. Mat.	10	2.14 ± .12 ^{a, w}	2.05 ± .12 ^{a, wx}	1.79 ± .13 ^{ab, wx}	1.64 ± .12 ^{b, w}	1.90 ± .06 ^w
40 wk	8	1.79 ± .14 ^{wx}	1.71 ± .14 ^x	1.66 ± .14 ^x	1.55 ± .14 ^{wx}	1.68 ± .07 ^{xy}
48 wk-L	6	1.38 ± .18 ^{c, x}	2.15 ± .14 ^{a, w}	2.08 ± .15 ^{ab, w}	1.63 ± .20 ^{bc, wx}	1.81 ± .08 ^{wx}
48 wk-NL	8	1.78 ± .16 ^{a, wx}	1.64 ± .18 ^{ab, x}	1.61 ± .13 ^{ab, x}	1.30 ± .12 ^{b, x}	1.58 ± .07 ^y
Mean		1.79 ± .07 ^a	1.88 ± .06 ^a	1.75 ± .06 ^a	1.51 ± .07 ^b	
------(Total carcass lipid weight (% of BW) ± SEM)-----						
Photostim.	8	13.7 ± .8 ^w	14.1 ± .8 ^{wx}	12.6 ± .8 ^x	12.3 ± .8 ^{wx}	13.2 ± .4 ^{wx}
Sex. Mat.	10	15.0 ± .8 ^{a, w}	14.4 ± .8 ^{ab, wx}	13.0 ± .8 ^{ab, x}	12.9 ± .8 ^{b, w}	13.8 ± .4 ^w
40 wk	8	14.0 ± .8 ^w	13.8 ± .8 ^{wx}	13.6 ± .8 ^{wx}	13.0 ± .8 ^w	13.6 ± .4 ^w
48 wk-L	6	10.5 ± 1.1 ^{b, x}	15.7 ± .8 ^{a, w}	15.8 ± .9 ^{a, w}	13.1 ± 1.2 ^{ab, w}	13.8 ± .5 ^w
48 wk-NL	8	13.2 ± 1.0 ^{wx}	12.8 ± 1.1 ^x	12.6 ± .8 ^x	10.3 ± .7 ^x	12.2 ± .4 ^x
Mean		13.3 ± .4 ^{ab}	14.2 ± .4 ^a	13.5 ± .4 ^a	12.3 ± .4 ^b	

^{a-c}Means within a row with no common superscripts differ significantly (P<.05).

^{w-y}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Photostim. = photostimulation (28 wk); Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment; L = laying birds; NL = non-laying birds.

³n = Average number of birds in each treatment.

TABLE II-13. Effect of feed allowance during rearing (0-28 wk) on total carcass ash weight and weight as a percentage of body weight at photostimulation and selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
------(Total carcass ash (g) ± SEM)-----						
Photostim.	8	323 ± 16	305 ± 16 ^x	302 ± 16 ^x	296 ± 16 ^x	307 ± 8 ^y
Sex. Mat.	10	341 ± 15	345 ± 15 ^x	331 ± 15 ^{wx}	339 ± 15 ^w	339 ± 7 ^{wx}
40 wk	8	353 ± 16	328 ± 16 ^x	336 ± 16 ^{wx}	328 ± 16 ^{wx}	336 ± 8 ^{wx}
48 wk-L	6	310 ± 21 ^b	389 ± 16 ^{a,w}	373 ± 17 ^{a,w}	333 ± 23 ^{ab,wx}	351 ± 10 ^w
48 wk-NL	8	338 ± 19	312 ± 21 ^x	317 ± 15 ^x	321 ± 14 ^{wx}	322 ± 9 ^x
Mean		333 ± 8	336 ± 8	332 ± 7	323 ± 8	
------(Total carcass ash (% of BW) ± SEM)-----						
Photostim.	8	2.37 ± .12 ^x	2.32 ± .12 ^y	2.40 ± .12 ^y	2.57 ± .12	2.42 ± .06 ^{xy}
Sex. Mat.	10	2.39 ± .11 ^x	2.43 ± .11 ^{xy}	2.42 ± .11 ^{xy}	2.66 ± .11	2.47 ± .05 ^{xy}
40 wk	8	2.78 ± .12 ^w	2.69 ± .12 ^{wx}	2.79 ± .12 ^{wx}	2.78 ± .12	2.76 ± .06 ^w
48 wk-L	6	2.37 ± .15 ^{b,x}	2.86 ± .12 ^{a,w}	2.84 ± .13 ^{a,w}	2.69 ± .17 ^{ab}	2.67 ± .07 ^{wx}
48 wk-NL	8	2.54 ± .14 ^{wx}	2.54 ± .15 ^{wxy}	2.49 ± .11 ^{xy}	2.60 ± .10	2.54 ± .06 ^x
Mean		2.49 ± .06 ^b	2.57 ± .06 ^{ab}	2.59 ± .06 ^{ab}	2.66 ± .06 ^a	

^{a-b}Means within a row with no common superscripts differ significantly (P<.05).

^{w-y}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Photostim. = photostimulation (28 wk); Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment; L = laying birds; NL = non-laying birds.

³n = Average number of birds in each treatment.

TABLE II-14. Effect of feed allowance during rearing (0-28 wk) on total carcass water weight and weight as a percentage of body weight at photostimulation and selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
------(Total carcass water (kg) ± SEM)-----						
Photostim.	8	9.14 ± .29 ^{a,wx}	8.81 ± .29 ^{a,wx}	8.57 ± .29 ^{ab}	7.79 ± .29 ^{b,x}	8.58 ± .15 ^{xy}
Sex. Mat.	10	9.48 ± .26 ^{a,w}	9.52 ± .26 ^{a,w}	9.35 ± .28 ^a	8.58 ± .26 ^{b,w}	9.23 ± .13 ^w
40 wk	8	8.47 ± .29 ^x	8.23 ± .29 ^x	8.14 ± .29	8.03 ± .29 ^{wx}	8.22 ± .15 ^y
48 wk-L	6	9.35 ± .37 ^{wx}	8.96 ± .29 ^{wx}	8.67 ± .31	8.49 ± .41 ^{wx}	8.87 ± .18 ^{wx}
48 wk-NL	8	9.14 ± .34 ^{wx}	8.59 ± .37 ^x	8.72 ± .28	8.69 ± .25 ^w	8.78 ± .16 ^x
Mean		9.12 ± .14 ^a	8.82 ± .14 ^{ab}	8.69 ± .13 ^b	8.31 ± .14 ^c	
------(Total carcass water (% of BW) _i ± SEM)-----						
Photostim.	8	67.0 ± 1.2 ^x	66.9 ± 1.2	67.9 ± 1.2	67.4 ± 1.2	67.3 ± .6
Sex. Mat.	10	66.3 ± 1.0 ^x	67.0 ± 1.0	68.4 ± 1.1	67.5 ± 1.0	67.3 ± .5
40 wk	8	67.0 ± 1.2 ^x	67.3 ± 1.2	67.5 ± 1.2	68.0 ± 1.2	67.4 ± .4
48 wk-L	6	74.7 ± 1.5 ^{a,w}	65.9 ± 1.2 ^b	65.9 ± 1.2 ^b	68.5 ± 1.6 ^b	68.8 ± .7
48 wk-NL	8	68.1 ± 1.3 ^x	68.5 ± 1.5	68.3 ± 1.1	70.1 ± 1.0	68.7 ± .6
Mean		68.6 ± .6	67.1 ± .5	67.6 ± .5	68.3 ± .5	

^{a-c}Means within a row with no common superscripts differ significantly (P<.05).

^{w-y}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Photostim. = photostimulation (28 wk); Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment; L = laying birds; NL = non-laying birds.

³n = Average number of birds in each treatment.

Average Body Weight (kg)

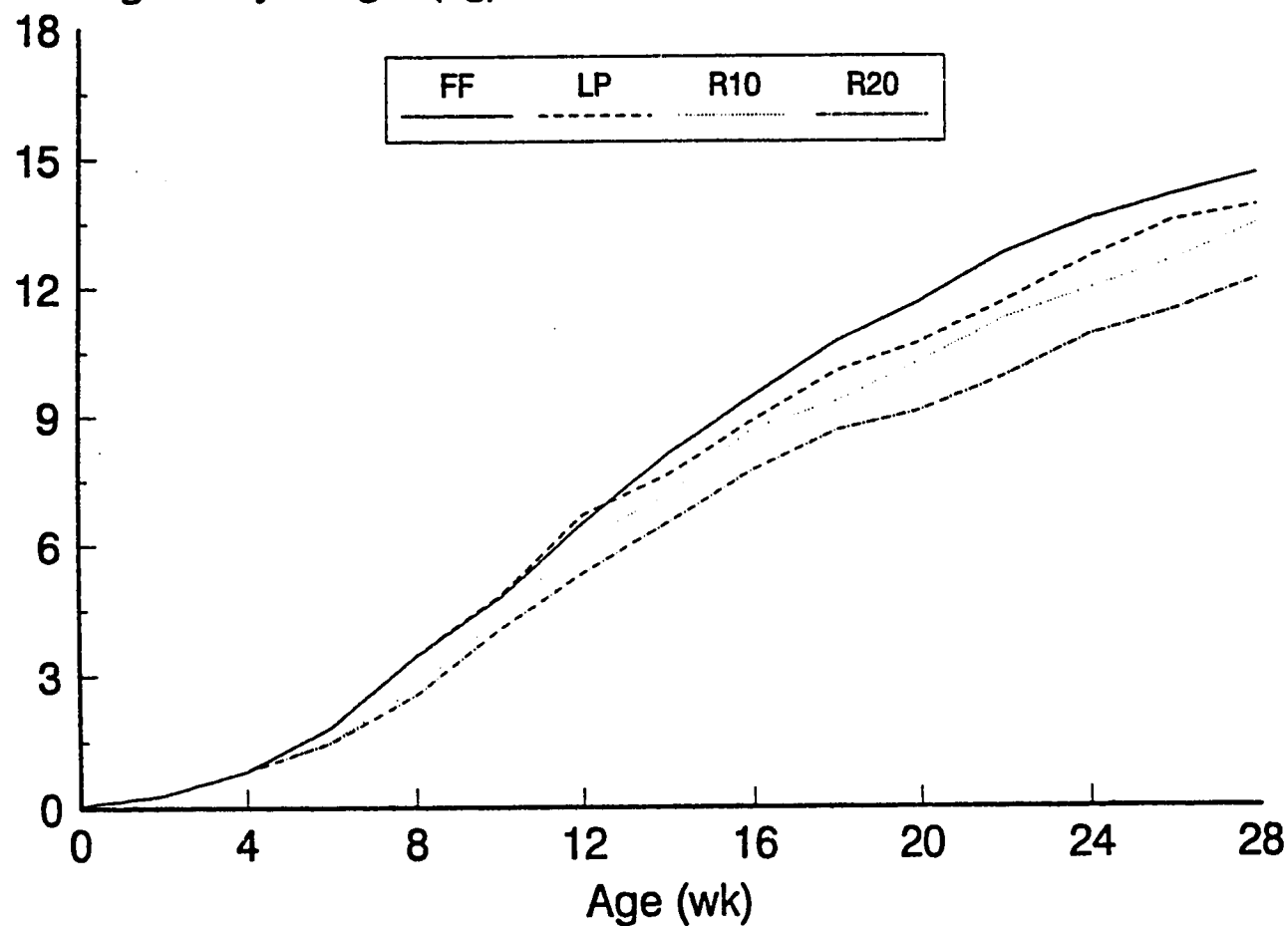


FIGURE II-1 Grower period (0 to 28 wk) body weights male-line breeder hen candidates reared under the following feeding regimens: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight.

Average Body Weight (kg)

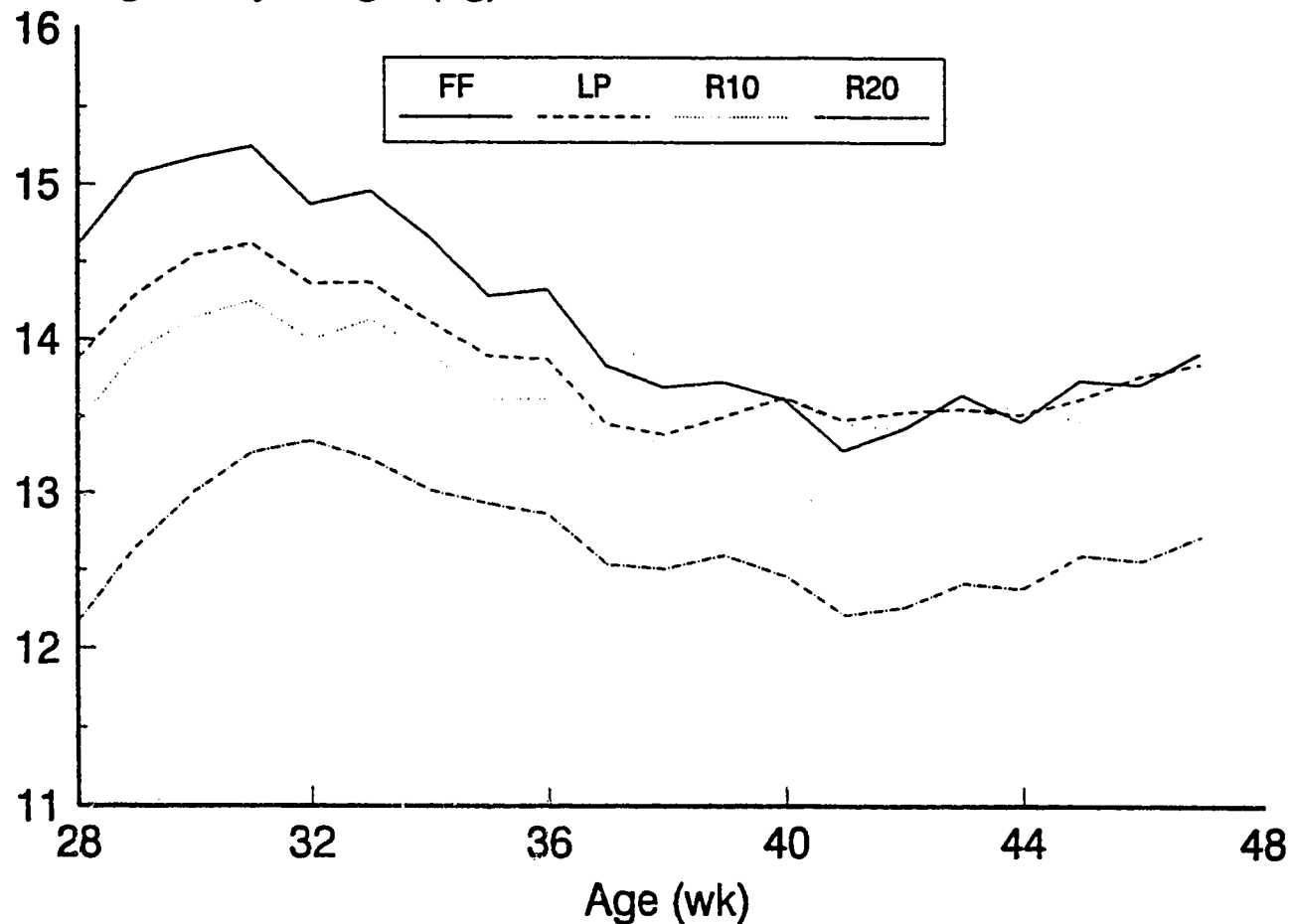
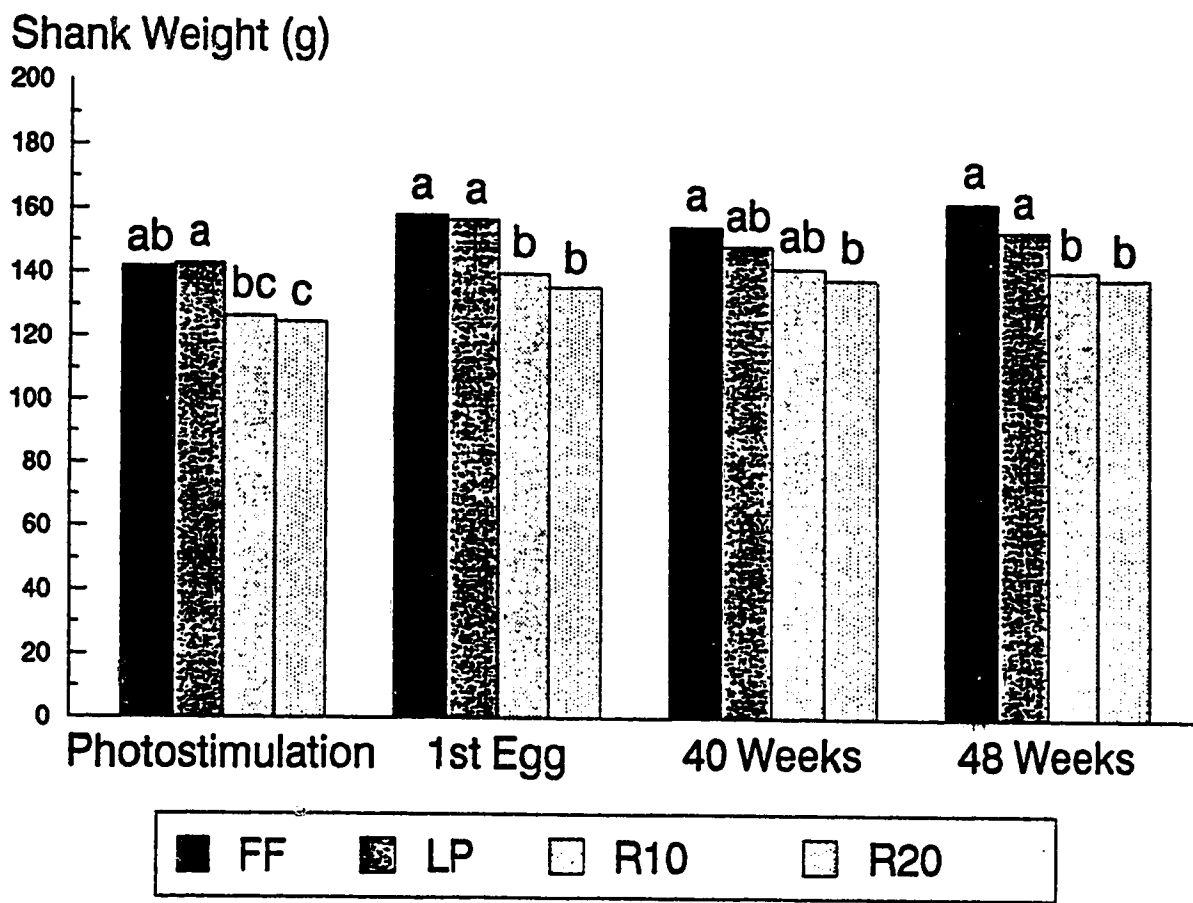


FIGURE II-2 Breeder period (29 to 48 wk) body weights male-line breeder hens reared under the following feeding regimens: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight.



Values within cluster with no common letters differ significantly ($P < 0.01$)

FIGURE II-3 Effect of feed allowance during rearing (0-28 wk) on shank weight at photostimulation, and selected times during the breeder period (29-48 wk), when reared under the following feeding regimens: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. Shank is defined as the portion of the leg from the hock joint down to and including the foot.

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III. THE USE OF FEED RESTRICTION FOR IMPROVING REPRODUCTIVE TRAITS IN MALE-LINE LARGE WHITE TURKEY HENS: 2. OVARY MORPHOLOGY AND LAYING TRAITS¹

Introduction

A negative correlation has been observed between body weight and egg production in turkeys (Nestor, 1971; Nestor *et al.*, 1980). In broiler breeders, obesity is generally associated with reduced egg production, fertility and hatchability (Wilson and Harms, 1986). Selection for rapid growth rate has increased the number of large ovarian follicles (Nestor *et al.*, 1970, 1980, 1981; Bacon *et al.*, 1972; Hocking, 1992a). With increased follicle numbers, the production of two or more ovulable follicles, in the form of multiple follicle sets, is more likely to occur, (Nestor *et al.*, 1980; Hocking, 1987, 1989, 1992a, 1992b), thereby increasing the potential for multiple ovulations. Multiple follicle sets are the major cause of lower egg numbers through the production of defective eggs (Jaap and Muir, 1968; van Middelkoop, 1971, 1972; Nestor and Bacon, 1972; Hocking, 1992b), having poor hatchability (Cherms and Wolff, 1968; Stephenson and Krause, 1988). Reducing body size and the associated fat content can result in improved egg production through a decrease in the number of follicles and the incidence of defective eggs (Miles and Leeson, 1990; Hocking, 1992b).

Male-line turkeys have been almost exclusively selected for growth characteristics. As a result, the expected rate of lay for a male-line hen is less than half that of smaller female line birds (Hocking, 1992a). The reproductive fitness of a male-line hen of today gives a possible picture of what turkeys may be like in the future if current selection trends continue. The presence of high numbers of follicles and multiple follicle sets in these large turkeys (Hocking, 1992a), combined with poor egg production, is cause for taking a close look at what may be gained from feed restriction.

¹ The content of this chapter was presented at the 82nd annual meeting of the Poultry Science Association, held in East Lansing, Michigan. July 26-29, 1993. Poultry Sci. 72 (Suppl 1):68. (Abstr.)

Various forms of nutrient restriction have been examined in turkey feed restriction programs of the past, including high fiber or low energy diets, low protein diets, and quantitative feed restriction, which includes skip-a-day and limited daily access feeding. Feed restriction has been implemented almost exclusively during rearing. In general, feed restricted turkeys exhibit a reduction in body weight and a delay in sexual maturity, while egg weight, fertility and hatchability are not affected (Hester and Stevens, 1990). More variable effects have been observed with egg production. Some restriction programs have resulted in improvements in egg production (Balloun, 1974; McCartney *et al.*, 1977; Miles and Leeson, 1990; and Hocking, 1992b), and others have been detrimental to egg production (Touchburn *et al.*, 1968; Krueger *et al.*, 1978; Voitle and Harms, 1978; and Meyer *et al.*, 1980). Smaller types of bird appear to be more sensitive to the effects of restriction (Whitehead, 1989), whereas larger strains are not affected to the same extent under similar conditions (Hocking, 1992a). Egg production is usually improved in part through the reduction in defective egg production in restriction treatments (Voitle *et al.*, 1973; Andrews and Morrow, 1978; Hocking, 1992b).

Until the recent work of Hocking and associates, there was little information reported on the effects of feed restriction on ovarian morphology in the modern turkey strains. New research on ovarian morphology, and analysis of laying patterns in male-line hens is practically nonexistent. The purpose of this experiment was to determine the effects of low protein and limited daily access forms of feed restriction during rearing on ovarian morphology, egg production, laying patterns, and egg characteristics of male-line Large White turkey breeder hens throughout the breeder period.

Materials and Methods

Stocks and Management

Two hundred day-old female poults from a male parent line were acquired from Hybrid Turkeys². The poults were reared to 28 wk of age in floor pens (4.75 m X 5.85 m). Poults were fed

² Hybrid Turkeys Inc., 9 Centennial Drive, Kitchener, ON. N2B-3E9

ad libitum until 4 wk of age, when restriction treatments began. Treatments consisted of a full-fed control (FF), and three feed restricted groups. The low protein treatment (LP) was a qualitatively restricted group, receiving a 12% C.P. diet *ad libitum* in the period from 12 to 20 weeks of age, rather than the 18% and 15% C.P. diet in this time period. Restricted -10% BW (R10), and Restricted -20% BW (R20) were quantitatively restricted groups, with feed withheld at a level that would result in birds either 10% or 20% lighter than the FF controls. At photostimulation (28 wk), turkeys were placed on an *ad libitum* breeder diet.. Except for the pre-starter diet (0-4 weeks), all diets were corn-soy based and formulated following breeder guidelines, the details of which are presented in Section II. All diets were fed in a mash form. Water was available *ad libitum* from suspended bell drinkers during the light period.

The poults received 24 hours of light on day 1 (24L:0D). The photoperiod was set at 23L:1D from 2 to 5 d, and 14L:10D between 5 d and 14 wk of age. Daylength was reduced to 8L:16D at 14 wk, 7L:17D at 18 wk, 6L:18D at 22 wk and 5L:19D at 26 wk of age. Photoperiod for the breeder period, beginning at 28 wk of age, was 14L:10D. Daylength was increased by 1 h at 34, 38 and 42 wk of age to a maximum photoperiod of 17L:7D.

Feed intake was calculated on a weekly basis for all treatments. Individual BW was recorded bi-weekly to 28 wk of age and weekly thereafter.

Trap nests (60 cm X 60 cm X 60 cm) were placed in each pen at 28 wk of age. Beginning at 30 wk of age, birds were palpated in the morning for the presence of a hard-shelled egg in the shell gland. Turkeys with eggs were placed in the nest to encourage use of the nests and to reduce floor laying. By 36 wk of age, birds were only checked near predicted times of lay to reduce any potential problems as a result of human interference.

Ovarian Morphology

At photostimulation (28 wk of age), eight randomly selected birds were removed from each treatment for carcass analysis as described in Section II. Ovary, stroma (ovary without large follicles), and oviduct weights were recorded for each bird, along with the number, weight and

diameter of normal ovarian follicles greater than 10 mm in diameter (if present). Incidence of follicular atresia or evidence of internal ovulation was recorded upon removal of the ovary. The large follicles from each hen were sorted into groups of similar size (differing by less than 1 g or 1 mm diameter) to determine the extent of potential multiple ovulations. The proportion of large follicles in each bird existing alone, in a double set, or in a triple set or greater was determined.

At sexual maturity (oviposition of first egg), ten pre-selected birds from each treatment were analyzed as described above. The ovaries of these birds were inspected for the total number of post-ovulatory follicles (POF). The number of POF present that could not be explained through oviposition records as well as through eggs in the reproductive tract were recorded. A further eight birds per treatment were examined at mid-laying cycle (40 wk), which corresponded with the lowest BW of the breeder period. At the end of the experiment (48 wk), hens remaining in lay were processed, to a maximum of eight randomly selected birds per treatment. Data from hens with regressed ovaries were not used in the analysis. Ovaries were considered regressed when their weight was less than 25 g in a previously laying hen. Atretic follicles were not weighed or sorted, and follicle data were not recorded for highly atrophied ovaries remaining in the normal weight range.

Laying Records and Interpretations

Individual laying records were kept throughout the breeder period. Daily records included time of lay and egg weight for all eggs laid. Incidence of soft-shelled, membranous, deformed and double yolked eggs were also recorded on an individual basis. The incidence of multiple ovulations was calculated. Multiple ovulations consisted of double yolked eggs and all multiple egg combinations within the period of a day. Records were used to calculate the production of total eggs produced and settable eggs produced for each treatment. Non-settable eggs included double yolked, thin-shelled, misshapen, membranous, and small (< 70 g). Production values were calculated based on both the total number of hens in the pen, and on the number of hens in lay in the pen. A hen without a recorded oviposition for two wk was considered to be out of lay. The proportion of birds

no longer in production were calculated through time for each treatment. Age at sexual maturity and total period of lay were also taken from the records. Data were summarized for the early lay period (31 to 40 wk), and the late lay period (40 to 48 wk) for defective egg production, multiple ovulations, and proportion of non-laying birds. Egg production was calculated to 40 and to 48 wk of age.

Time of oviposition records were used to determine both sequence length and inter sequence pause length for each hen as described by Robinson *et al.* (1990). Sequences were defined as a period of consecutive ovipositions terminated by a pause of 1 d or more. The laying period (31 to 48 wk) was broken down into nine, 14 d periods, and the average sequence length for each section calculated. A sequence overlapping into two periods was used in the calculations for both. Mean sequence length during early and late lay (30-40 wk and 40-48 wk respectively), length of the longest sequence (prime sequence), and day of commencement of the prime sequence were determined. The bi-weekly sequence means were sorted by length into various groups (1 d, 1.1-2 d, 2.1-3 d and 3.1 or more d), and the proportion of sequences in each group calculated for each treatment in early and late lay. Inter sequence pause length was evaluated in the same manner as described above. A pause was defined as the period of time between the terminal egg of one sequence and the first egg of the following sequence. Mean pause length during early and late lay, as well as the proportion of pauses in various groups (1 d, 1.1-2 d, 2.1-3 d and 3.1 or more d) were determined for early and late lay.

Egg quality and Component Values

All settable eggs collected had their shell quality tested through determination of egg specific gravity. Mean specific gravity was summarized for early and late lay. Eggs were weighed, followed by being hard boiled for 30 min. Eggs were broken open, components separated, and weights taken of the yolk, albumen, and shell and membranes. Weight loss from boiling was theorized to be proportionally similar for the yolk and albumen due to osmotic water movements. A correction factor for weight loss therefore divided the weight difference between the yolk and albumen

according to the proportion of egg weight they represented. Average values for eggweight, yolk, albumen, and shell and membranes were determined on a weekly basis, as well as percentages of total eggweight for yolk, albumen, and shell and membranes. Egg data were summarized for early and late lay.

Statistical Analysis

Data were evaluated by analysis of variance using the General Linear Models (GLM) procedures (SAS Institute, 1985). Preliminary analyses indicated the variation among pens was essentially the same as the variation among birds within pens. On this basis the pen variation was combined with the bird variation to form the error variation. Feeding regimens (treatments) were compared within periods of interest and / or times in the growth and production cycle. For immature reproductive tract components, and prime sequence length, sources of variation were treatments and birds within treatments. Egg production and percentage defective egg types were analyzed at the pen level, as this was the lowest level of variability for this factor. Mature reproductive tract components, ovary morphology data, proportion of non-laying birds, laying patterns, and egg characteristics were analyzed across both treatment and time. Sources of variation were treatment, time, and treatment * time interaction. Differences between treatments in a time period were examined, as well as differences in time within a treatment. Differences between means were evaluated with the TTEST procedure (SAS Institute, 1985). Pearson correlation coefficients (Steel and Torrie, 1980) were computed as a measure of relationships among several body components and production parameters. The Pearson correlation coefficients were computed across all treatments. Unless otherwise stated, all statements of significance were based on testing at the .05 level.

Results

Ovary Morphology

At photostimulation (28 wk of age), there was no observable development of the reproductive tract (Table III-1). There were significant differences between treatments at this time. Ovary weight in the FF treatment birds (6.0 g) was significantly greater than that of the R10 treatment birds (4.9 g). The mean FF treatment birds oviduct weight, at 4.2 g, was nearly double the average weight of the oviducts of the R10 and R20 treatment birds (54% of FF weight).

Day of sexual maturity was slightly delayed in the birds that were feed restricted during rearing, with a significant delay of 2.7 d occurring in the R20 treatment compared to the FF treatment value. Comparison of the reproductive tract components at sexual maturity demonstrates a lack of difference between treatments for ovary, stroma, and oviduct weight (Table III-2), and weight as a percentage of BW (Table III-3). Average ovary, stroma, and oviduct weights were 215, 37, and 119 g respectively at this time. At sexual maturity FF, LP, R10, and R20 hens had an average of 4.8, 5.2, 4.9, and 4.9 POF respectively. The number of POF were found to be positively correlated to fatpad size ($r = .39$, $P \leq .01$), negatively correlated with breast muscle weight ($r = -.34$, $P \leq .03$), and had no relationship with BW.

The weight of the ovary and stroma decreased significantly in the restricted treatments between sexual maturity and 40 wk of age (Table III-2). Ovary weight did not change in the FF hens during this time period, while stroma weight was significantly lower in the older birds, as it was in the other treatments. The R20 treatment was the only treatment to have a significant decrease in ovary weight both on an actual weight, and on a percentage of BW basis (Table III-2, III-3). R20 treatment ovary weight as a percentage of BW dropped from a high at sexual maturity (1.68% vs. a mean of 1.46% in the other treatments) to almost the lowest treatment level at 40 wk of age (1.38% vs. a range of 1.32 to 1.52%) (Table III-2). Between 40 and 48 wk of age, the ovaries of the restricted hens increased slightly, while ovary weight decreased in the FF treatment hens (Table III-2). Ovary weight was found to be correlated to BW ($r = .49$, $P \leq .0001$), and fatpad weight ($r = .37$, $P \leq .0004$). Oviduct weight was correlated to ovary weight ($r = .37$, $P \leq .0004$), and fatpad weight

($r = .34$, $P \leq .001$), but not to BW. Oviduct weight increased with age in all treatments, with a significant increase in the FF treatment between sexual maturity and 48 wk of age (Table III-2), and in the FF and LP treatments when oviduct weight is calculated as a percentage of BW (Table III-3). On average, oviduct weight was significantly greater at 48 wk (140 g) than at sexual maturity or at 40 wk of age (85 and 88% of 48 wk values respectively) (Table III-2). The FF treatment oviduct weight at 48 wk of age was numerically greater than for the restriction treatment oviduct weights both on an actual weight and on a percentage of BW basis (Table III-2, III-3).

Throughout the laying cycle, the number of large ovarian follicles did not differ between treatments. On average, the FF treatment had significantly more follicles than the R10 treatment, with 15.6 compared to 13.8 (Table III-4). In all treatments there was a significant reduction in follicle numbers between sexual maturity and 40 wk of age, averaging a five follicle (27%) reduction (Table III-4). The number of large follicles was correlated with BW ($r = .50$, $P \leq .0001$), and ovary size ($r = .64$, $P \leq .0001$). Unlike ovary size, however, this trait was not related to fatpad size. The percentage of recorded ovipositions that were determined to be the result of multiple ovulation did not differ significantly between treatments or with time (Table III-4). In the 31-40 wk range, however, the LP treatment laid 4.2% of its eggs in multiples compared to a 2.4% value for the R20 treatment.

The large follicles were sorted into groups of similar size, and the proportion of follicles existing alone, in a double set of similar size, or in a set of three or more follicles is presented in Table III-5. At sexual maturity there were 4% of follicles existing alone on average, compared to 54% in sets of three or more. Through time there was a significant increase in the incidence of single follicle sets, and significant decrease in sets of three or more, with values of 28% and 14% respectively at 48 wk of age. A summary of the affect of time on follicle distribution is presented in Figure V-3 (Appendix 1). Significant treatment differences were observed in the incidence of follicles existing alone at 40 and 48 wk of age, with higher proportions of single follicles occurring in the more severe rearing restriction programs (Table III-5). The R20 treatment had an average of 34% of its follicles occurring alone, while the R10, LP, and FF treatments had means of 30, 21, and

11% respectively for this time period. There were no significant differences in the incidence of follicles in sets of three or more (Table III-5), although the overall treatment means for the R10 and R20 treatments was about 5% lower than that of the LP and FF treatments (26 vs. 32% respectively). The treatment effect on follicle arrangement is summarized in Figure V-4 (Appendix 1). The incidence of follicles in sets of three or more was correlated with ovary size ($r = .49$, $P \leq .0001$).

Egg Production and Negative Production Factors

The production of unsettable eggs did not differ significantly between treatments or with time, and averaged 9 and 8% of total egg production in early and late lay respectively (Table III-4). Defective egg production decreased in the restriction treatments, and increased in the FF treatment. The analysis of the incidence of the different types of defective eggs is presented in Table III-6. The R20 treatment hens laid significantly fewer double yolked eggs in early lay, significantly fewer thin-shelled eggs in late lay, and significantly more misshapen eggs in late lay than any other groups of hens. The FF treatment had the highest incidence of double yolked egg production and thin-shelled egg production. In early lay, the production of small eggs (<70 g), was higher in the restriction treatments, and increased with the severity of the restriction program during rearing. In late lay, however, no small eggs were produced in the restriction treatments, while 3% of FF treatment production were small eggs. The percentage of membranous eggs decreased with time on average, representing 4.1 and 2.8% of total egg production in early and late lay respectively.

Egg production was calculated on the basis of birds in the pen, and on the basis of the birds in the pen which were in production (Table III-7). There were no significant differences in total or settable egg production to 40 or to 48 wk of age. Egg production to 48 wk per layer, however, was numerically increased in the restriction treatments, and increased in these treatments with the severity of the rearing restriction program. Settable egg production was the highest in the R20 treatment with 55.4 eggs per layer, and the egg production of the R10, LP, and FF treatments were 95, 93, and 88% of this level respectively. Total egg production (percent) over time is presented per bird present

in Figure III-1, and per laying bird in Figure III-2. Settable egg production over time is presented per bird present in Figure III-3, and per layer in Figure III-4. The R20 treatment had the highest rate of peak production in early lay in each of these figures. When production was calculated per bird present, the LP treatment had the highest rate of production throughout most of the latter laying period (Figure II-1, III-3). When production was based on hens in production, the R20 treatment peaked with the highest rate of production early in lay, and had the highest rate of egg production for the duration of the laying period (Figure II-2, II-4).

The differences between egg production per bird and egg production per layer are due to the proportion of birds in the pen which are not in production. In early lay, although the average was only 6%, a significantly higher proportion of birds in the R20 treatment were out of production (Table III-8). During the second half of the laying cycle, an average of 44% of birds were out of production. The R20 treatment had the most difficulty sustaining lay with 54% of the birds out of production in this period, followed by the R10, FF, and LP treatments, with 47, 43, and 32% non-layers respectively. The percentage of non-layers through time is presented in Figure V-5 (Appendix 1).

The incidence of follicular atresia on the ovary can be an indicator of excess follicle production. Atresia was significantly more frequent in R20 treatment birds, although it had disappeared in these birds by 48 wk of age (Figure III-8). The overall average was 26% in R20 birds, followed by 21, 17, and 11% in the R10, LP, and FF treatments respectively. On average, there was a significantly higher incidence of internal ovulation in the FF treatment than in the R20 treatment (Table III-8). The incidence of internal ovulation in the FF treatment was 32% on average, and 20, 22, and 7% in the LP, R10, and R20 treatments respectively. The incidence of internal ovulation was positively correlated to BW ($r = .34$, $P \leq .001$).

Laying Patterns

Prime sequence length did not differ between treatments, and the day of commencement of the prime sequence was similar (Table III-9). The length of the prime sequence was correlated to

settable egg production to 40 wk ($r = .42$, $P \leq .0003$), and to 48 wk of age ($r = .61$, $P \leq .002$). Although not correlated to BW at sexual maturity, prime sequence length was negatively correlated with BW at 40 wk of age ($r = -.30$, $P \leq .046$). The day of prime sequence commencement was negatively correlated with egg production to 40 wk, but not significantly ($P \leq .07$). Sequence length was longer in the restriction treatments during early lay, and increased with the severity of the rearing restriction program. In this period, sequence length was significantly improved in the R20 treatment (2.1 d) compared to the FF treatment (1.8 d). During the second half of lay there were no differences observed in sequence length, with an average of 1.4 d. Changes in sequence length over time are presented in Figure V-6 (Appendix 1). Pause length was significantly higher in the FF treatment early in lay than in all of the restriction treatments, with a pause length of 2.2 d compared to an average of 1.5 d in the other treatments (Table III-9). There was a significant increase in pause length in the LP treatment late in lay, resulting in an overall pause length mean which was significantly shorter in the R10 and R20 treatments (1.7 and 1.5 d respectively) than in the FF and LP treatments (2.3 and 2.3 d respectively)

Average sequence and pause lengths were calculated per bird for two week periods during the laying cycle. These means were sorted into sequence and pause length ranges, and the proportion of total sequences or pauses for each range calculated for 31 to 40 wk, and 40 to 48 wk of age. The proportion of sequences from 2-3 d, and sequences >3 d were both significantly reduced on average from early to late lay (Table III-10). Both 1 d, and 1-2 d sequences were significantly increased from early to late lay. The FF treatment had significantly more 1 d sequences than the LP and R20 hens did. The R20 treatment had numerically more 2-3, and >3 d sequences. Pauses of 1 d decreased with time on average, while pauses of 2-3 d or >3 d increased (Table III-11). The FF and LP treatments had significantly fewer 1 d pauses than the R10 treatment, significantly more 2-3 d pauses than the R20 treatment, and significantly more pauses >3 d than the R10 and R20 treatments had.

Egg Characteristics

Eggweight increased significantly in all treatments between the time periods of early and late lay (Table III-12). Eggweight was consistently the greatest in the R10 treatment, followed by the FF, LP, and R20 treatments. The R20 treatment eggweights were consistently significantly lower than those of all other treatments, with eggweights of 3 to 6% lighter. Changes in eggweight over time are presented in Figure V-7 (Appendix 1). Egg specific gravity was not strongly related to egg size, as the eggs laid in late production by the R10 hens were the largest eggs, with the highest specific gravity (Table III-12). Egg specific gravity decreased slightly with time. Specific gravity was the poorest in the FF treatment, with an average value of 1.082, and increased incrementally in the LP, R10, and R20 treatments to a maximum average of 1.084.

The weight of the yolk, albumen, and shell of the eggs all significantly increased on average between early and late lay (Table III-13). As a percentage of eggweight, yolk weight significantly increased while albumen weight significantly decreased in time. Despite having the smallest egg weight, the R20 treatment eggs had a significantly larger yolk size than the FF and LP treatments. Yolk weight through time is presented in Figure V-8 (Appendix 1). In early production, the R10 and R20 treatments deposited a significantly lower percentage of albumen into their eggs than the FF and LP treatments did. Shell deposition as a percentage of eggweight was significantly better in the restricted treatments than in the FF treatment, and was incrementally improved through the LP and R10 treatment to the R20 treatment.

Discussion

The weight of the ovary and oviduct at photostimulation can possibly be used as predictors of age of sexual maturity. Although ovary and oviduct weights at this time represented only 2.5% of their sexually mature weight, treatments with heavier reproductive tract components became sexually mature earlier. The lack of treatment differences in ovary, stroma, and oviduct weight at time of photostimulation (Table III-2) suggests that a relatively constant amount of growth must

occur in the reproductive tract in order for sexual maturity to be achieved, hence the delay in treatments with smaller components at photostimulation.

The ovary of the R10 treatment was 5% lower in weight on average than the ovaries of the other treatments (Table III-2). This difference was associated with an average large follicle number 8% below the mean of the other treatments (Table III-4), and an average egg yolk size 2% greater than in the other treatments (Table III-13). The weight of the liver, where the majority of the yolk components are synthesized (Leveille *et al.*, 1975), is correlated with ovary size (Section II), and was lowest in the R10 treatment. It appears that a reduced amount of yolk precursors are being made available in the R10 treatment for yolk deposition, and yet the concentration of precursors per follicle is greater, resulting in a decreased ovary size and an increased yolk size.

At sexual maturity, there was an average of 4.9 unexplained post-ovulatory follicles on the ovary. These follicles represent ovulations which were not accounted for by the first egg, or by an egg in the oviduct. On average, birds in treatment groups ovulated an average of five times before an ova generated an egg. The fate of these missing follicles is unknown, and hence we suggest the term "phantom follicles". It is suspected that oviduct immaturity may be the limiting factor in the determination of sexual maturity in the male-line hen. Oviduct size was not related to POF numbers, although these birds were examined at sexual maturity, when the oviduct growth requirements have likely been met. Data on the morphology of the oviduct and ovary in the week before sexual maturity may be beneficial to the understanding of this phenomenon. The relationship between POF and fatpad size may be involved in the loss of potential eggs. Abdominal fat would be indicative of a general fatness, an excess of which may be a hindrance to infundibular motility, and a detriment to sperm storage capabilities (McDaniel *et al.*, 1981). Oviduct weight was also correlated to fat levels, but not to BW. Data revealing the fat and protein content of the oviduct, which was numerically heavier in the FF treatment (Table III-2) would specify whether or not a relationship existed with adipose tissue.

Feed restriction typically reduces the number of developing large follicles, which will decrease the frequency of multiple follicle set formation, and the incidence of defective eggs (Miles

and Leeson, 1990; Hocking, 1992b). Hocking (1992a) found that quantitative feed restriction not only reduced multiple follicle set formation, but also reduced stroma weight. Reduced stroma weight could have long term effects on egg production through a decreased quantity of small follicles. In the current study, stroma weight at 48 wk and average follicle numbers in the R10 treatment were significantly lower than in the FF treatment. In all treatments there was a significant decrease in stroma weight and follicle numbers in time (Table III-2, III-4). Feed restriction slightly reduced the incidence of multiple ovulations, but had no apparent effect on defective egg production (Table III-4). Andrews and Morrow (1978) observed a significant reduction in both misshapen and soft-shelled eggs in turkeys feed restricted during rearing. Hocking (1992b) reported similar results, with significant reductions in double yolk and soft shelled eggs. The R20 treatment group in the present study displayed a significant reduction in double yolked eggs early in lay, and in thin shelled eggs on average, while the average incidence of misshapen eggs was significantly higher (Table III-6).

Follicle numbers were reduced in restriction treatments between 6% (LP and R20) and 11% (R10) on average (Table III-4). These differences resulted in a significant reduction in multiple follicle sets in the R10 and R20 treatments. The distribution of follicles into single, double, or triple and greater sets in the LP treatment was similar to that of the FF treatment, while the follicular distribution of the R10 and R20 treatments was also very similar (Table III-5). At sexual maturity, between 95 and 98% of follicles were in multiple sets, with sets of three or more follicles representing nearly 60% of this in all but the R20 treatment, where it was 40%. These levels are not in agreement with the range of 25 to 50% observed in smaller turkey strains on full-feeding (Hocking, 1992a; Hocking *et al.*, 1992), or in male-line hens heavier than those of the current study, where a high of 70% was observed (Hocking, 1992a). By 40 wk of age, the proportion of multiple follicles had dropped significantly in the R10 and R20 treatments, and by 48 wk of age averaged 65% for these two treatments, compared to 85 and 75% for the FF and LP treatments respectively. The proportion of follicles in sets of three or more follicles was numerically different in the R10 and R20 treatments, averaging 25% compared to 33 and 31% for the FF and LP treatments respectively. The decline in multiple follicles is due to the reduction in follicle numbers, as follicular recruitment

and maturation declines with age (Hocking *et al.*, 1988). It is not known why the turkeys reared under quantitative feed restriction condition organized a similar amount of follicles to the other treatments differently. They may be acting more like an egg strain, where egg production has been observed to be greater than in a meat strain with similar follicle numbers in late production (Bacon *et al.*, 1972).

The ovary of the FF treatment hens did not decrease in weight between sexual maturity and 40 wk to the same degree that was observed in the restricted treatments. As a result, at 40 wk of age the FF treatment had 2 to 2.5 more large follicles than the other treatments (Table III-4), which resulted in 10 to 25% more multiple follicle sets (Table III-5), and 1.5 to 3.5 fewer settable eggs per bird than the other treatment groups (Table III-7). These differences demonstrate a numerically negative relationship between follicle numbers and egg production. These results are consistent with trends observed with selection for increased BW, where egg production decreases, and follicle numbers and multiple follicle sets increase (Nestor *et al.*, 1980). Feed restriction appears to have the same effect in these turkeys as selection for reduced BW would.

There were treatment differences in the rate of follicular atresia and the rate of internal ovulation. Incidence of atresia of the large follicles increased with the severity of the rearing restriction program, while the incidence of internal ovulation decreased (Table III-8). Atresia is the normal fate of excess follicles in the hierarchy, with the expected incidence in full-fed meat-type turkeys being about 35% (Bacon *et al.*, 1972; Hocking *et al.*, 1992). Feed restriction has been shown to reduce the incidence of atresia to a 13% incidence (Hocking *et al.*, 1992), a level comparable to what has been observed in turkey egg lines (Bacon *et al.*, 1972). Bacon *et al.* (1972) reported the incidence of internal ovulation to be 23% in meat lines compared to 13% in egg lines. The incidence of atresia in the current study increased incrementally from a low of 11% in the FF treatment to a high of 26% in the R20 treatment (Table III-8). Conversely, the incidence of internal ovulation decreased from a high of 32% in the FF treatment to a low of 7% in the R20 treatment. It could be that hormonal control of ovulation is not as strong in the larger turkeys, resulting in less restriction over timing of ovulation. If the hormonal events of ovulation are not followed properly,

the infundibulum will not be stimulated to surround the ovulating ovum, which may result in an internal ovulation. Pyrzak and Siopes (1989) reported that a portion of the turkeys in their experiment laid eggs throughout a 24 hour day, and theorized that the laying patterns of some hens are not synchronized to the light period. Hocking (1992a) observed an increased delay in the attainment of sexual maturity in male-line hens compared to female-line hens, and suspected reduced light sensitivity to be the cause. The increased incidence of internal ovulation in the larger treatment hens of the current study could also be due to reduced light sensitivity, as this would decrease the regularity of hormonal control over ovulation.

Sequence length is one of the key indicators of an improvement in reproductive performance. The primary way eggs are added is through an increase in sequence length (Anthony *et al.*, 1991). The length of the prime sequence is correlated with total egg production for the bird in turkeys (Lerner *et al.*, 1993), and in broiler breeders (Robinson *et al.*, 1993). Robinson *et al.* (1991), observed *ad libitum* fed hens to have a shorter prime sequence than restricted fed hens. In the current study, sequence length during early lay was improved with feed restriction, although more substantial differences were observed in the reduction of pause length (Table III-9). The R10 and R20 treatments had significantly reduced pause lengths on average compared to the FF and LP treatment birds. The primary area of improvement in pause length was a reduction in pauses of greater than three days (Table III-11). There were no differences in prime sequence length, although prime sequence length was correlated with egg production. Sequence length was observed to decrease with age, while pause length increased (Table III-11), which confirms what Lerner *et al.* (1993), and Robinson *et al.* (1990), report for the turkey and domestic fowl respectively. Improved sequence length contributes to improved chick production, as the production of first-of-sequence eggs is reduced. First-of-sequence eggs have been found to be less fertile, less hatchable, and more likely to undergo embryonic loss (Bacon and Nestor, 1979; Lerner *et al.*, 1993).

The eggs in the current study followed the published trends for changes throughout the laying cycle. The weight of the ovum at ovulation increased steadily throughout lay (Figure V-8: Appendix 1), which was a reflection of the increased time needed to reach maturity (Bacon and

Cherms, 1968; Sharp, 1989). The increase in yolk size related directly to an increase in egg size through time (Figure V-7: Appendix 1) (Bacon *et al.*, 1972), which would be expected to result in a larger poult size (Shanaway, 1984). The yolk:albumen ratio increased in time, as has been observed in broiler breeder stocks (O'Sullivan *et al.*, 1991), and shell weight increased in time (Rahn *et al.*, 1981), while shell quality declined (Table III-12, III-13).

Improved hatchabilities in eggs of restricted fed treatments is thought to be primarily due to better shell calcification brought about by reduced erratic oviposition, and by improved shell density if egg size has been reduced. In the current study, shell quality in late production was the best in the R10 treatment, which also was laying the largest eggs at this time. Shell deposition as a percentage of egg weight improved incrementally with the severity of the rearing restriction program (Table III-13). Egg weight in the R10 treatment was 1% higher on average than egg weight in the FF treatment, and shell weight was 3% higher. As there were no differences in defective egg production, efficiency of shell deposition appears to improve with the degree of feed restriction during rearing.

In early lay, eggs of the FF and LP treatment had a significantly higher proportion of albumen, and lower proportion of yolk than the eggs of the R10 and R20 treatments (Table III-13). These treatments are both exhibiting an effect of a low protein diet, which has been shown to increase the proportion of albumen at the expense of yolk (Ferket and Moran, 1986). The eggs of the R10 treatment were 4% lighter than the average egg weights of the other treatment (Table III-12), but did not exhibit a decreased yolk size. The difference in egg weight was accounted for almost completely by a reduction in albumen content (Table III-13). The implications of a larger yolk in a smaller egg on hatchability and poult size are not well understood.

At the end of the laying cycle, a high proportion of hens in all treatments had gone out of production (Table III-8). There were two peak times for hens to cease laying activity, 37 to 39 wk of age, and 41 to 44 wk of age (Figure V-5: Appendix 1). Some of these birds demonstrated broody behavior, while others simply stopped laying eggs. The first period followed shortly after a short heat wave, demonstrating the link between high temperature and elevated levels of broodiness (Thomason *et al.*, 1972; El Halawani *et al.*, 1984) Large turkeys are more susceptible to

broodiness, and have a poor ability to tolerate the stress of change. The second period (41 to 44 wk) followed soon after one third of the birds in each pen were removed for processing, which may have had negative effects on the social order in each pen. The proportion of non-production birds was reduced in the LP treatment compared to FF treatment levels. As the stock from which these birds originated have been reared under the LP treatment conditions for a number of generation, it is reasonable to expect that they are able to handle this type of rearing program. When these birds are reared under conditions they have not been bred to tolerate, however, such as in the FF, R10, and R20 treatments, a portion of the birds unable to handle the stressors of the new conditions may be expected not to thrive reproductively.

A poor persistency of lay has been observed previously in quantitative feed restriction experiments (Woodard *et al.*, 1974; Hocking, 1992b; Hocking *et al.*, 1992). The inability to sustain lay appears to be associated with feed restriction primarily when photostimulation is early. Early photostimulation alone will reduce persistency of lay (Hocking *et al.*, 1988), while restricting feed with a normal photostimulation time will not adversely affect the proportion of birds in lay (Hocking, 1992b; Hocking *et al.*, 1992). In the current study, the R20 treatment group showed a substantial increase in the percentage of non-layers compared to the FF treatment (Table III-8). This may be evidence that photostimulation is occurring too early in this treatment. Further support exists in the state of the ovary at sexual maturity. The weight of the ovary and of the stroma as a percentage of BW was the greatest in this treatment group (Table III-3). There was a significant delay in the attainment of sexual maturity in the R20 treatment compared to the FF treatment. The number of large follicles decreased incrementally from FF treatment levels in the LP and R10 treatments, but then rose again in the R20 treatment (Table III-4). Early photostimulation is associated with elevated follicle numbers (Hocking, 1992a; Hocking *et al.*, 1992).. Early photostimulation has been shown to increase the incidence of small eggs (Woodard *et al.*, 1974), particularly when in combination with feed restriction. Birds of the R10 and R20 treatments in the current study exhibited a numerical increase in small egg production in early lay (Table III-6). Taken together, this evidence demonstrates that at 28 wk of age the body of the more severely restricted birds may be

too immature to handle egg production. Photostimulation should probably be delayed by several weeks in this type of restriction treatment to better take advantage of the anticipated benefits for reproductive traits.

Qualitative (LP) and quantitative (R10 and R20) forms of feed restriction both affected reproductive traits in the male-line turkey hen. In particular, they numerically reduced average follicle numbers, proportion of multiple ovulations, and incidence of double yolked eggs. Egg production was numerically improved over FF treatment levels, and yolk weight, shell weight, and specific gravity were all significantly improved in the restriction treatments. Although the LP treatment brought about differences in certain traits, the R10 and R20 treatments were more effective at altering egg characteristics such as yolk size and egg quality, reducing average pause length, and at reducing multiple follicle sets on the ovary. The R20 treatment best altered follicular arrangements in a positive manner, improved sequence length, had the highest peak rate of egg production, and improved egg numbers per bird in production.

The R10 and R20 treatments, although similar to the LP treatment in some respects, gave the hen an improved state of reproductive fitness. For male-line hens, with their unnaturally high proportions of multiple follicle sets, short laying sequence lengths, and apparent resistance to compositional change under restriction conditions (Section II), any changes in reproductive fitness are beneficial. The R10 and R20 treatments were best able to shift ovary morphology and laying patterns to a more normal state. More substantial change may be possible with more severe rates of restriction, if certain issues are addressed. The problem of poor persistency of lay may be lessened when severe restriction is done in combination with a delayed age of photostimulation. The release of birds from the restriction program at photostimulation should be gradual, as a large proportion of growth between photostimulation and first egg is in the ovary. A reduced degree of restriction in this period may limit excess follicle development. There is the potential to gain up to five more eggs near the onset of lay, if the phenomenon of the phantom follicles at sexual maturity is addressed. Due to the poor state of reproductive fitness in male-line hens, feed restriction programs of some kind no longer appear to be an option, but a necessity.

TABLE III-1. Effect of feed allowance during rearing (0-28 wk) on the development of the reproductive tract at Photostimulation (28 wk).

Component	n ²	Feeding Regimen ¹				SEM
		FF	LP	R10	R20	
<u>Ovary</u>						
(g)	8	6.01 ^a	5.33 ^{ab}	4.88 ^b	5.31 ^{ab}	.35
(% of BW)	8	.043 ^{ab}	.040 ^{ab}	.038 ^b	.045 ^a	.002
<u>Oviduct</u>						
(g)	8	4.20 ^a	3.29 ^{ab}	2.43 ^b	2.10 ^b	.45
(% of BW)	8	.031 ^a	.024 ^{ab}	.019 ^b	.018 ^b	.003

^{a-b}Means within a row with no common superscripts differ significantly ($P < .05$).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²n = Average number of birds in each treatment.

TABLE III-2. Effect of feed allowance during rearing (0-28 wk) on the weight of the reproductive tract at selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
(Weight (g) ± SEM)						
Ovary:						
Sex. Mat.	10	211 ± 12	231 ± 12 ^x	201 ± 12 ^x	220 ± 12 ^x	215 ± 6 ^x
40 wk	8	206 ± 15 ^a	179 ± 14 ^{ab,y}	165 ± 13 ^{b,y}	172 ± 14 ^{ab,y}	180 ± 7 ^y
48 wk	6	184 ± 17	186 ± 14 ^y	199 ± 14 ^{xy}	206 ± 18 ^{xy}	194 ± 8 ^y
Mean		201 ± 8	198 ± 8	188 ± 8	199 ± 9	
Stroma:						
Sex. Mat.	10	35.8 ± 1.7 ^x	39.7 ± 1.7 ^x	36.8 ± 1.8 ^x	37.2 ± 1.7 ^x	37.4 ± .9 ^x
40 wk	8	28.1 ± 2.5 ^y	27.5 ± 2.1 ^y	27.7 ± 2.1 ^y	29.3 ± 2.2 ^y	28.2 ± 1.1 ^y
48 wk	6	31.9 ± 2.5 ^{a,xy}	26.7 ± 2.1 ^{ab,y}	24.2 ± 2.1 ^{b,y}	27.2 ± 2.7 ^{ab,y}	27.4 ± 1.2 ^y
Mean		32.0 ± 1.3	31.2 ± 1.1	29.4 ± 1.2	31.2 ± 1.3	
Oviduct:						
Sex. Mat.	10	117 ± 9 ^y	118 ± 8	120 ± 9	119 ± 9	119 ± 4 ^y
40 wk	8	128 ± 11 ^{xy}	120 ± 10	118 ± 10	125 ± 10	123 ± 5 ^y
48 wk	6	154 ± 12 ^x	140 ± 10	141 ± 10	126 ± 14	140 ± 6 ^x
Mean		133 ± 6	126 ± 6	126 ± 6	123 ± 6	

^{a-b}Means within a row with no common superscripts differ significantly ($P < .05$).

^{xy}Means within a column with no common superscripts differ significantly ($P < .05$).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment.

³n = Average number of birds in each treatment.

TABLE III-3. Effect of feed allowance during rearing (0-28 wk) on the development of the reproductive tract as a percentage of body weight at selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
(Weight (% of BW) ± SEM)						
Ovary:						
Sex. Mat.	10	1.47 ± .08	1.47 ± .08	1.45 ± .09	1.68 ± .09 ^x	1.54 ± .04 ^x
40 wk	8	1.52 ± .11	1.40 ± .10	1.32 ± .09	1.38 ± .10 ^y	1.40 ± .05 ^y
48 wk	6	1.39 ± .12	1.35 ± .10	1.46 ± .10	1.61 ± .13 ^{xy}	1.45 ± .06 ^{xy}
Mean		1.46 ± .06	1.44 ± .05	1.41 ± .05	1.55 ± .06	
Stroma:						
Sex. Mat.	10	.25 ± .01 ^b	.27 ± .01 ^{ab,x}	.27 ± .01 ^{ab,x}	.29 ± .01 ^{a,x}	.27 ± .01 ^x
40 wk	8	.21 ± .02	.22 ± .02 ^y	.23 ± .02 ^x	.23 ± .02 ^y	.22 ± .01 ^y
48 wk	6	.25 ± .02 ^a	.20 ± .02 ^{b,y}	.18 ± .02 ^{b,y}	.21 ± .02 ^{ab,y}	.21 ± .01 ^y
Mean		.23 ± .01	.23 ± .01	.22 ± .01	.24 ± .01	
Oviduct:						
Sex. Mat.	10	.82 ± .07 ^y	.80 ± .06 ^y	.87 ± .07	.92 ± .07	.85 ± .03 ^y
40 wk	8	.94 ± .08 ^{xy}	.94 ± .08 ^{xy}	.95 ± .07	1.00 ± .08	.96 ± .04 ^x
48 wk	6	1.17 ± .09 ^x	1.02 ± .08 ^x	1.04 ± .08	.98 ± .10	1.05 ± .04 ^a
Mean		.98 ± .05	.92 ± .04	.96 ± .04	.96 ± .05	

^{a-b}Means within a row with no common superscripts differ significantly ($P < .05$).

^{x-y}Means within a column with no common superscripts differ significantly ($P < .05$).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment.

³n = Average number of birds in each treatment.

TABLE III-4. Effect of feed allowance during rearing (0-28 wk) on the number of large follicles, multiple ovulation days, unsettable egg production, calculated at selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
Number of large follicles⁴						
Sex. Mat.	10	19.1 ± .7 ^x	18.7 ± .7 ^x	17.1 ± .8 ^x	18.7 ± .8 ^x	18.4 ± .4 ^x
40 wk	8	15.0 ± 1.0 ^y	12.8 ± .9 ^y	12.6 ± .9 ^y	13.0 ± .9 ^y	13.4 ± .5 ^y
48 wk	6	12.6 ± 1.0 ^y	12.1 ± .9 ^y	11.6 ± .9 ^y	12.5 ± 1.2 ^y	12.3 ± .5 ^y
Mean		15.6 ± .5 ^a	14.6 ± .5 ^{ab}	13.8 ± .5 ^b	14.7 ± .5 ^{ab}	
Multiple ovulations (%)⁵						
31 to 40 wk	24	3.5 ± .7	4.2 ± .7	3.9 ± .7	2.4 ± .7	3.5 ± .4
40 to 48 wk	15	4.7 ± 1.3	2.2 ± 1.3	3.4 ± 1.3	4.4 ± 1.3	3.7 ± .8
(31 to 48 wk)	20	4.1 ± .6	3.7 ± .6	3.8 ± .6	2.8 ± .6	
Unsettable eggs (%)						
31 to 40 wk	24	8.2 ± 2.7	9.1 ± 2.7	11.4 ± 2.7	8.5 ± 2.7	9.3 ± 1.4
40 to 48 wk	15	13.6 ± 5.7	5.3 ± 5.7	7.0 ± 5.7	5.8 ± 5.7	7.9 ± 3.0
(31 to 48 wk)	20	10.9 ± 3.2	7.2 ± 3.2	9.2 ± 3.2	7.1 ± 3.2	

^{a-b}Means within a row with no common superscripts differ significantly (P<.05).

^{x-y}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment.

³n = Average number of birds in each treatment.

⁴Follicles = Large yolky ovarian follicles greater than 10 mm in diameter.

⁵Estimate of multiple ovulations include double yolked eggs and all multiple egg combinations.

TABLE III-5. Effect of feed allowance during rearing (0-28 wk) on the distribution of large follicles in single, double, and triple hierarchical arrangements of size at selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
-----(% of follicles in each arrangement ± SEM)-----						
Single:						
Sex. Mat.	10	2.2 ± 4.5	2.7 ± 4.5 ^y	5.2 ± 4.8 ^y	5.3 ± 4.8 ^y	3.8 ± 2.3 ^y
40 wk	8	6.8 ± 6.4 ^c	16.0 ± 5.8 ^{bc,xy}	23.9 ± 5.4 ^{ab,x}	33.2 ± 5.8 ^{a,x}	20.0 ± 2.9 ^x
48 wk	6	14.8 ± 6.4 ^b	26.1 ± 5.4 ^{ab,x}	35.9 ± 5.4 ^{a,x}	34.2 ± 7.2 ^{a,x}	27.7 ± 3.1 ^x
Mean		7.9 ± 3.4 ^c	14.9 ± 3.1 ^{bc}	21.7 ± 3.0 ^{ab}	24.2 ± 3.5 ^a	
Double:						
Sex. Mat.	10	39.0 ± 6.0 ^y	38.4 ± 6.0 ^y	39.3 ± 6.4 ^y	54.1 ± 6.4	42.7 ± 3.1 ^y
40 wk	8	72.0 ± 8.5 ^{a,x}	66.1 ± 7.8 ^{ab,x}	63.8 ± 7.2 ^{ab,x}	46.1 ± 7.8 ^b	62.0 ± 3.9 ^x
48 wk	6	67.0 ± 8.5 ^x	59.2 ± 7.2 ^x	51.4 ± 7.2 ^{xy}	54.5 ± 9.6	58.0 ± 4.1 ^x
Mean		59.3 ± 4.5	54.6 ± 4.1	51.5 ± 4.0	51.6 ± 4.6	
Triple or greater:						
Sex. Mat.	10	58.9 ± 6.5 ^x	58.9 ± 6.5 ^x	55.0 ± 6.9 ^x	41.8 ± 6.9 ^x	53.6 ± 3.4 ^x
40 wk	8	21.2 ± 9.2 ^y	17.9 ± 8.4 ^y	12.3 ± 7.8 ^y	20.7 ± 8.4 ^{xy}	18.0 ± 4.2 ^y
48 wk	6	18.2 ± 9.2 ^y	14.7 ± 7.8 ^y	12.7 ± 7.8 ^y	11.3 ± 10.3 ^y	14.2 ± 4.4 ^y
Mean		32.8 ± 4.9	30.5 ± 4.4	26.7 ± 4.3	24.6 ± 5.0	

^{a-c}Means within a row with no common superscripts differ significantly (P<.05).

^{x-y}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment.

³n = Average number of birds in each treatment.

TABLE III-6 Effect of feed allowance during rearing (0-28 wk) on the production of various forms of defective eggs at selected times during the breeder period (29-48 wk).

Egg type	n ²	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
——(% incidence of defective egg type ± SEM)——						
Double yolk						
31 to 40 wk	735	2.6 ± .5 ^a	2.3 ± .5 ^{ab}	2.4 ± .5 ^a	1.0 ± .5 ^b	2.1 ± .3
40 to 48 wk	180	3.1 ± 1.1	1.0 ± 1.0	1.4 ± 1.0	2.1 ± 1.0	1.9 ± .5
(31 to 48 wk)	915	2.8 ± .6	1.7 ± .6	1.9 ± .5	1.5 ± .6	
Thin-shelled						
31 to 40 wk	735	1.2 ± .4	1.2 ± .4	1.5 ± .4	.6 ± .4	1.1 ± .2
40 to 48 wk	180	2.5 ± .9 ^a	2.1 ± .8 ^{ab}	2.3 ± .7 ^a	.0 ± .8 ^b	1.7 ± .4
(31 to 48 wk)	915	1.8 ± .5 ^a	1.6 ± .5 ^a	1.9 ± .4 ^a	.3 ± .4 ^b	
Misshapen (flat)						
31 to 40 wk	735	.15 ± .21	.00 ± .21	.13 ± .20	.49 ± .20 ^z	.19 ± .10 ^z
40 to 48 wk	180	.00 ± .42 ^b	.52 ± .40 ^{ab}	.46 ± .37 ^b	1.57 ± .40 ^{a,y}	.64 ± .20 ^y
(31 to 48 wk)	915	.08 ± .23 ^b	.26 ± .22 ^b	.30 ± .21 ^b	1.03 ± .21 ^a	
Membranous						
31 to 40 wk	735	2.8 ± .7 ^b	4.5 ± .7 ^{ab}	5.3 ± .7 ^a	4.0 ± .7 ^{ab}	4.1 ± .4
40 to 48 wk	180	4.9 ± 1.5	1.6 ± 1.4	2.8 ± 1.3	2.1 ± 1.4	2.8 ± .7
(31 to 48 wk)	915	3.9 ± .8	3.1 ± .8	4.0 ± .7	3.0 ± .8	
Small (< 70 g)						
31 to 40 wk	735	1.4 ± .5	1.5 ± .5	2.1 ± .5 ^y	2.2 ± .4 ^y	1.8 ± .2 ^y
40 to 48 wk	180	3.1 ± .1 ^a	.0 ± .1 ^b	.0 ± .1 ^{b,z}	.0 ± .1 ^{b,z}	.8 ± .5 ^z
(31 to 48 wk)	915	2.2 ± .5 ^a	.7 ± .5 ^b	1.1 ± .5 ^{ab}	1.1 ± .5 ^{ab}	

^{a-b}Means within a row with no common superscripts differ significantly (P<.05).

^{y-z}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²n = Average number of eggs processed in each treatment.

TABLE III-7 Effect of feed allowance during rearing (0-28 wk) on total and settable egg production in male-line Large White turkey hens.

Variable	n ²	Feeding Regimen ¹				SEM
		FF	LP	R10	R20	
-----Egg number-----						
<u>Total egg production</u>						
Eggs per bird ⁴						
31 to 40 wk	24	27.8	31.4	30.5	29.4	2.1
31 to 48 wk	20	43.5	46.2	46.2	44.2	4.9
Eggs per layer ⁵						
31 to 40 wk	24	29.6	32.2	32.3	32.3	1.6
31 to 48 wk	16	53.7	55.8	58.8	60.2	1.9
<u>Settable egg production</u>						
Eggs per bird						
31 to 40 wk	24	25.4	28.3	26.7	26.8	1.8
31 to 48 wk	20	39.4	42.7	41.4	40.7	4.6
Eggs per layer						
31 to 40 wk	24	27.1	29.1	28.3	29.5	1.1
31 to 48 wk	16	48.6	51.7	52.8	55.4	2.4

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²n = Average number of birds in each treatment.

³Sexual maturity defined as day of first egg, calculated as days past photostimulation.

⁴Eggs per bird = mean egg production for birds present.

⁵Eggs per layer = mean egg production for birds in production.

TABLE III-8. Effect of feed allowance during rearing (0-28 wk) on the occurrence of non-laying hens, and on the presence of atretic follicles or evidence of internal ovulation at selected times during the breeder period (29-48 wk).

Time ²	n ³	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
-----(% incidence ± SEM)-----						
% Non-layers						
31 to 40 wk.	24	5.4 ± .4 ^{b,z}	5.1 ± .4 ^{b,z}	5.1 ± .3 ^{b,z}	7.7 ± .3 ^{a,z}	5.8 ± .2 ^z
40 to 48 wk	15	43.0 ± .7 ^{c,y}	31.5 ± .7 ^{d,y}	46.6 ± .6 ^{b,y}	54.2 ± .7 ^{a,y}	43.8 ± .3 ^y
(31 to 48 wk)	20	24.2 ± .4 ^c	18.3 ± .4 ^d	25.8 ± .4 ^b	31.0 ± .4 ^a	
Follicular atresia						
Sex. Mat.	10	.0 ± 12.5 ^b	9.1 ± 11.9 ^{ab}	22.2 ± 13.2 ^{ab}	40.0 ± 12.5 ^a	17.8 ± 6.3
40 wk	8	12.5 ± 14.0	12.5 ± 14.0	12.5 ± 14.0	37.5 ± 14.0	17.8 ± 7.0
48 wk	6	20.0 ± 17.7	28.6 ± 15.0	28.6 ± 15.0	.0 ± 19.8	19.3 ± 8.5
Mean		10.8 ± 8.6	16.7 ± 7.9	21.1 ± 8.1	25.8 ± 9.1	
Internal ovulation						
Sex. Mat.	10	30.0 ± 12.5	18.2 ± 11.9	22.2 ± 13.2	20.0 ± 12.5	22.6 ± 6.3 ^{xy}
40 wk	8	25.0 ± 14.0	.0 ± 14.0	.0 ± 14.0	.0 ± 14.0	6.3 ± 7.0 ^y
48 wk	6	40.0 ± 17.7	42.9 ± 15.0	42.9 ± 15.0	.0 ± 19.8	31.4 ± 8.4 ^x
Mean		31.7 ± 8.6 ^a	20.3 ± 7.9 ^{ab}	21.7 ± 8.1 ^{ab}	6.7 ± 9.1 ^b	

^{a-b}Means within a row with no common superscripts differ significantly (P<.05).

^{x-z}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²Processing times: Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment.

³n = Average number of birds in each treatment.

TABLE III-9 Effect of feed allowance during rearing (0-28 wk) on prime sequence timing and length, and on average sequence and pause length at selected times during the breeder period (29-48 wk).

Variable	n ²	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
(Days ± SEM)						
Prime sequence length ³ (d)	24	3.61 ± .37	4.00 ± .39	3.42 ± .37	4.11 ± .34	3.79 ± .37
Day of prime sequence ⁴	24	36.3 ± 1.5	36.4 ± 1.6	33.6 ± 1.5	36.9 ± 1.4	35.8 ± 1.5
<u>Mean sequence length (d)</u>						
31 to 40 wk	24	1.82 ± .07 ^{b,y}	1.95 ± .07 ^{ab,y}	1.98 ± .07 ^{ab,y}	2.13 ± .07 ^{a,y}	1.97 ± .04 ^y
40 to 48 wk	7	1.44 ± .13 ^z	1.47 ± .13 ^z	1.39 ± .12 ^z	1.45 ± .14 ^z	1.44 ± .07 ^z
(31 to 48 wk)	16	1.63 ± .08	1.71 ± .07	1.68 ± .07	1.79 ± .07	
<u>Mean pause length (d)</u>						
31 to 40 wk	24	2.19 ± .14 ^a	1.49 ± .14 ^{b,z}	1.53 ± .14 ^b	1.44 ± .13 ^b	1.66 ± .07 ^z
40 to 48 wk	7	2.34 ± .26 ^b	3.12 ± .23 ^{a,y}	1.80 ± .23 ^{bc}	1.63 ± .23 ^c	2.22 ± .12 ^y
(31 to 48 wk)	16	2.27 ± .15 ^a	2.31 ± .14 ^a	1.67 ± .13 ^b	1.53 ± .15 ^b	

^{a-c}Means within a row with no common superscripts differ significantly (P<.05).

^{y-z}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²n = Average number of birds in each treatment.

³Prime sequence defined as the longest sequence of the laying cycle, typically occurring early in lay.

⁴Day of prime sequence defined as day of prime sequence commencement, calculated as days past photostimulation.

TABLE III-10. Effect of feed allowance during rearing (0-28 wk) on the distribution of egg laying sequences¹ into different length categories during the breeder period (29-48 wk).

Variable	n ³	Feeding Regimen ²				Mean
		FF	LP	R10	R20	
-----(% of sequences in each range ± SEM)-----						
<u>1 day:</u>						
31 to 40 wk	24	16.8 ± 3.4 ^{a,z}	7.4 ± 3.6 ^{ab,z}	7.4 ± 3.4 ^{b,z}	11.9 ± 3.3 ^{ab}	10.9 ± 1.7 ^z
40 to 48 wk	7	37.9 ± 6.5 ^{a,y}	27.3 ± 6.1 ^{ab,y}	34.3 ± 5.9 ^{ab,y}	18.5 ± 6.7 ^b	29.5 ± 3.2 ^y
<u>1.1 to 2 days:</u>						
31 to 40 wk	24	58.4 ± 4.9 ^a	62.8 ± 5.1 ^a	62.0 ± 4.7 ^a	43.1 ± 4.7 ^{b,z}	56.6 ± 2.4 ^z
40 to 48 wk	7	51.7 ± 10.6	66.7 ± 9.2	62.9 ± 9.4	70.4 ± 9.6 ^y	62.9 ± 4.4 ^y
<u>2.1 to 3 days:</u>						
31 to 40 wk	24	20.8 ± 4.0	26.6 ± 4.2 ^y	25.0 ± 3.9 ^y	31.1 ± 3.9 ^y	25.9 ± 2.0 ^y
40 to 48 wk	7	6.9 ± 7.5	6.1 ± 7.0 ^z	2.9 ± 6.8 ^z	11.1 ± 7.8 ^z	6.7 ± 3.6 ^z
<u>3.1 or more:</u>						
31 to 40 wk	24	4.0 ± 2.2 ^b	3.2 ± 2.3 ^b	5.6 ± 2.1 ^b	13.8 ± 2.1 ^{a,y}	6.6 ± 1.1 ^y
40 to 48 wk	7	3.4 ± 4.1	.0 ± 3.9	.0 ± 3.8	.0 ± 4.2 ^z	.9 ± 2.0 ^z
<u>Means</u>						
(31 to 48 wk):						
1 d	16	27.4 ± 3.7 ^a	17.4 ± 3.5 ^b	20.8 ± 3.4 ^{ab}	15.2 ± 3.8 ^b	
1.1 to 2 d	16	55.1 ± 5.1	64.7 ± 5.0	62.4 ± 4.8	56.7 ± 5.3	
2.1 to 3 d	16	13.8 ± 4.3	16.3 ± 4.1	13.9 ± 3.9	21.2 ± 4.3	
3.1 or more d	16	3.7 ± 2.4	1.6 ± 2.2	2.8 ± 2.2	6.9 ± 2.4	

^{a-b}Means within a row with no common superscripts differ significantly (P<.05).

^{y-z}Means within a column with no common superscripts differ significantly (P<.05).

¹Laying sequence is defined as a series of ovipositions occurring on consecutive days.

²Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

³n = Average number of birds in each treatment.

TABLE III-11. Effect of feed allowance during rearing (0-28 wk) on the distribution of pauses¹ sorted into different length categories during the breeder period (29-48 wk).

Variable	n ³	Feeding Regimen ²				Mean
		FF	LP	R10	R20	
-----(% of pauses in each range ± SEM)-----						
<u>1 day:</u>						
31 to 40 wk	24	28.7 ± 4.7 ^b	41.5 ± 4.8 ^{ab,y}	48.1 ± 4.5 ^a	42.2 ± 4.5 ^a	40.1 ± 2.3 ^y
40 to 48 wk	7	20.7 ± 8.7 ^{ab}	6.1 ± 8.2 ^{b,z}	31.4 ± 7.9 ^a	25.9 ± 9.0 ^{ab}	21.0 ± 4.2 ^z
<u>1.1 to 2 days:</u>						
31 to 40 wk	24	42.6 ± 5.0	56.8 ± 5.2	41.7 ± 4.8	51.4 ± 4.8	45.6 ± 2.5
40 to 48 wk	7	44.8 ± 9.2	48.5 ± 8.7	45.7 ± 8.5	63.0 ± 9.6	50.4 ± 4.5
<u>2.1 to 3 days:</u>						
31 to 40 wk	24	12.9 ± 2.9 ^a	7.4 ± 3.0 ^{ab,z}	6.5 ± 2.8 ^{ab}	4.6 ± 2.8 ^b	7.8 ± 1.4 ^z
40 to 48 wk	7	20.7 ± 5.4 ^a	21.2 ± 5.1 ^{a,y}	17.1 ± 5.0 ^{ab}	3.7 ± 5.6 ^b	15.7 ± 2.6 ^y
<u>3.1 or more:</u>						
31 to 40 wk	24	15.8 ± 2.6 ^a	4.2 ± 2.7 ^{b,z}	3.7 ± 2.5 ^b	1.8 ± 2.5 ^b	6.4 ± 1.3 ^z
40 to 48 wk	7	13.8 ± 4.9 ^{ab}	24.2 ± 4.5 ^{a,y}	5.7 ± 4.4 ^b	7.4 ± 5.1 ^b	12.8 ± 2.4 ^y
<u>Means</u>						
<u>(31 to 48 wk):</u>						
1 d	16	24.7 ± 4.9 ^b	23.8 ± 4.8 ^b	39.8 ± 4.6 ^a	34.1 ± 5.0 ^{ab}	
1.1 to 2 d	16	43.7 ± 5.3	47.6 ± 5.0	43.7 ± 4.9	57.2 ± 5.5	
2.1 to 3 d	16	16.8 ± 3.1 ^a	14.3 ± 3.0 ^a	11.8 ± 2.8 ^{ab}	4.1 ± 3.1 ^b	
3.1 or more d	16	14.8 ± 2.8 ^a	14.2 ± 2.7 ^a	4.7 ± 2.6 ^b	4.6 ± 2.8 ^b	

^{a-b}Means within a row with no common superscripts differ significantly (P<.05).

^{y-z}Means within a column with no common superscripts differ significantly (P<.05).

¹Pause is defined as a break of one or more days between sequences in which no ovipositions occur.

²Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

³n = Average number of birds in each treatment.

TABLE III-12 Effect of feed allowance during rearing (0-28 wk) on egg weight and specific gravity at selected times during the breeder period (29-48 wk).

Variable	n ²	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
(Value ± SEM)						
<u>Egg weight (g)</u>						
31 to 40 wk	664	87.0 ± .3 ^{ab,z}	86.7 ± .3 ^{b,z}	87.7 ± .3 ^{a,z}	84.3 ± .2 ^{c,z}	86.4 ± .1 ^z
40 to 48 wk	169	94.0 ± .6 ^{ab,y}	92.6 ± .6 ^{b,y}	94.9 ± .5 ^{a,y}	89.4 ± .5 ^{c,y}	92.8 ± .3 ^y
(31-48 wk)	833	90.5 ± .3 ^b	89.7 ± .3 ^c	91.3 ± .3 ^a	86.9 ± .3 ^d	
<u>Egg specific gravity</u>						
31 to 40 wk	637	1.082 ± .000 ^d	1.083 ± .000 ^c	1.084 ± .000 ^b	1.085 ± .000 ^{a,y}	1.084 ± .000
40 to 48 wk	164	1.081 ± .001 ^c	1.082 ± .001 ^b	1.084 ± .001 ^a	1.083 ± .001 ^{b,z}	1.083 ± .000
(31-48 wk)	801	1.082 ± .000 ^d	1.083 ± .000 ^c	1.084 ± .000 ^b	1.084 ± .000 ^a	

^{a-d}Means within a row with no common superscripts differ significantly (P<.05).

^{y-z}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²n = Average number of eggs processed in each treatment.

TABLE III-13 Effect of feed allowance during rearing (0-28 wk) on egg yolk, albumen, and shell weights, and percentage of egg weight at selected times during the breeder period (29-48 wk).

Egg component	n ²	Feeding Regimen ¹				Mean
		FF	LP	R10	R20	
----- (Weight (g) ± SEM) -----						
<u>Yolk</u>						
31 to 40 wk	637	23.1 ± .1 ^b	23.1 ± .1 ^b	23.7 ± .1 ^a	23.4 ± .1 ^a	23.4 ± .1 ^z
40 to 48 wk	167	27.1 ± .2 ^b	27.2 ± .2 ^b	27.9 ± .2 ^a	27.4 ± .2 ^{ab}	27.4 ± .1 ^y
(31-48 wk)	804	25.1 ± .1 ^c	25.2 ± .1 ^{bc}	25.8 ± .1 ^a	25.4 ± .1 ^b	
<u>Albumen</u>						
31 to 40 wk	637	54.8 ± .2 ^a	54.5 ± .2 ^a	54.7 ± .2 ^a	51.9 ± .2 ^b	54.0 ± .1 ^z
40 to 48 wk	167	57.6 ± .5 ^a	55.8 ± .4 ^b	57.1 ± .4 ^a	52.6 ± .4 ^c	55.8 ± .2 ^y
(31-48 wk)	804	56.2 ± .3 ^a	55.1 ± .2 ^b	55.9 ± .2 ^a	52.3 ± .2 ^c	
<u>Shell + membrane</u>						
31 to 40 wk	637	9.05 ± .04 ^b	9.11 ± .04 ^b	9.31 ± .04 ^a	9.03 ± .04 ^b	9.12 ± .02 ^z
40 to 48 wk	167	9.56 ± .08 ^{bc}	9.71 ± .07 ^b	9.89 ± .07 ^a	9.39 ± .07 ^c	9.64 ± .04 ^y
(31 to 48 wk)	804	9.30 ± .04 ^{bc}	9.41 ± .04 ^b	9.60 ± .04 ^a	9.21 ± .04 ^c	
----- (Weight (% of egg weight) ± SEM) -----						
<u>Yolk</u>						
31 to 40 wk	637	26.7 ± .1 ^{c,z}	26.7 ± .1 ^{c,z}	27.1 ± .1 ^{b,z}	27.8 ± .1 ^{a,z}	27.1 ± .1 ^z
40 to 48 wk	167	28.7 ± .2 ^{c,y}	29.4 ± .2 ^{b,y}	29.4 ± .2 ^{b,y}	30.7 ± .2 ^{a,y}	29.6 ± .1 ^y
(31 to 48 wk)	804	27.7 ± .1 ^c	28.1 ± .1 ^b	28.2 ± .1 ^b	29.3 ± .1 ^a	
<u>Albumen</u>						
31 to 40 wk	637	62.9 ± .1 ^{a,y}	62.8 ± .1 ^{a,y}	62.3 ± .1 ^{b,y}	61.5 ± .1 ^{c,y}	62.4 ± .1 ^z
40 to 48 wk	167	61.1 ± .2 ^{a,z}	60.9 ± .2 ^{b,z}	60.2 ± .2 ^{b,z}	58.8 ± .2 ^{c,z}	60.2 ± .2 ^y
(31 to 48 wk)	804	62.0 ± .1 ^a	61.4 ± .1 ^b	61.2 ± .1 ^b	60.1 ± .1 ^c	
<u>Shell + membrane</u>						
31 to 40 wk	637	10.42 ± .03 ^{d,y}	10.52 ± .03 ^c	10.61 ± .03 ^{b,y}	10.71 ± .03 ^{a,y}	10.57 ± .02 ^y
40 to 48 wk	167	10.16 ± .08 ^{b,z}	10.48 ± .08 ^a	10.44 ± .07 ^{a,z}	10.53 ± .07 ^{a,z}	10.40 ± .03 ^z
(31 to 48 wk)	804	10.29 ± .04 ^c	10.50 ± .03 ^b	10.53 ± .03 ^{ab}	10.61 ± .03 ^a	

^{a-c}Means within a row with no common superscripts differ significantly (P<.05).

^{y-z}Means within a column with no common superscripts differ significantly (P<.05).

¹Feeding Regimen: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. All treatments full-fed during breeder period.

²n = Average number of eggs processed in each treatment.

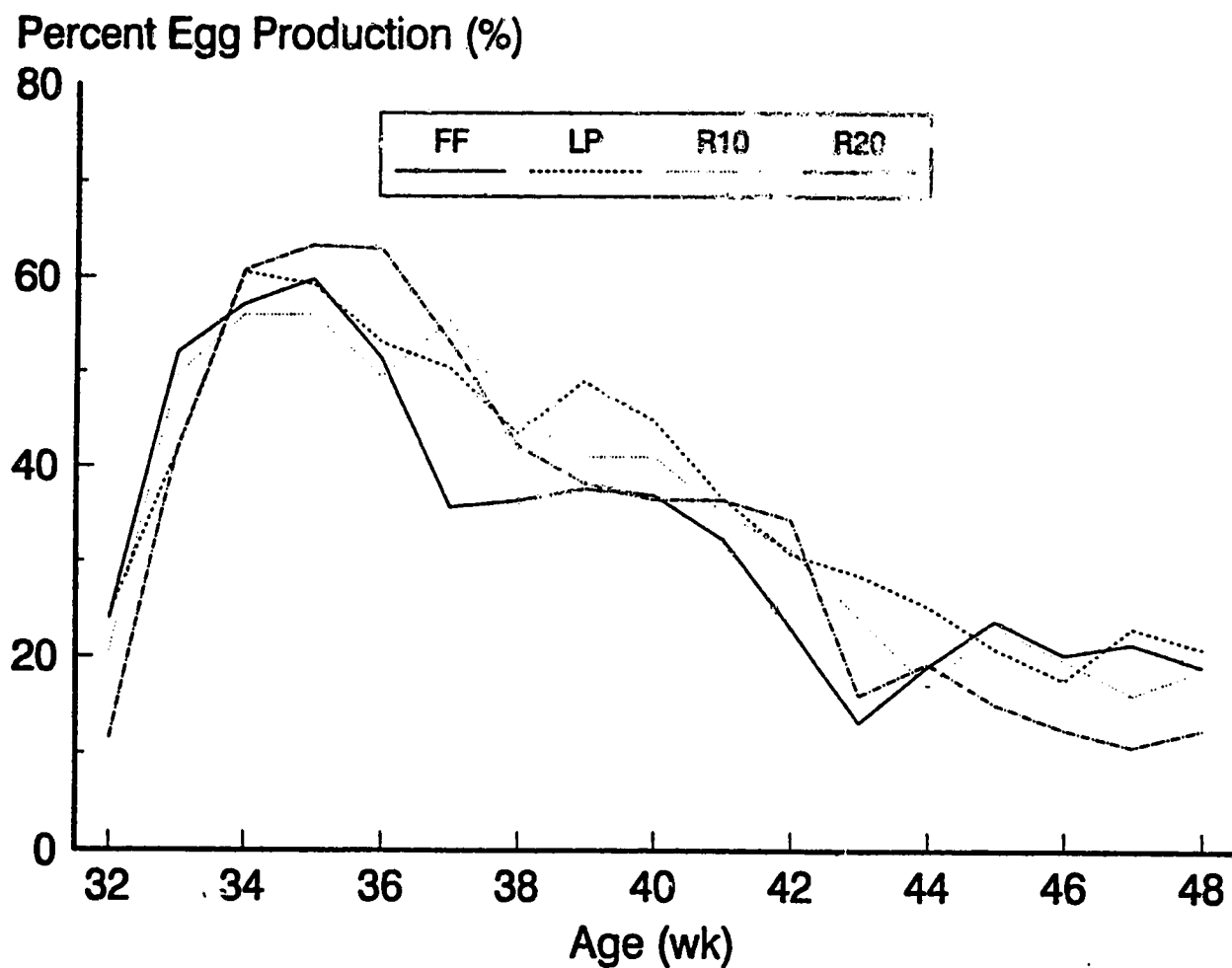


FIGURE III-1 Effect of feed allowance during rearing (0-28 wk) on total hen-day egg production in male-line breeder hens during the breeder period (29-48 wk) with treatments as follows: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight.

Percent Egg Production (%)

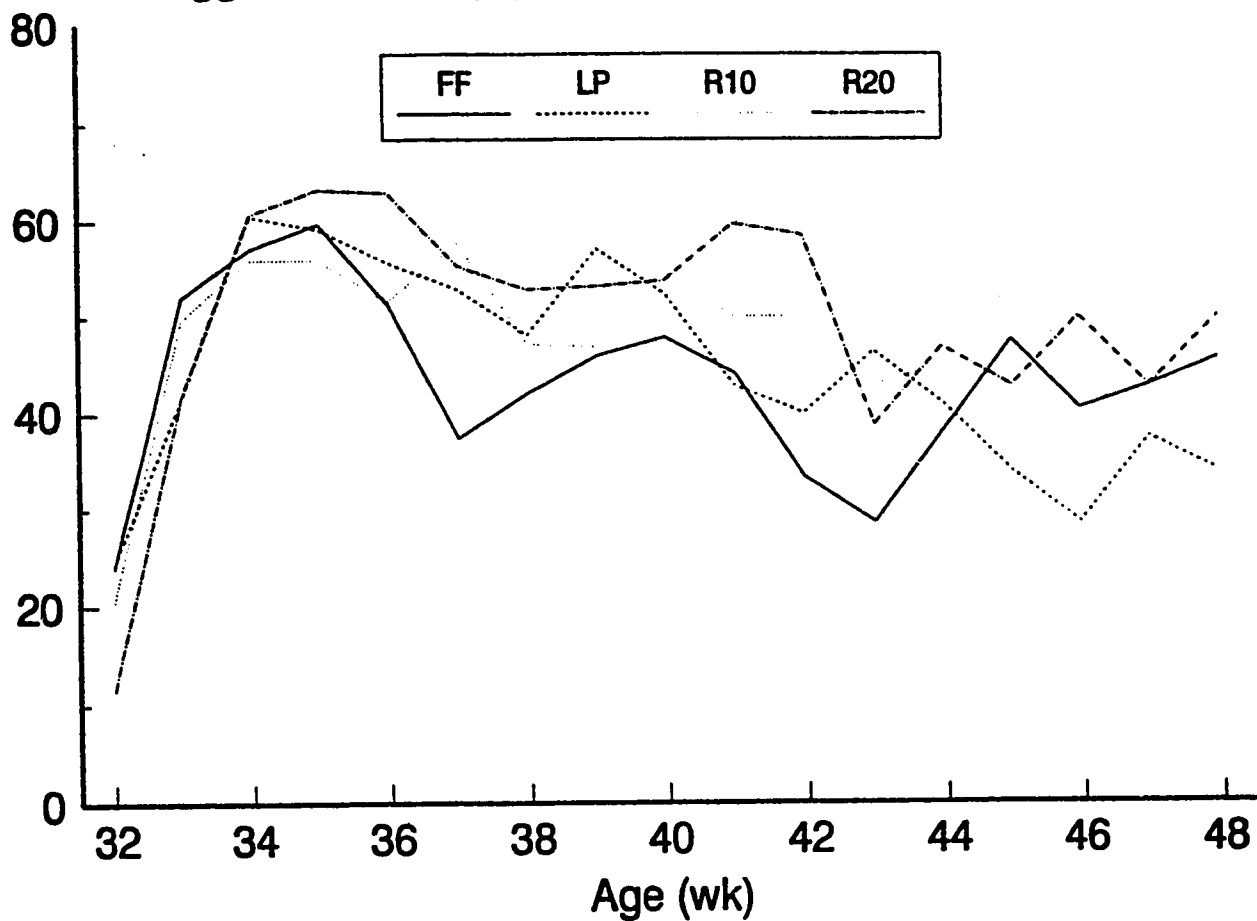


FIGURE III-2 Effect of feed allowance during rearing (0-28 wk) on total layer-day egg production in male-line breeder hens during the breeder period (29-48 wk) with treatments as follows: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. Layer-day production calculated using only hens in production.

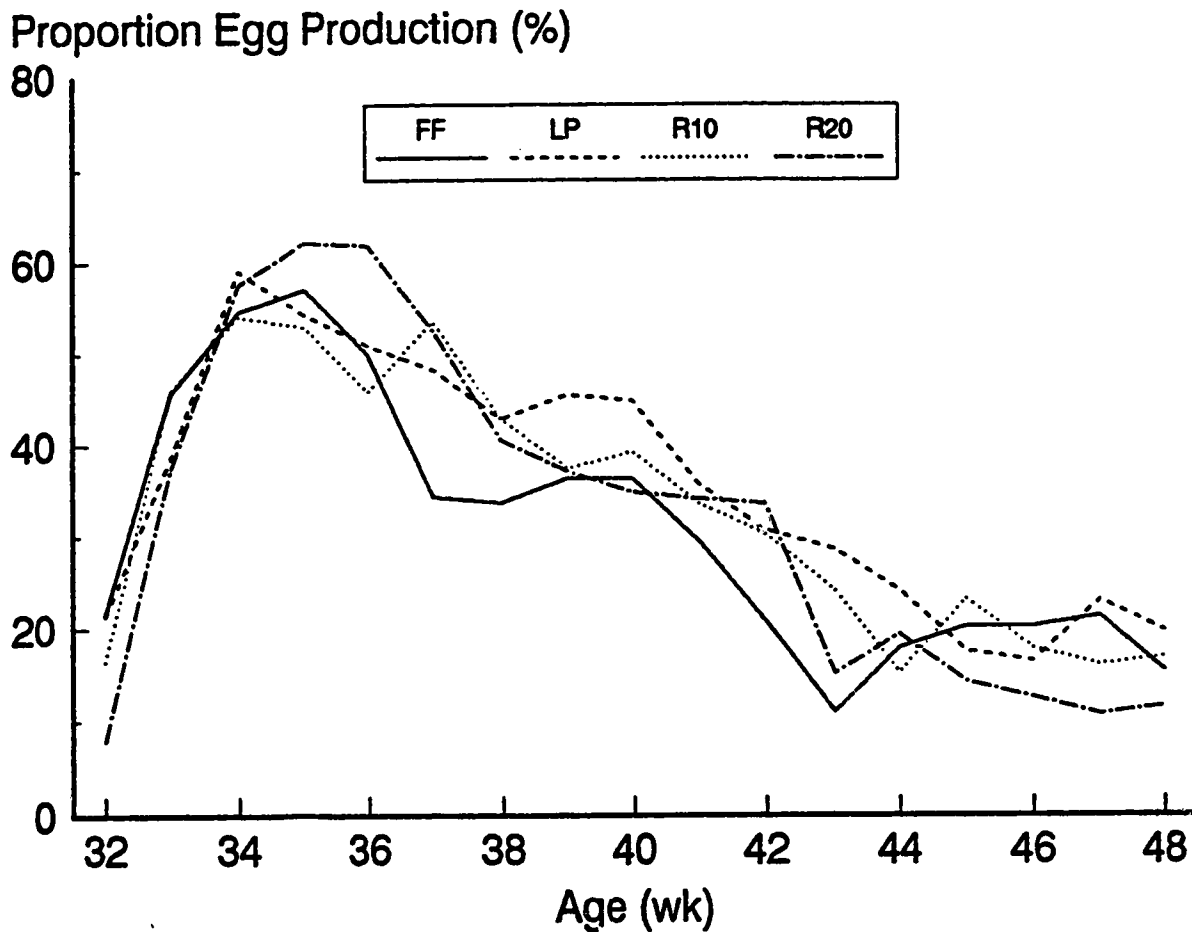


FIGURE III-3 Effect of feed allowance during rearing (0-28 wk) on settable hen-day egg production in male-line breeder hens during the breeder period (29-48 wk) with treatments as follows: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight.

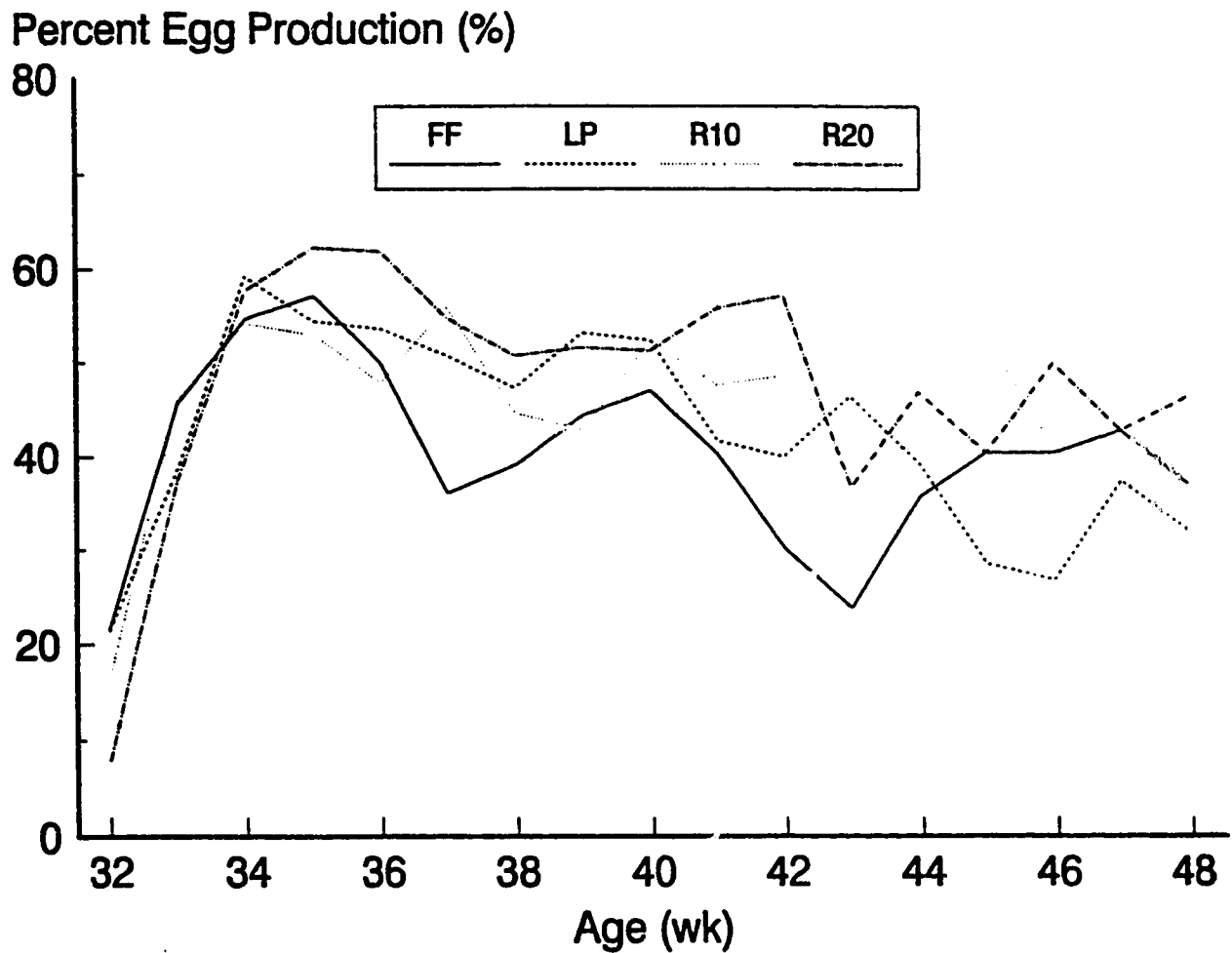


FIGURE III-4 Effect of feed allowance during rearing (0-28 wk) on settable layer-day egg production in male-line breeder hens during the breeder period (29-48 wk) with treatments as follows: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight. Layer-day production calculated using only hens in production.

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IV. GENERAL DISCUSSION AND CONCLUSIONS

Feed restriction in turkey breeder hen candidates has been studied for two reasons. Firstly, a reduction in body size due to restriction would reduce feed costs, particularly in the holding period just prior to the breeder period. Secondly, reduced body size and altered body composition may improve egg production by countering some of the negative effects selection for growth traits have had on reproductive efficiency.

Broiler breeder restriction programs are the source of restriction techniques for use in turkeys. Broiler breeder hen candidates are feed restricted beginning at an early age (Costa, 1981), to circumvent reproductive problems brought about by selection for growth (Siegel and Dunnington, 1985). Less is known about the effects of feed restriction in turkeys than in broiler breeders. In recent years, turkey breeders have begun to increase in BW more substantially between generations because of a shifting of selection emphasis towards growth in female line (Miles and Leeson, 1990). A negative relationship has been observed between BW and egg production in turkeys (Nestor, 1971; Nestor *et al.*, 1980). The male-line breeder hen is likely the most reproductively unfit hen in poultry production, as expected rates of lay are less than half that of the female-line turkeys (Hocking, 1992a).

The male-line hen was selected as the model for the current study because of its extreme size and poor egg production. Feed restriction studies in the past have utilized much smaller birds, with more variable results for egg production (Hester and Stevens, 1990). With the current selection practices focusing heavily on BW gain, a study of responses of a male-line bird to feed restriction may give a preview of what to expect in the coming years.

Section II and III report the results of a study of the effects of several feed restriction programs during the rearing period on growth, feed intake, carcass composition, ovarian morphology, egg production, and egg laying patterns. The restriction programs (low protein, LP; restricted BW by 10 or 20%, R10 and R20) were effective in reducing body weight at photostimulation. It was possible to manage a growth curve either 10 or 20% below the full-fed

(FF) control curve by altering daily feed allowance (Section II). Feed intake was significantly reduced during rearing in the R10 and R20 treatment birds. The LP treatment, with *ad libitum* access to a low protein feed, hardly reduced its feed consumption, eliminating the potential for any feed savings beyond a reduced protein intake (Section II). Feed intake was increased between 28 wk and first egg in restricted treatment birds. This was probably to compensate for a lack of body stores to support ovary formation and the onset of egg production. For the remainder of the breeder period feed intake was again reduced, however, nullifying concerns about increased rates of feed intake in previously restricted birds canceling the value of previous feed savings.

Flock uniformity in restriction treatments involving limited daily access to feed is of concern. During rearing, uniformity in the R10 and R20 treatment groups was significantly worse than the *ad libitum* fed treatments between 13 and 28 wk of age, with no negative effects prior to this (Section II). Under conditions of limited feed, the aggressive birds will consume extra feed, and grow disproportionately larger (Petitte *et al.*, 1981). Full-feeding during rearing removed the uniformity problem, as smaller birds were allowed to catch up in size. It may be useful to consider using diluted daily feed allotments during quantitative feed restriction to extend feed availability. This method of feed extension has been found to improve uniformity over time in broiler breeder stocks (Zuidhof *et al.*, 1993).

The body composition of the smaller restricted birds was altered in early lay. Restricted birds had a reduced breast muscle size, and abdominal fatpad weight, except for the LP fatpad, which was significantly heavier on average (Section II). The LP treatment birds appeared to have consumed excess feed during rearing to compensate for the lack of protein in the diet. The extra energy consumed was stored as fat. Low protein diets are frowned upon for broiler breeders, as the birds are heavier, and fatter at photostimulation than are quantitatively restricted birds (Leeson and Summers, 1991). The differences in body weight and composition had faded by 40 wk of age. In effect, feed restriction programs had gently lowered the peak of the growth curve through the stage of maximum body size, and allowed the curve to intersect the FF treatment growth curve mid-way through the breeder cycle. The growth curve of the R20 treatment did not intersect the main curve,

reflecting stunted growth due to feed restriction. The implications of this permanently reduced body size is further potential for feed savings during the breeder period because of a lower basal metabolic requirement.

Feed restriction during the rearing period reduced the average number of large follicles on the ovary, which resulted in a lower proportion of multiple ovulations, and incidence of double yolked eggs during the breeder period. Egg traits, such as the proportion of yolk and shell in the egg, and specific gravity were significantly improved. Sequence length was significantly lengthened in R20 treatment birds, and pause length was significantly decreased in birds of the R10 and R20 treatments. R10 and R20 treatment birds also had a significantly reduced proportion of multiple follicle sets, and the R20 treatment had the highest rate of egg production in early lay (Section III). Quantitative feed restriction had a negative effect on persistence of lay, particularly in the R20 treatment. If persistence of lay is ignored, however, the R20 treatment hens were the most reproductively fit hens in the experiment. Reduced persistency of lay is associated with early photostimulation (Hocking *et al.*, 1988) more than with feed restriction, as persistency of lay is not affected in birds photostimulated at a later time (Hocking, 1992b; Hocking *et al.*, 1992). If photostimulation were slightly delayed to allow for a more complete physiological maturity, persistence of lay in these birds would likely improve. A more severe restriction may then be able to generate further improvements to reproductive traits.

The key time period in the growth cycle of large turkey breeder hens is the days between photostimulation and first egg. In this time period, a large portion of feed intake and growth is focused on development of the reproductive tract. In birds reared under restriction conditions, part of the energy in this period was diverted to expansion of the fatpad and breast muscle tissue, resulting in fewer precursors being available for excess ovary development (Section II). Hocking *et al.* (1989) found that to be truly effective in controlling follicle numbers at sexual maturity in broiler breeders, some level of feed restriction should continue until point of lay. Male-line breeder hens would likely also benefit from this type of management, as less energy would be available for ovarian expansion. The period between photostimulation and first egg is also of interest because of

the phenomenon of phantom follicles. If these follicles can be captured, up to five more eggs per bird can be produced. A further understanding of oviduct maturation is necessary, as this seems to be the limiting factor in the attainment of sexual maturity.

Despite the improvements that were possible in this study for reproductive traits due to changes in body composition and breeder eating patterns, the problems with reproductive fitness in large turkeys are far from solved. Male-line turkeys are more resistant to change due to feed restriction than smaller lines are (Hocking 1992a). Strain differences may alter reproductive traits, and the effects of feed restriction on them. Future research will need to focus on how lipids are utilized for ovary growth and fat storage. These birds were less fat than those studied by Hocking (1992a), but had a greater number of large ovarian follicles. These turkeys in general were not very fat, and if lipids could be diverted away from the ovary, it would be beneficial to reproductive performance.

The turkey breeding companies may need to re-examine their priorities for future selection. Growth selection has occurred for years with little consideration given to the effects on ovary morphology. The ovary is the key component to propagation of the species, and if it is dysfunctional, so is the industry. The turkey industry is pushing the limits of carcass trait development with its high growth rates, feed efficiencies, and meat yields. Tipping the selection scale so far in one direction can only be done for so long, however, before something gives. Birds are now becoming too large too quickly to be able to support their own weight, and the reproductive system of the large breeder hens is in disarray. Perhaps we need to take a step back, and slow the growth rates slightly to create a more reproductively fit bird. This does not mean that genetic advancement has to be relinquished, however, as these goals may be possible through changes to bird management.

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V. APPENDIX I.

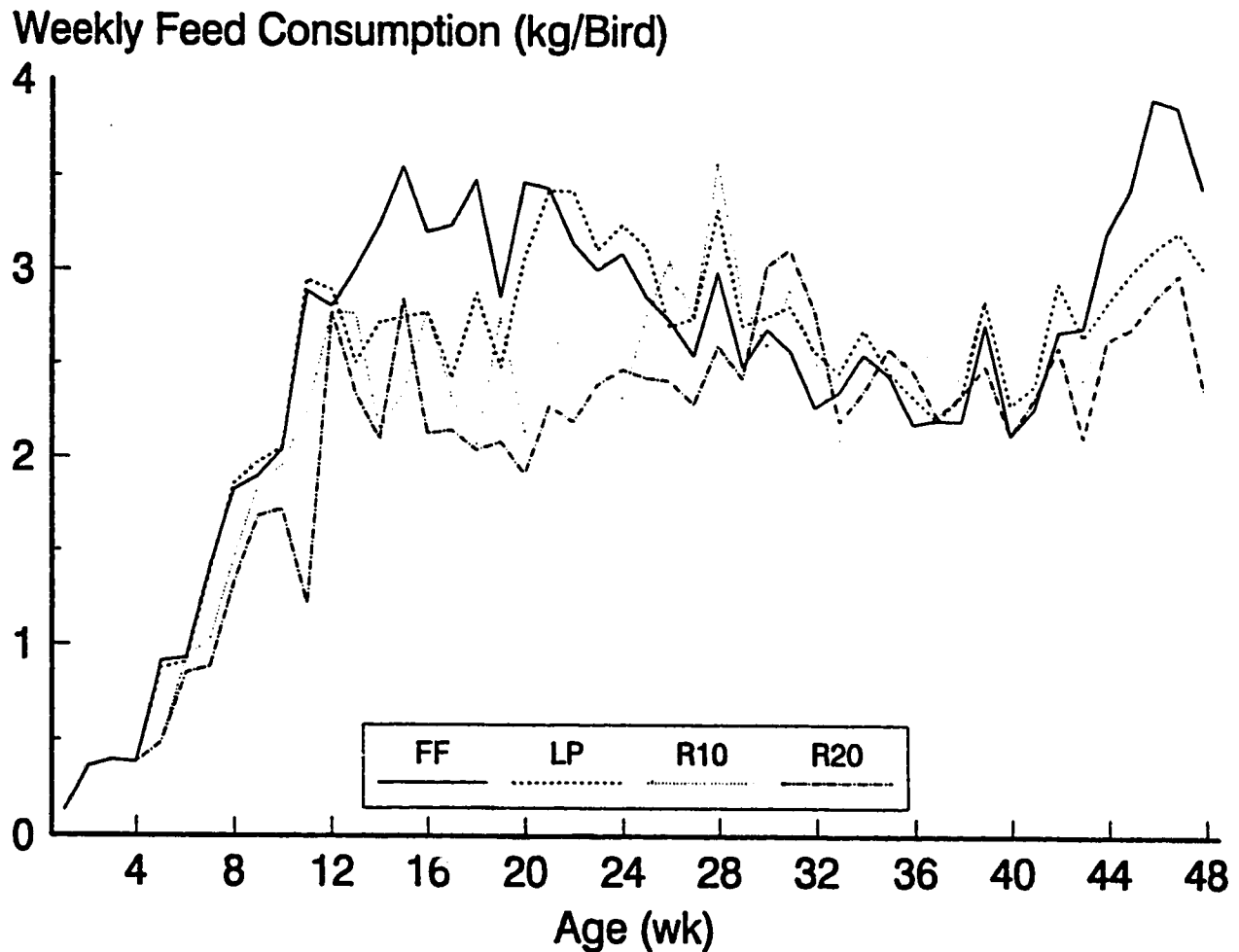


FIGURE V-1 Weekly individual feed consumption values during the grower (0 to 28 wk) and breeder period (29 to 48 wk) for male-line breeder hens reared under the following feeding regimens: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight.

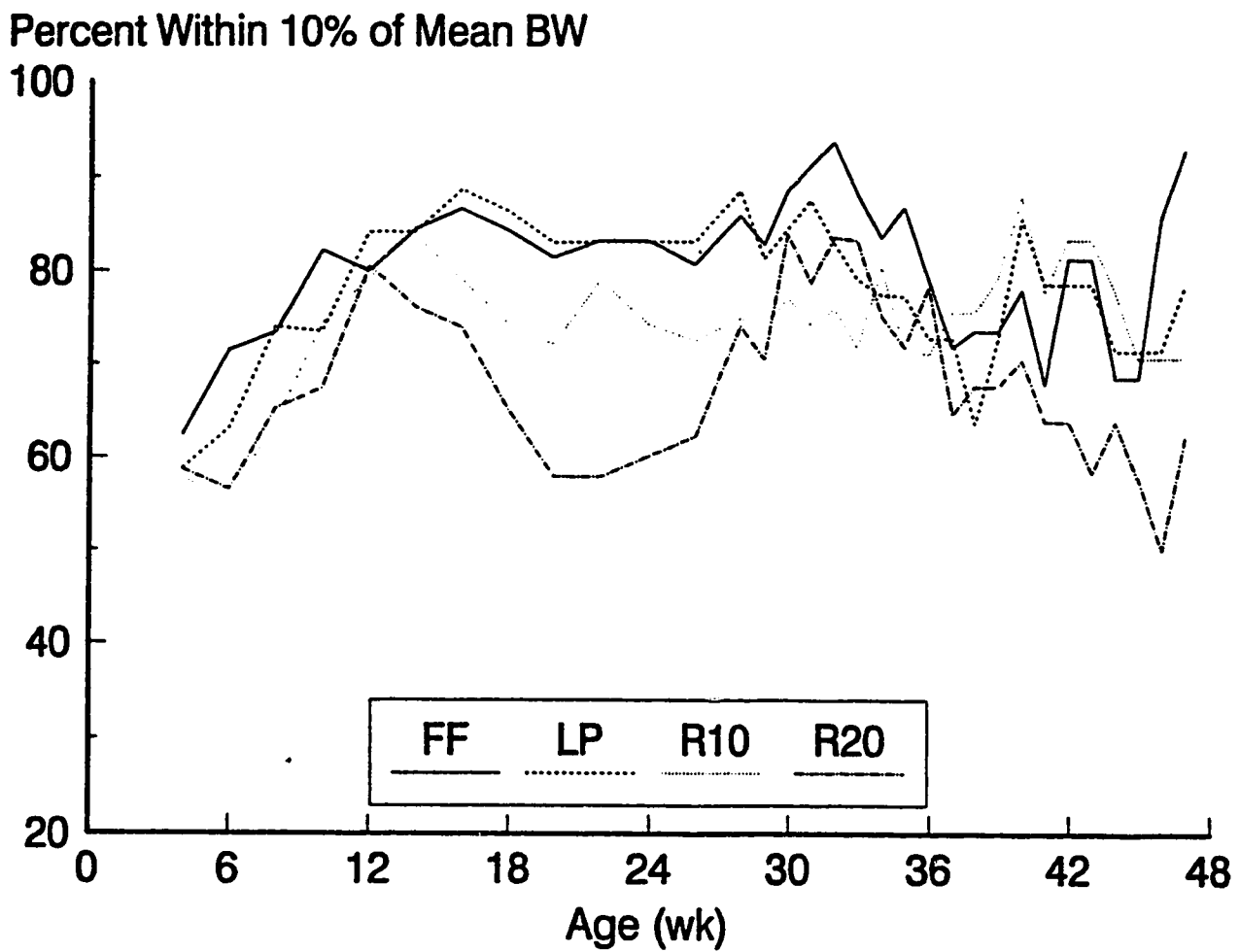
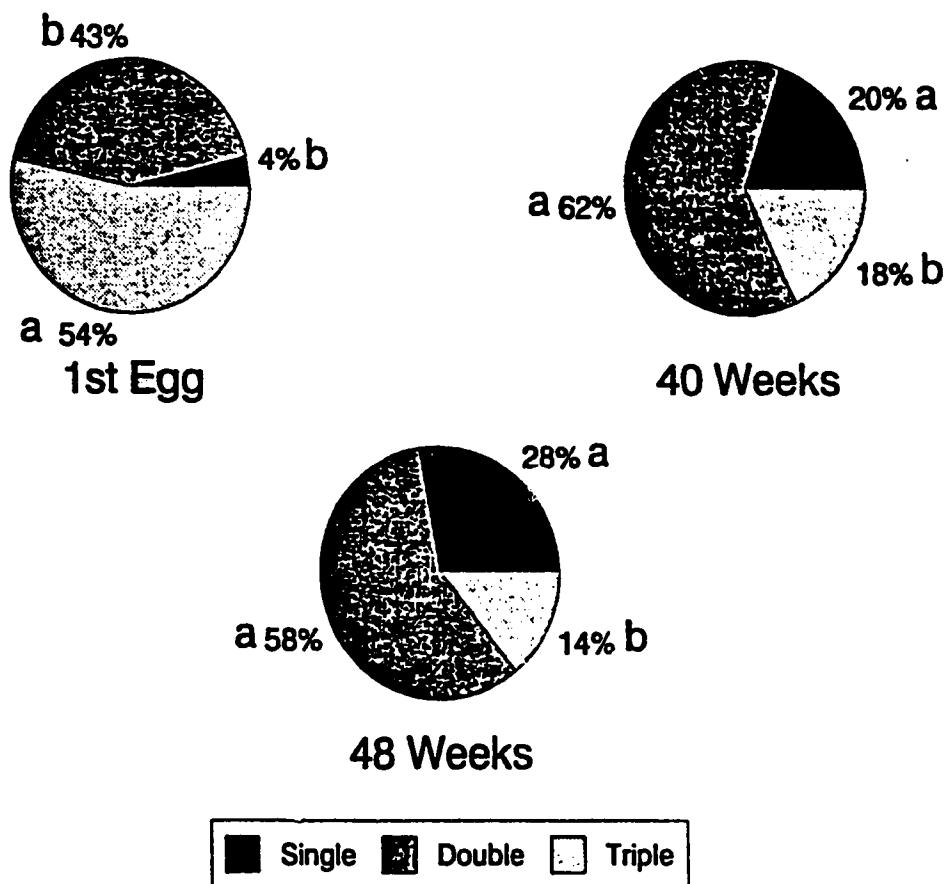
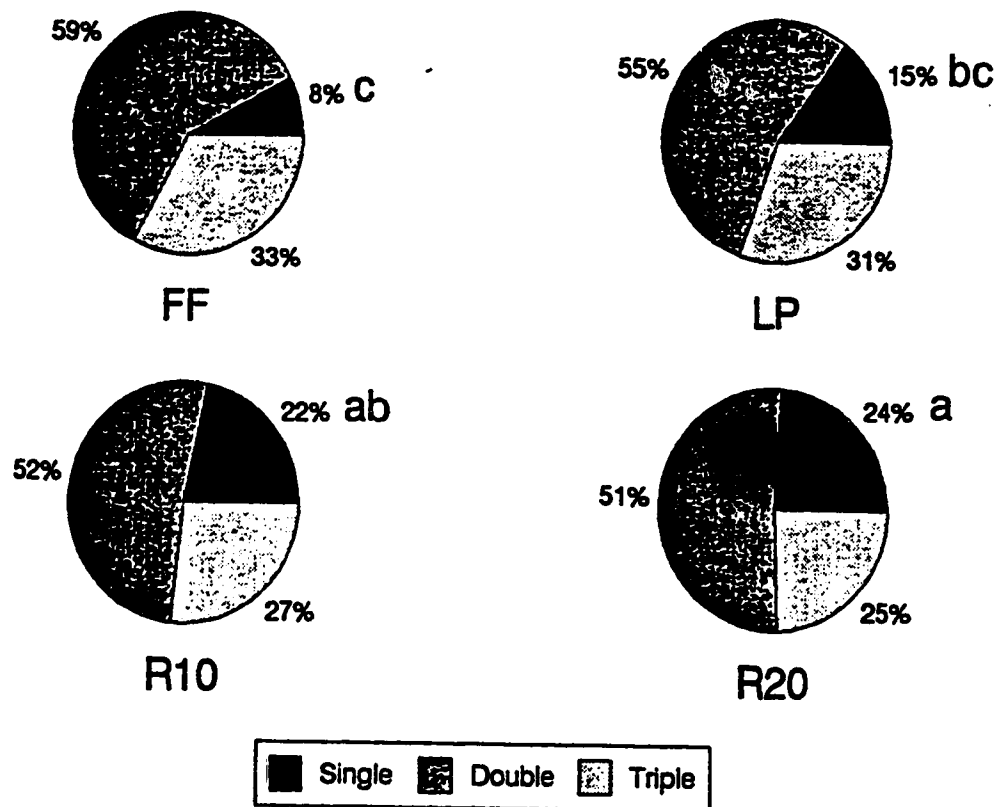


FIGURE V-2 Flock uniformity values ($\pm 10\%$ of mean body weight) for the grower (0-28 wk) and breeder period (29 to 48 wk) for male-line turkey breeder hens reared under the following feeding regimens: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight.



Values without common letters differ significantly for each slice type ($P < 0.0001$)

FIGURE V-3 Summary of the effect of feed allowance during rearing (0-28 wk) on the distribution of large follicles in single, double, and triple hierarchical arrangements of size at selected times during the breeder period (29-48 wk). Summary times were as follows: Sex. Mat. = sexual maturity (first egg); 40 wk = mid-breeding cycle; 48 wk = end of experiment.



Values without common letters differ significantly ($P < 0.004$)

FIGURE V-4 Treatment summary of the effect of feed allowance during rearing (0-28 wk) on the distribution of large follicles in single, double, and triple hierarchical arrangements of size during the breeder period (29-48 wk) in the following treatments: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight.

Proportion Non-Layers (%)

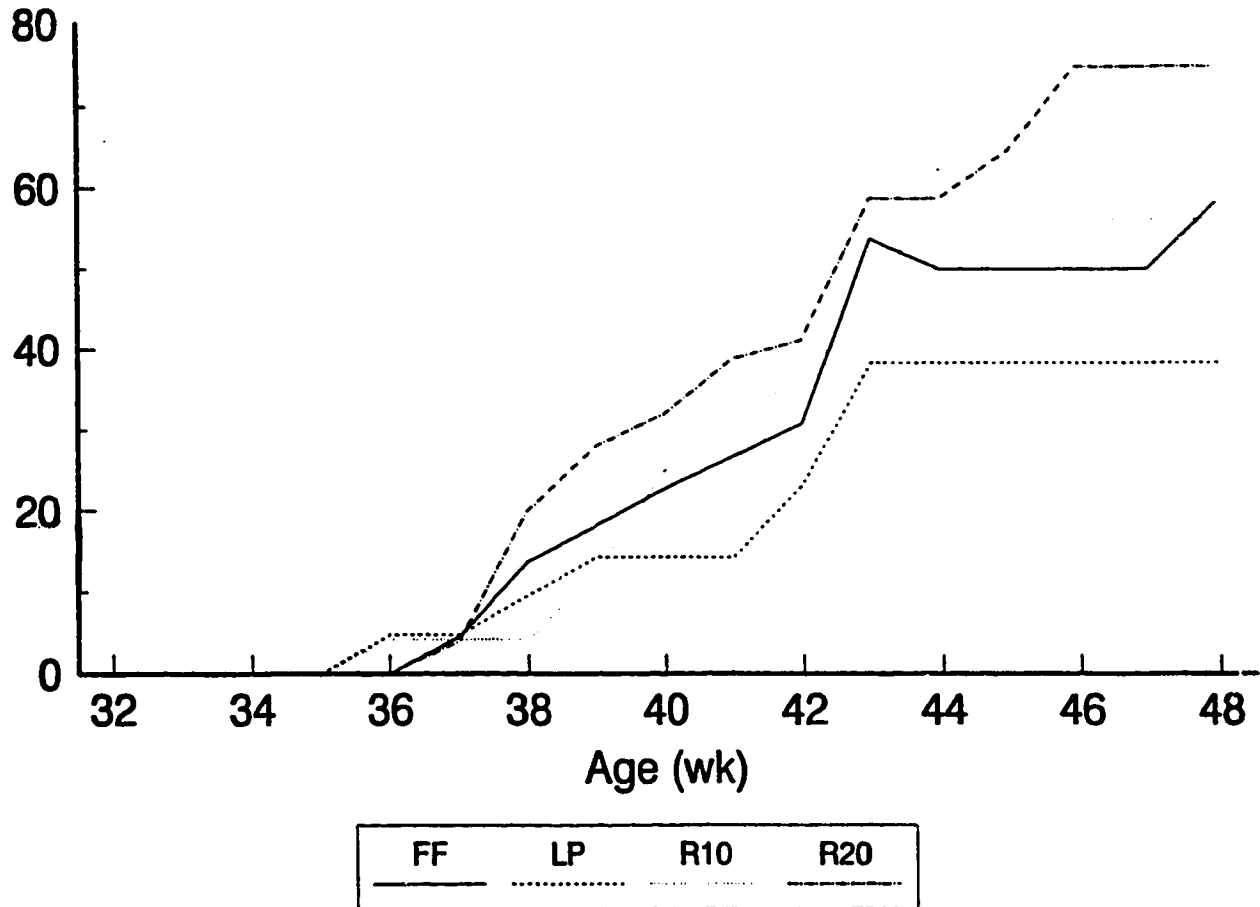


FIGURE V-5 Effect of feed allowance during rearing (0-28 wk) on the proportion of male-line breeder hens going out of production during the breeder period (29-48 wk) when reared under the following feeding regimens: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight.

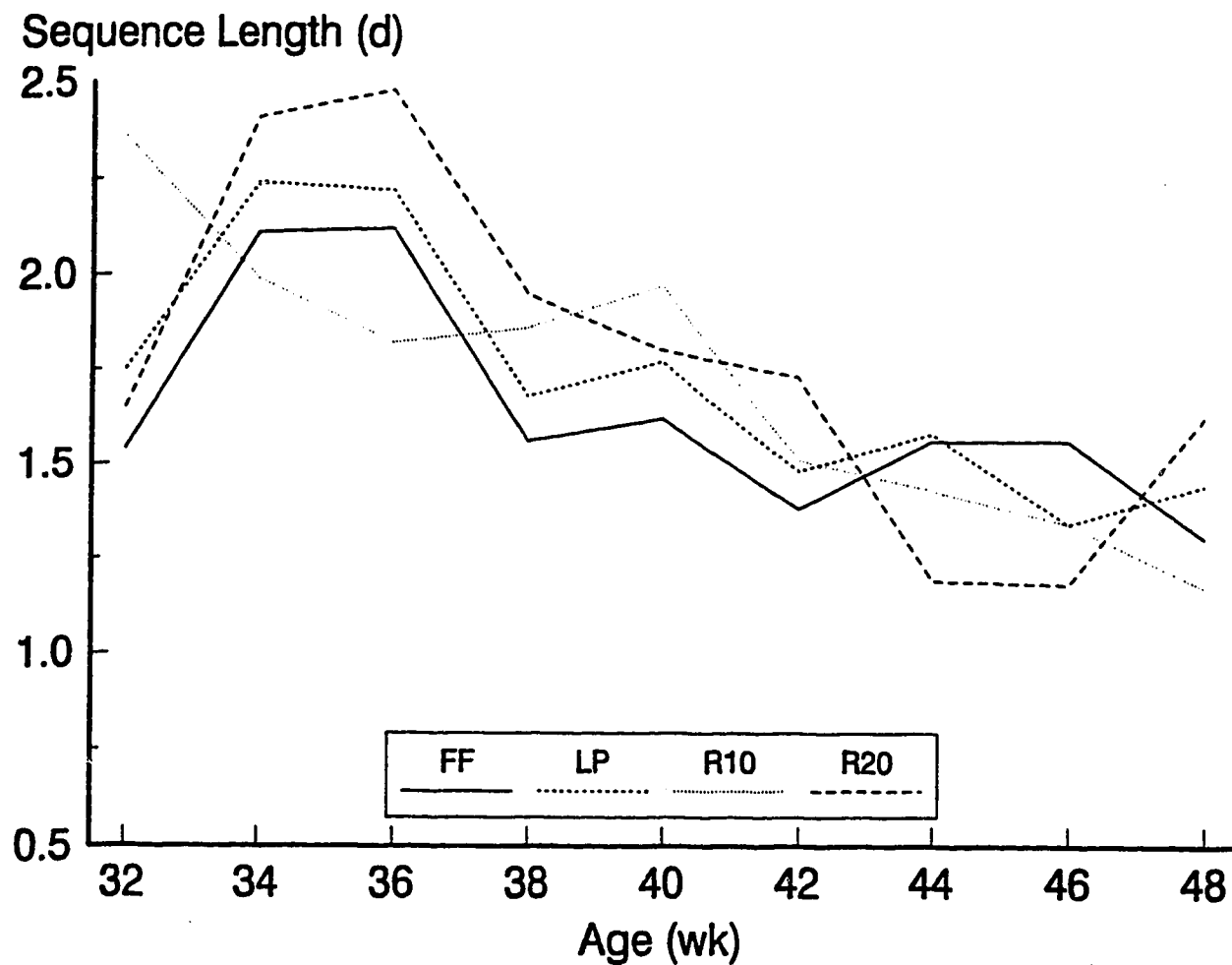


FIGURE V-6 The effect of feed allowance during rearing (0-28 wk) on average sequence length during the breeder period (29-48 wk). Rearing feeding regimens were as follows: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight.

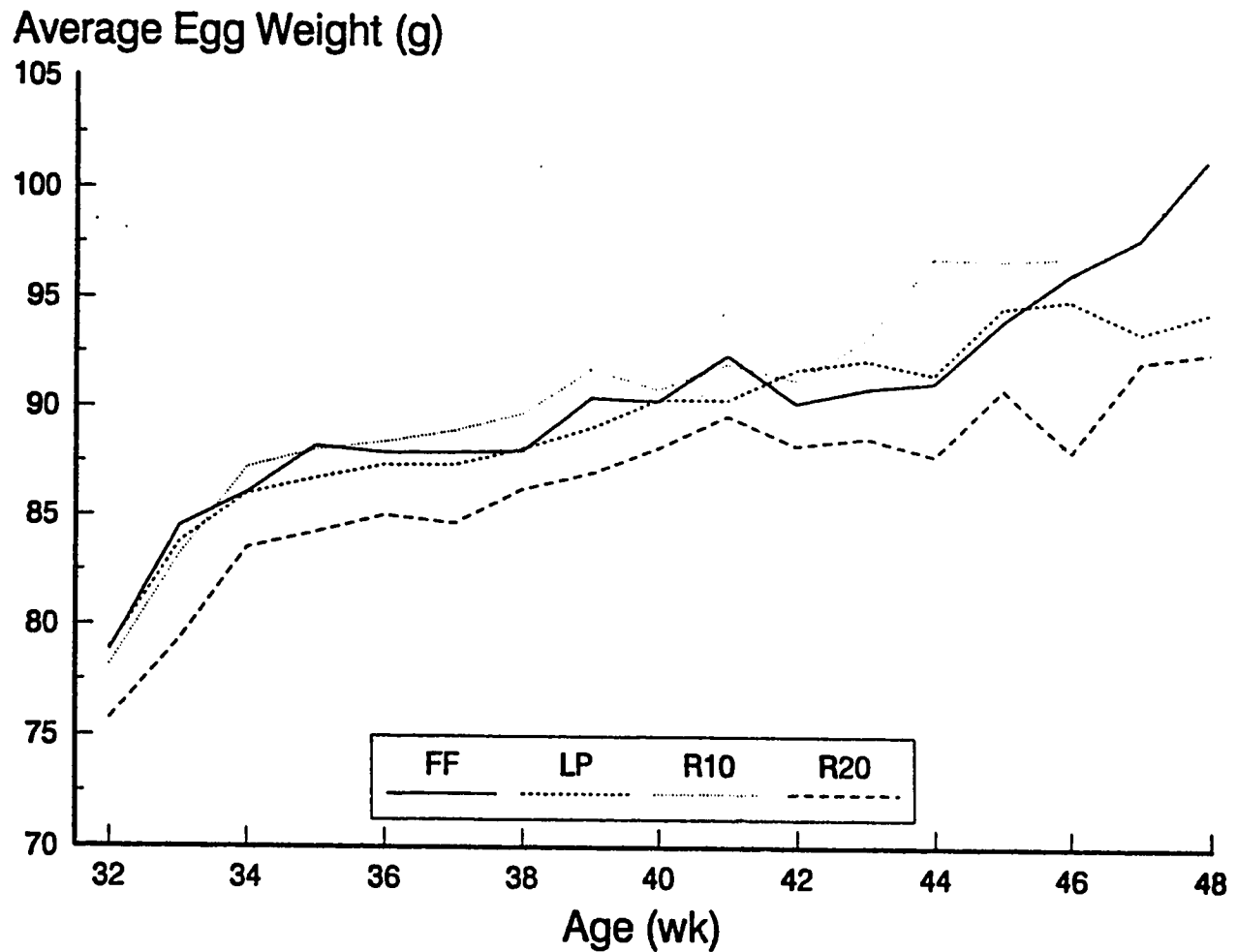


FIGURE V-7 Effect of feed allowance during rearing (0-28 wk) on egg weight during the breeder period (29-48 wk) in male-line turkey breeder hens reared under the following feeding regimens: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight.

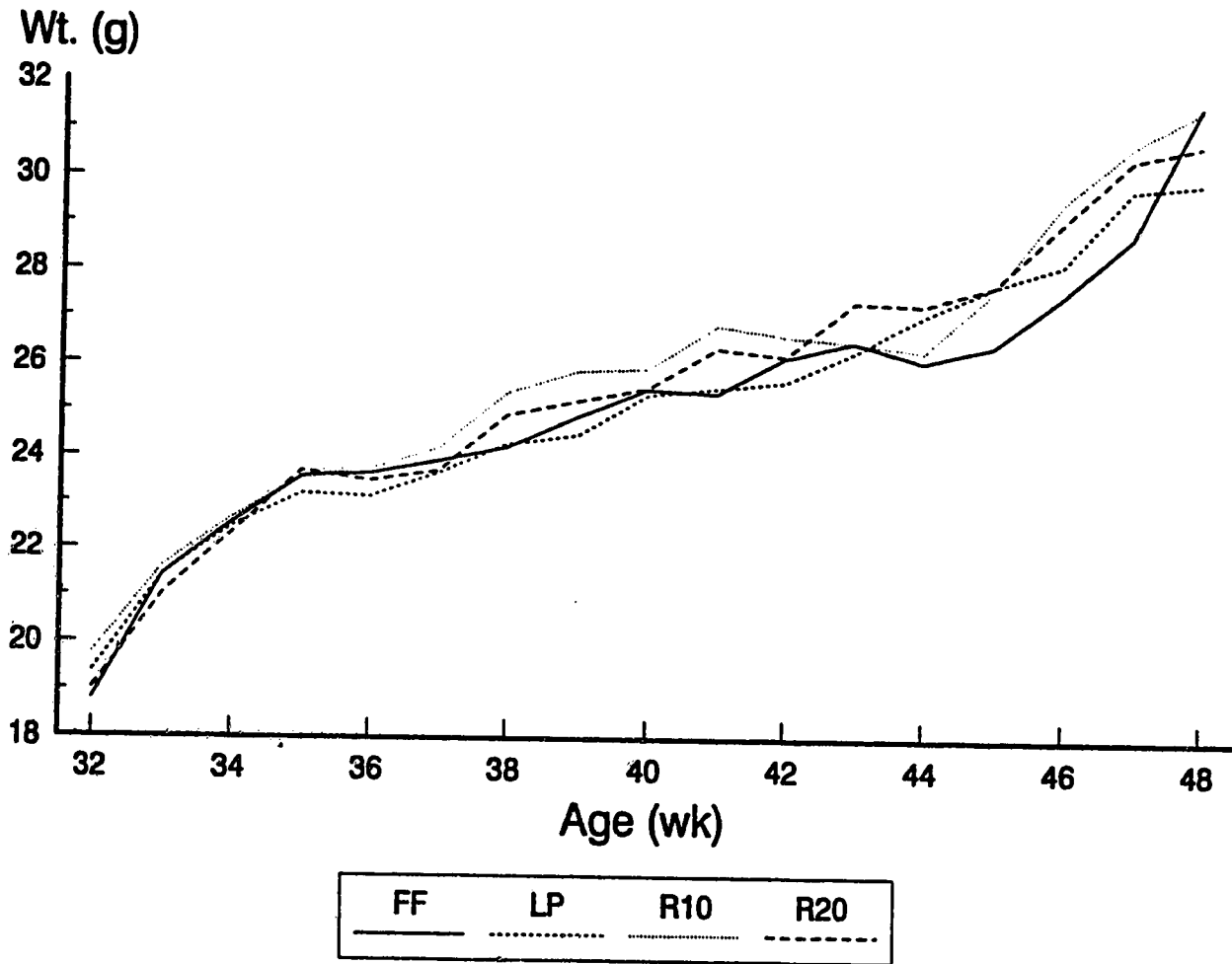


FIGURE V-8 Effect of feed allowance during rearing (0-28 wk) on yolk weight during the breeder period (29-48 wk) in male-line turkey breeder hens reared under the following feeding regimens: FF = full-fed; LP = low protein diet from 12 to 20 wk; R10 and R20 = body weight restricted during rearing to 10 or 20% less respectively than full-fed treatment body weight.