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Bioenergetics Of Breeding House Sparrows

David George Krementz

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BIOENERGETICS OF BREEDING HOUSE SPARROWS

by

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submitted in partial fulfilment

of the requirements for the degree of

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ABSTRACT

Between April, 1981 and July, 1983, I collected 563 (211 male, 352 female) house sparrows (Passer domesticus) around London, Ontario, weighed their nutrient reserves (protein, fat, calcium) and determined their food habits, to see if nutrient reserves proximately control clutch size in this species. Daily energy demands during egg production were evaluated by analyzing changes in nutrient reserves. Captive house sparrows were studied to determine if stored fat was deposited in eggs.

The proportions of males and females that consumed high-protein foods varied with the seasonal availability of insects. Insect use was low until egg laying but then increased and remained high thereafter. Insect consumption by males and females was similar throughout breeding. The proportion of males and females that ate calciferous material was constant (low) until egg production began. Then most females, but few males, consumed calciferous materials. After laying, female consumption of calciferous materials declined and equaled that of males.

Before egg production began, males used protein and fat but not calcium reserves; protein and fat reserves of females were constant but calcium was accumulated. Because the proportion of females that consumed calciferous materials did not change during prereproduction, females must have accumulated calcium through increased retention of calcium from their normal diet. After egg production began, male nutrient

reserves remained constant through postreproduction. Female protein and calcium reserves declined linearly during egg production; fat reserves, however, increased while 50% of the fat in a clutch was being allocated, and declined rapidly thereafter. The use of protein and fat reserves was independent of clutch size as all postlaying females had at least enough protein and fat to build an additional egg. Protein and calcium reserves of postlaying females remained constant but fat increased.

Maximum daily energy required for egg production was, at most, 50% of basal metabolic rate. Fat ingested by captive house sparrows was deposited daily in the developing follicles and fat not put into follicles went to fat depots, which were used rapidly. I conclude that, although female house sparrows do use nutrient reserves during egg laying, their clutch size is not controlled thereby.

To the memory of John James Audubon

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Neither this thesis nor my understanding of physiological ecology could have evolved without the help of Dave Ankney. I am deeply indepted to him on both counts. I feel honored to have had the chance to work and hunt with Dave.

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LIST OF ABBREVIATIONS

Abbreviation	Description
BM	Breast Muscle
BMR	Basal Metabolic Rate
CARC	Carcass
DAY	Day of Laying
DEE	Daily Energy Expenditure
EI	Early Incubation
FMR	Femur Length
GZ	Gizzard
LAY	Laying
LDW	Lean Dry Weight
LEG	Leg Bones
LI/N	Late Incubation/Nestling
LM	Leg Muscle.
LV	Liver
POST	Postreproductive
PRD	Prereproductive
PRL	Prelaying
SMR	Standard Metabolic Rate
STERN	Sternum
TBC	Total Body Calcium
TBF	Total Body Fat
TBP	Total Body Protein
TCARC	Total Carcass Dry Weight

Both the nutrient and energetic demands of egg production in non-passerines, especially anseriforms, are great (King 1973, Ricklefs 1974, Milne 1976, Siegfried et al. 1976, Korschgen 1977, Ankney and MacInnes 1978, Peterson and Ellerson 1979, Raveling 1979, Krapu 1981, Alisauskas 1982, Drobney 1982, Reinecke et al. 1982, Tome 1983, Ankney 1984). These demands can be so great that the final clutch size of some species, e.g. snow goose (Chen caerulescens, Ankney and MacInnes 1978) is proximately controlled by endogenous (stored) nutrient and/or energy reserves. While endogenous nutrient and energy reserves are necessary in non-passerines for the production of eggs, the situation for passerines remains unclear.

From the few extensive studies conducted on the bioenergetics of breeding passerines, the results have been conflicting. The red-billed quelea (Quelea quelea), a nomadic highly colonial subtropical granivore, stores protein reserves before egg production and offsets endogenous reserve use during egg laying through increased exogenous (daily) intake of high protein and calciferous foods (Jones 1976, Jones and Ward 1976). Jones and Ward (1976) concluded that egg production was limited by a minimum endogenous reserve level. The grey-backed camaroptera (Camaroptera brevicaudata), an aseasonally multi-brooded tropical insectivore, stores protein before egg production possibly to meet specialized amino acid needs while endogenous fat was stored to provide energy for the loss in feeding time resulting from searching for calciferous materials (Fogden and Fogden 1979). Courtship feeding in the grey-backed camaroptera is probably important in meeting nutrient and energy demands (Fogden and Fogden 1979). Based on the timing and magnitude of endogenous reserve

fluctuations in the grey-backed camaroptera, Fogden and Fogden (1979) concluded that neither endogenous nor exogenous reserves were proximately controlling clutch size. The brown-headed cowbird (Molothrus ater), a temperate granivorous nest parasite, stores neither protein, fat nor calcium before egg production nor does it utilize endogenous protein, fat nor calcium during egg production (Ankney and Scott 1980). Moreover, the brown-headed cowbird diet shifts from mainly seeds before, to mainly insects and calciferous materials during egg production (Ankney and Scott 1980). Ankney and Scott (1980) concluded that clutch size was not proximately controlled by endogenous reserves.

The house sparrow (Passer domesticus), a circumpolar seasonally multi-brooded granivore, according to Schifferli (1976) stores protein, fat and calcium before egg production. During egg laying protein and calcium intake increases to offset the use of endogenous reserves (Schifferli,1976). Although egg production ceases before endogenous reserves are depleted, Schifferli (1976) concluded that nutrient stores could be "biologically significant" in meeting the "strenuous" demands of reproduction. Pinowska (1975,1979) found female house sparrows to differentially accumulate fat and store protein before egg production, and to increase protein and calcium intake during egg laying to offset use of endogenous reserves. She concluded that clutch size was proximately controlled by the initial amount of fat stored when egg production began (Pinowska,1979).

Thus Jones and Ward (1976) and Pinowska (1979) concluded that clutch size was proximately controlled by endogenous reserve use and/or storage, while Ankney and Scott (1980), Schifferli (1976), and

Fogden and Fogden (1979) concluded that clutch size was not proximately controlled by endogenous reserve use and/or storage.

Energetically, egg production places less demand on passerines (45 - 58% of Basal Metabolic Rate (BMR)), than on anseriforms (156 - 239% of BMR) (King 1973). But still, to add 58% of daily BMR onto the normal daily energy demands of a female may represent a burden so great that clutch size could be limited. Kendeigh (1973) investigated the added energy demand of reproduction in house sparrows by determining the index for the incipient metabolic capacity of work. This index is the difference between BMR and the potential energy that is readily mobilizable or the amount of energy in excess of maintenance activities which can be allocated to other purposes, e.g. egg production. According to Kendeigh (1973) this index peaks during the breeding season in house sparrows because of a combination of lowered BMR from ambient temperatures approaching the thermoneutral zone and the decline in energy being allocated to other functions, e.g. transportation. Thus, if there is to be any period during the year when a female would be most capable of meeting extra energy demands, that time would be during the breeding season. Further, if the energetic demands of egg production are potentially limiting then why is the daily energetic cost of egg production (10.9 kJ·bird^{-1}·day^{-1}, Kendeigh 1973) only 34% of the daily energetic cost of nestling care (32.2 kJ·bird^{-1}·day^{-1}, Schifferli, 1976)?

In spite of the above evidence regarding passerine energetics and the conflicting results from studies of endogenous nutrients in breeding passerines, researchers continue to claim that the production of eggs by passerine females is stressful (Fogden 1972, Jones and Ward

1976, Schifferli 1976, Stobo and McLaren 1976, Greenlaw 1978). If stress is defined as a potentially lethal demand on nutrients and/or energy, I doubt that egg production in passerines is stressful. I investigated the bioenergetics of breeding house sparrows to establish: 1) are nutrient reserves (protein, fat, calcium) stored before rapid follicular development and 2) does nutrient reserve use during egg production and/or the meeting of a minimum nutrient reserve level during egg production limit clutch size?

I chose the house sparrow for the following reasons. First, I feel that Pinowska's work (1979), which has been widely cited, incorporated several major methodological errors; she assumed that 1) all female house sparrows bred synchronously and sequentially throughout the breeding season, i.e. if a female was collected during the third nesting peak of the breeding season, that female was assumed to have already bred twice (see Section 2.3), and 2) that all preovulatory follicles >2.0 mm in diameter would eventually ovulate, whether those follicles were yolky or not (see Section 2.3). Second, the biology of the house sparrow has been extensively studied yielding a broad data base upon which to consult. And finally, the house sparrow is an abundant and readily obtainable study animal.

2. MATERIALS & METHODS

2.1 Study Area

The study area included both suburban and rural sites within a 50 km radius of London, Ontario (43°02'N, 81°09'W). Almost all suburban work was conducted on the University of Western Ontario campus in London. Rural sites included farms- corn or wheat; ranches- dairy, sheep, and/or pig; and mixed operations. Feedlot operations were not used. A large and varied study area was utilized 1) to avoid repeated sampling of the same local populations and 2) to average out any peculiar population traits (after Lowther 1979).

A total of 125 nest boxes (15 X 13 X 10 cm) were located at some of the sites (between 10 and 30 boxes per site) to obtain clutch size data and from which to collect eggs and breeding females. Nest boxes were placed on trees, utility poles, fence posts and abandoned barns. No nest boxes were located where the nest microclimate was altered by man-made waste heat, i.e. nest boxes were never located inside or on barns in production, or houses in use (see Will 1973, Pinowska 1979). At the end of each breeding season, all nest boxes where occupancy by house sparrows was less than 50% were moved and located elsewhere.

2.2 Collecting House Sparrows

House sparrows were collected by using mist nets, Potter live traps, nest box traps, or by drugging with alpha-chlotalose, but primarily by shooting. Shotguns (.410 and .12 gauge) and rifles (.22 pellet gun and .22 caliber rifle) were used. Shot sizes included # 7½,

8, 9 and 12. To correct for fluctuations in internal nutrient reserves over the daylight period (Kendeigh et al. 1969), I attempted to collect house sparrows before noon; >95% of collected house sparrows were taken between 0800 and 1200 EST. Birds were collected from March to May 1981, March to July 1982, and January to May 1983.

2.3 Categorization of House Sparrows

Collected house sparrows were assigned to 1 of 7 categories - Winter, Prereproductive (PRD), Prelaying (PRL), Laying (LAY), Postlaying (POST), Early Incubation (EI), or Late Incubation/Nestling (LI/N). I defined these as follows:

Winter- Males or females collected during January or February.

Prereproductive- Females collected after February but with no yolky pre- or postovulatory follicles: males collected after February and before the first PRL female was collected during that year. This period, on average, spanned 2 months.

Prelaying- Females collected with yolky preovulatory follicles but no oviducal egg or postovulatory follicles: males collected after the first PRD female up to the date when 50% of the collected females had entered LAY (after Caughley and Caughley 1974). Biologically, this period lasted 4 days (see Section 3.1.2.2).

Laying- Females collected with an oviducal egg or if no oviducal egg was present, the largest postovulatory follicle weighed more than 2.1 mg (the smallest postovulatory follicle of a female with an oviducal yolk weighed 2.2 mg): males collected between the date when 50% of the collected females had entered LAY and the date when 50% of the collected females had entered POST. Biologically, this period could last from 3 to 6 days.

Postlaying- Females collected with no yolky preovulatory follicles or oviducal egg and largest postovulatory follicle weighing less than 2.2 mg; or if no pre- or postovulatory follicle(s) was present, then females which possessed a vascularized, wrinkled and/or flaky brood patch also qualified (see Pinowska 1979): males collected after 50% of the collected females had entered POST. Biologically, this period could last up to 2 weeks.

It was possible to further subdivide POST females into 2 additional categories (Early Incubation or Late Incubation/Nestling) based on morphological characteristics (see below); however using Caughley and Caughley's (1974) method for further subdividing POST males proved fruitless because sample sizes were too small.

Early Incubation- Females collected without an oviducal egg or postovulatory follicle weighing more than 2.2 mg but with at least 1 postovulatory follicle.

Late Incubation/Nestling- Females collected with no pre- or postovulatory follicles but possessing a vascularized, wrinkled and/or flaky brood patch.

In addition to the above I also defined the following broader categories.

Prereproductive- includes all birds collected during the WINTER and PRD periods. When discussing this period, I also refer to nutrient reserve dynamics between the PRD and PRL periods.

Reproductive- includes all birds collected during the PRL and LAY periods. When possible, these birds were classified according to the number of days before or after they ovulated their first yolk (after Schifferli 1976). House sparrows require 4 days to complete rapid follicular development (see Section 3.1.2.2); on the fourth morning (DAY 0), the first egg is ovulated. The day before is DAY -1 while the day after is DAY +1, etc. (Appendix 1). Pinowska (1979) used a slightly different DAY classification scheme. Her DAY 0 was equivalent to my DAY -1, i.e. on her DAY 0, the female had no postovulatory follicle. To expedite matters, I standardized the DAY classification of Pinowska (1979) according to Schifferli's (1976) scheme.

Postreproductive- includes all birds collected during the POST period which includes all EI and LI/N individuals. Here, discussions may incorporate findings on the nutrient reserve dynamics between the LAY and POST periods.

No collections were made after the first fledgling house sparrow of that breeding season was seen to insure that the previous breeding history of those individuals was known, i.e. they had to have been nesting for the first time in that breeding season. This precaution excluded individuals which may have begun their second or later clutch of the breeding season but did not preclude collecting re-nesters. Re-nesters are those females which lost their first clutch and began a second clutch within the first peak in nesting. Following my criterion, there can be no doubt as to the previous breeding history of an individual, unlike Pinowska's (1979) criteria. Pinowska (1979) assumed, based on the regularity of breeding peaks of the house sparrow population she monitored, that individuals had bred synchronously and sequentially in relation to the population, i.e. each female renested as soon as possible after each successful nesting. However, Pinowska (1979) found nonbreeding females during every peak in nesting. Because of the frequency of nonbreeding females and because the population was not marked, I cannot accept her basic assumption.

Other researchers have investigated if house sparrows nest synchronously and sequentially. Summers-Smith (1963) noted that house sparrows will nest sequentially but not necessarily in the same box; he did not state if the population bred synchronously and sequentially. North (1973) seriously doubted whether the same house sparrow pair nested sequentially in the same nest box throughout the breeding season. Weaver (1942, 1943) deduced that while a pair may use only a single nest box over the breeding season, that pair may wait 1 or more months between broods. Although Summers-Smith (1963) was the

only researcher of the above 3 to use a banded population, the available evidence on whether a house sparrow population nests synchronously and sequentially remains unclear.

Females nesting during the first peak in nesting tend to be more than 1 year old (Summers-Smith 1963, Dawson 1972).

Thus by collecting first breeders, both previous breeding history and age were controlled.

The actual or potential clutch size of a female was determined by counting the number of consecutive pre- and postovulatory follicles (after Pinowska 1979) under the following criteria: 1) since only 3 yolky preovulatory follicles could be distinguished in PRL or LAY females collected before noon (Schifferli 1976, pers. observ.), I arbitrarily decided that females with the penultimate or the penultimate and next smaller yolky preovulatory follicle be included for clutch size categorization; 2) no females with 4 or fewer consecutively smaller postovulatory follicles be used unless the largest postovulatory follicle weighed more than 2.2 mg; and 3) no females with more than 1 successive pre- or postovulatory follicles missing be included. These 3 criteria were necessary for the following reasons. Had I used females with DAY -3 preovulatory follicles, I could not have been certain if that female was going to develop 1 or more additional follicles. The only exception to this criterion was when a female had 3 yolky preovulatory follicles and 3 postovulatory follicles. These females would have laid 6 eggs since no clutches of 7 were found in nest boxes. Pinowska (1979) used a slightly different scheme for determining clutch size. She assumed that all preovulatory follicles >2.0 mm in width would ovulate, regardless of whether or not

those preovulatory follicles contained yellow yolk material. Using this scheme she believed that clutch size could be determined on DAY 0 for all clutches up to 6. Following this scheme in 1981, I regularly found that PRL and LAY females would have estimated clutches of more than 8. Clutches of >6 were never found in my nest boxes. Based on my tests, I believe the technique used by Pinowska (1979) for the determination of clutch size was incorrect. Had I used females with 4 or fewer consecutively smaller postovulatory follicles and the largest postovulatory follicle not weighing more than 2.2 mg, I could not have been certain that the female had smaller postovulatory follicles. Because postovulatory follicles are resorbed within several days (Schifferli 1976), I had difficulty recognizing follicles ovulated 4 days earlier. Thus, any female with 4 or fewer postovulatory follicles was difficult to classify and was not used in my estimate. Females with more than 1 successive pre- or postovulatory follicle missing were considered to be either re-nesters or were badly damaged and were not used.

Five clutch size categories were possible: 3,4,5,6 and unknown. Because of my criteria for determining clutch size, the number of days on which a particular clutch size could be distinguished varied in the following manner. Clutches of 3 could be distinguished for 3 days (DAY 0 to DAY +2); clutches of 4 for 3 days (DAY +1 to DAY +3); clutches of 5 for 2 days (DAY +2 to DAY+3); clutches of 6 for 3 days (DAY +3 to DAY +5); and clutches of unknown number for 9 days (DAY -3 to DAY +5) (Appendix 1). I could not determine clutch size until DAY 0 because of the above criterion #1.

2.4 Carcass Analysis

Upon collection, each bird was tagged individually and weighed to the nearest 1 g. Birds were then returned to the laboratory where the female reproductive tissues (ovary, oviduct and, if present, oviducal egg) and male reproductive tissues (testes) were removed. All reproductive tissues were placed in 10% formalin for later analysis.

Next, the brood patch was ranked according to the following criteria: 0.0- down feathers present on brood patch, feather follicles present; 0.5- down noticeably sparse, feather follicles present; 1.0- no down present but brood patch narrow (<1.5 cm), feather follicles present; 1.5- down gone, brood patch full width (>1.5 cm), feather follicles disappearing; 2.0- down gone, brood patch full width, feather follicles disappearing or absent, brood patch possibly vascularized or scaly in appearence; 2.5- down gone, brood patch full width, feather follicles absent, brood patch usually wrinkled in appearance; and 3.0- down gone, brood patch full width, feather follicles absent, brood patch wrinkled and pale (after Selander and Yang 1966, Pinowska 1979).

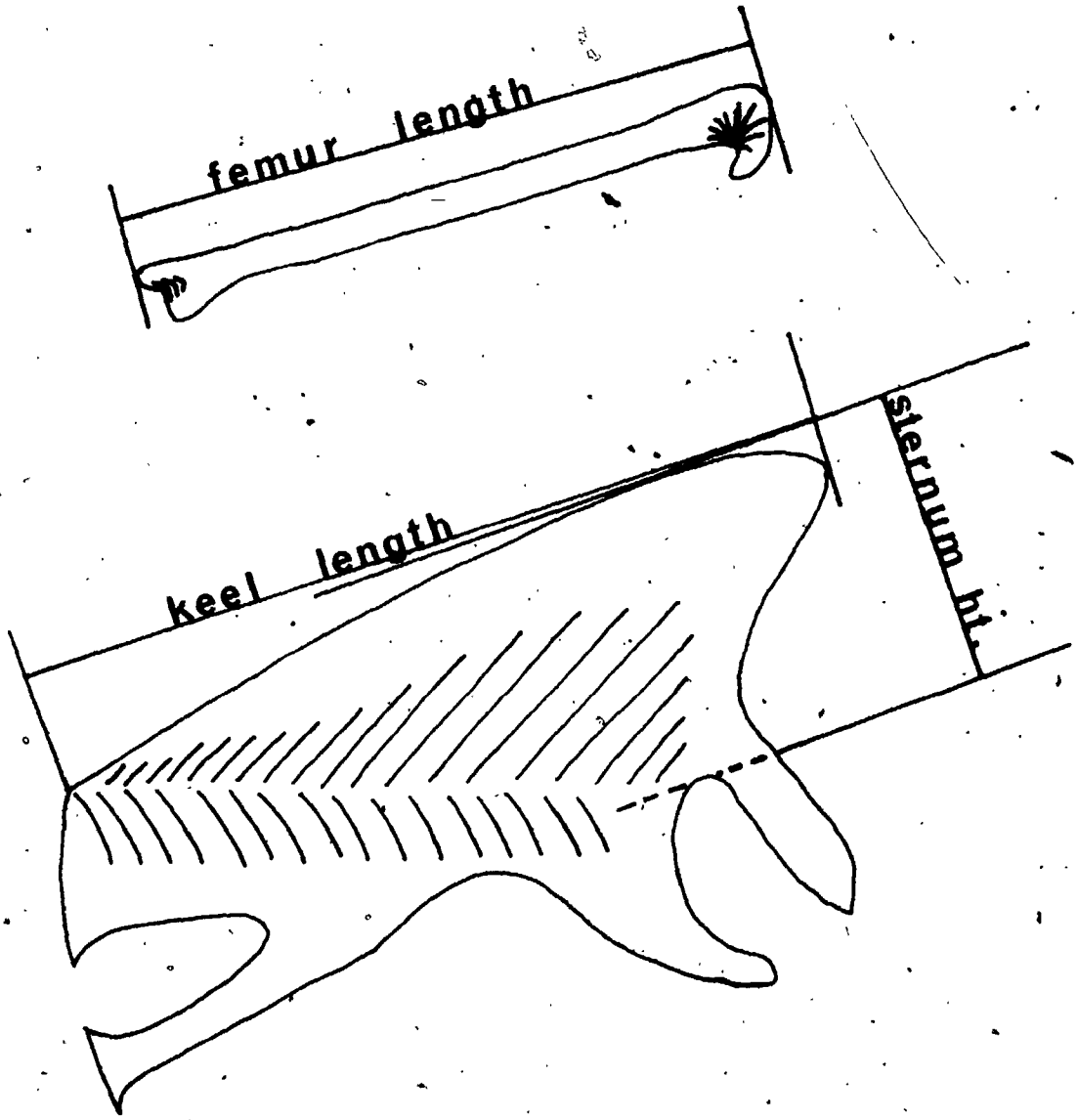
In 1981 I noticed that some individuals had distinctly notched retrices analogous to the notches present in young of the year waterfowl (Godin 1960). I therefore removed all rectrices to investigate the relationship between these notches and body condition indices. Following this the birds were bagged and frozen.

Final dissections were done as follows. The breast muscles (BM; pectoralis, supercoracoideus and coracobrachialis) and leg muscles (LM) (all those muscles having either their origin or insertion on the

femur or tibiotarsus) were unilaterally excised and weighed to the nearest 0.01 g. Values of BM and LM were doubled and presented herein. The contents of the esophagus, proventriculus and gizzard were removed and placed in 70% ethanol for later examination. The liver (LV) and gizzard (GZ) were removed, cleaned of adhering fat and weighed to the nearest 0.01 g. The small intestine, large intestine and cloaca were removed and stripped of contents. The sternum (STERN) and 1 set of "leg bones" (LEG; femur, tibiotarsus and fibula) were removed and placed in a dermestid beetle (Dermestes nidum) colony and cleaned of adhering flesh. Muscles, organs, bones and remaining carcass plus digestive tract (CARC) were placed individually in aluminum pans, dried in an oven at 90° C to a constant weight (Kerr et al. 1982) and then weighed individually to the nearest 0.01 g. STERN and LEG bones were weighed to the nearest 0.001 g. In retrospect the STERN and LEG bones should have been extracted to remove marrow fat; however, Raveling et al. (1978) stated that marrow fat was used before the LAY period. Thus, any changes during or after LAY could not be attributed to changes in marrow fat. The weight of all dried material yielded total carcass dry weight (TCARC). The femur length, keel length, and sternum height were measured with calipers to the nearest 0.05 mm (Fig. 1).

Testes were oven dried at 90° C to a constant weight and weighed to the nearest 0.001 g. All yolky follicles and postovulatory follicles were counted and removed. The ovaries, yolky follicles, postovulatory follicles, oviduct and oviducal eggs were oven dried at 90° C to a constant weight and weighed to the nearest 0.001 g.

Fig. 1. Skeletal measurements used to investigate body size variation of house sparrows.


femur length
keel length
sternum ht.

All dried material except the LEG, STERN and reproductive tissues, was then ground in a Wiley mill using a # 20 screen. In 1981 and 1982 the entire ground sample, 7-10 g, was extracted of neutral fats using petroleum ether for 12 h in a Soxhlet extractor. For logistical reasons, in 1983 a modified Soxhlet extractor was used which accomodated a maximum sample of 5 g. Thus, I calculated for each bird:

$$\text{Total Body Fat (TBF)} = \frac{\text{weight of fat in sample}}{\text{total weight of sample}} \times \text{TCARC} \qquad \text{Eq. 1}$$

and

$$\text{Lean Dry Weight (LDW)} = \text{TCARC} - \text{Total Body Fat} . \qquad \text{Eq. 2}$$

After analyzing the 1981 LEG and STERN samples, I decided to investigate calcium dynamics more completely. Thus the 1982 and 1983 lean dry weight samples were reground with each sample's corresponding LEG and STERN bones and dried. A 2 g subsample of this material was placed in a muffle furnace at 500° C for 6 h (Ricklefs 1974). The residue was used to estimate ash content for each bird using the following formula:

$$\text{ASH} = \frac{\text{weight of ash in sample}}{\text{total weight of sample}} \times \text{TCARC}. \qquad \text{Eq. 3}$$

In 1982 total body calcium (TBC) was determined by the following method. From each bird a 0.05 g sample of ASH was boiled in 10 ml 8N

HCl and cooled. Five ml of 2N HNO3 was added and the ASH boiled again. Ten ml of distilled, deionized water was added to the ASH to dilute the sample and to retain the calcium in solution. The residue was filtered off and the calcium containing filtrate diluted to 100 ml with 2000 ppm K solution. The filtrate was further diluted 10:1 twice with 2000 ppm K solution to bring the calcium content within the operating limits of an atomic absorption spectrophotometer. The calcium content of the diluted filtrate was determined by atomic absorption spectrophotometry on a Varion 1275. A nitrous oxide-acetylene flame was used to produce a flame high enough in temperature to avoid interference from P. Also the 2000 ppm K solution with which the sample was diluted should have further reduced interference from P. Calcium acid phosphate was used to prepare calcium standards which were treated in the same manner as the samples. The sample absorbancies were compared to these standards which yielded TBC.

Because of costs involved in using the Varion 1275, in 1983 a Varian Techtrom model AA-5 was used which was not capable of using a nitrous oxide-acetylene flame. Because this machine used a lower temperature oxide-acetylene flame, a 1000 ppm Lanthanum solution was needed in addition to the 2000 ppm K solution to reduce P interference due to Ca ionization in the flame (G. Fairchild, pers. comm.).

TBC determinations were expensive so I emphasized TBC determinations on PRL, LAY, and EI individuals.

Then I calculated for each bird:

Total Body Protein (TBP) = LDW - ASH. Eq. 4

TBP is a more accurate index of protein than LDW. When Schifferli (1976) investigated protein dynamics he devised an index of body protein based on the structural size ("diagonal" measurement, essentially the sternum length plus coracoid length), flight muscle mass (BM) and nonmetabolizable protein (protein remaining after an individual had starved to death). Because Schifferli (1976) noted that variation in individual muscle mass was high, he corrected for structural size. By accounting for individual differences in structural size, he felt that any additional variation in protein reserves would result from breeding stress. I believe there are some problems with this method. First, the index assumes that all individuals are alike in their ability to collect, store and use protein. Second, the index assumes that weight changes in the flight muscles are representative of weight changes in the rest of the body (see Section 3.1.1.1, Fogden and Fogden 1979). Finally the index implies that only females with above average protein levels have protein available for reproduction. Yet Schifferli (1976) points out that females never approach the LDW level when a house sparrow starves to death. I therefore did not correct for structural size when analyzing protein dynamics.

BM, LM, LV, GZ, CARC, LDW and TBP were all used to index protein; TBF was used as an index of neutral fat; LEG, STERN and TBC were used as indices of calcium.

2.5 Definition of Nutrient Reserves

Three nutrients (protein, fat, calcium) were monitored, but most readers have trouble accepting that calcium is a nutrient rather than a mineral. According to Wolf and Hainsworth (1978:347) nutrients are, "... those chemicals in a diet that are necessary for survival and reproduction but which need not be important as immediate sources of energy." Using this definition, calcium can be considered as a nutrient because it is among the 3 heaviest egg components by dry weight (Romanoff and Romanoff 1949). So calcium satisfies the requirement of being necessary for reproduction but not important as a source of energy.

Below are the definitions of each endogenous nutrient reserve.

Protein reserves- all proteins in excess of the amount of LDW remaining in a house sparrow after starvation (5.41 g, Schifferli 1976) minus the maximum TBC weight (0.39 g) encountered in my study.

Fat reserves- all fats in excess of the amount of fat remaining in a house sparrow after starvation (0.25 g, Schifferli 1976). Fat reserves only include fats from nonreproductive tissues.

Calcium reserves- all calcium in excess of the mean winter TBC levels (1983 data, 0.12 g) encountered in my study.

2.6 Food Habits

I originally planned to examine the less biased esophageal contents because animal material passes through the digestive tract at a different rate than plant material (Swanson and Bartonek 1970). Too few birds had esophageal contents to warrant only esophogeal food

examination, therefore proventricular and gizzard contents were included.

Contents were placed in a gridded petri dish and examined with a binocular microscope at 12.5X magnification and ranked as follows: 1) 100% plant; 2) Plant + trace of animal (5% of total area); 3) Both plant and animal; 4) Animal + trace of plant (5% of total area); and 5) 100% animal (after Ankney and Scott 1980).

Calciferous material was also measured in each food sample according to presence/absence. Calciferous material included mollusc shell (identified by W. W. Judd), avian eggshell and calciferous grit.

No correction for a sample was made if it contained more than 1 type of calciferous material, i.e. if a sample contained just eggshell, or just mollusc shell, or eggshell and mollusc shell, they were scored the same.

2.7 Egg Collection and Analysis

In 1982 eggs were collected from nest boxes at 6 sites to determine variation in egg composition for use in calculating nutrient requirements for reproduction. Eggs were collected on the day of laying and replaced with dummy eggs to encourage the female to continue laying. Each removed egg was weighed to the nearest 0.01 g and placed in an airtight plastic container and refrigerated until further analysis. To avoid excessive water loss from refrigerated eggs, final analyses of eggs were made within 1 week of collection (Ricklefs 1984).

Eggs were then boiled and separated into shell, albumen and yolk. These components were oven dried at 75° C to a constant weight and weighed to the nearest 0.001 g. I attempted to extract neutral fats from the yolks using petroleum ether in a Goldfisch extractor for 6 h. Because the resulting coefficients of variation greatly exceeded 25%, I opted not to use my estimates of yolk fat. Instead I used the estimated yolk fat percent (59.09% of yolk dry weight, Schifferli 1976) to determine the amount of fat in my yolks. The percent yolk fat estimated by Schifferli (1976) is well within the range recorded for altricial species (King 1973, Ricklefs 1974).

2.8 Yolk/Dye Experiments

A breeding colony of house sparrows was established in an aviary at the University of Western Ontario in 1982. Ten cages (1.5 W X 2.5 H X 5.0 L m) were each supplied with 4 nest boxes, 1 roost box (1 m^3) heated with a 40 W light bulb painted black and 2 coniferous trees for roosting. Seven pairs of house sparrows were placed into each cage during the fall of 1982. Individuals succumbing before April 1983 were replaced with an individual of the same sex. I thought that after April 1983, additions of new birds would disrupt breeding activity of established pairs already present and thus no more birds were added after that month. Food, water, 'Callgro Shellmaker No. 3 grit' and cuttlefish bone were provided ad libitum. The fall/winter diet consisted of mixed bird seed, ad libitum.

Beginning in April 1983, I prepared a 1:1 mixture of 'Purina Eggena' and mixed birdseed, and coated it with peanut butter until the

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entire mixture appeared granular. Into this breeding mash was also added Sudan black B until the mixture was uniformly black. Sudan black B is a nontoxic lipophilic dye which is bound to yolk fats synthesized in the liver (L.E. Astheimer, pers. comm.). Whether Sudan black B was bound to fats in adipocyte tissues is unknown. This food/dye mixture was provided until the first egg in a cage was discovered. Upon discovery of that egg, I removed all dyed food from that cage and replaced it with the same mixture of breeding mash but undyed. This unmarked mash was made available until the last egg of any clutch was laid in that cage, i.e. if another female in that same cage began a clutch while the first female was still laying, I continued the undyed breeding mash until the female laying her last egg was finished. All eggs were removed daily and replaced with dummy eggs to encourage females to continue laying.

Following Grau's (1976) methodology, I removed eggs, degassed them in a vacuum overnight, and then froze them at -20° C for at least 48 h. Each frozen egg was placed in 10% formalin and heated to 65° C for 24 h. The shell and albumen were then removed and discarded. The yolk was cut in half through the blastoderm; one half of the section was stained in 6% potassium dichromate and the remaining half left in 10% formalin.

Each half was independently examined under a binocular microscope at 12.5 - 40X magnification. After the total number of bands in each yolk half had been counted, representative color diagrams of each yolk half were drawn to note the relative location of dye. It was sometimes necessary to thin section the yolk (2 mm sections) and use transmitted light to distinguish banding patterns. Caution should be exercised

when using both reflected and transmitted light for drawing profiles since the light/dark banding patterns appear reversed depending on the light source.

2.9 Pooling Data

Because severe winter weather can significantly alter body size in local house sparrow populations (Bumpus 1899, Lowther 1977, Murphy 1980, Johnston and Fleischer 1981, Fleischer and Johnston 1982), it was necessary to test for between-year body size differences.

Structural size measurements rather than tissue weights are usually used for such analyses to avoid potential confounding interactions from factors such as capture time, breeding status and short term climatic effects. Four structural size variables (total body length, sternum length, sternum height and femur length) were compared against LDW to determine which variable correlated best with structural size and body mass. Body mass here implies the potential for supporting tissue. To control for seasonal differences in body mass, these correlations were conducted on only PRD individuals. While all measurements were correlated significantly with either 1 or both sexes' LDW, femur length (FMR) had the highest, by sex, coefficients of determination (male $r^2 = 0.33$, $df = 33$, $p < 0.001$; female $r^2 = 0.23$, $df = 101$, $p < 0.001$). Thus FMR was used to investigate body size variation over time and season.

Body size variation between-years was tested by comparing, within sex, PRD FMR's collected before 1201 h. These criteria controlled for variation in body mass resulting from variation in collection time,

skeletal weight and muscle mass. No significant difference in FMR was detected between years for either sex (1-way ANOVA: male $F = 0.32$, $df = 35$, $p > 0.50$; female $F = 0.12$, $df = 100$, $p > 0.50$). However one may be incorrect to assume that all subsequent individuals in the sequential breeding stages are represented by the PRD sample. There was no significant difference in FMR between any breeding stages (2-way ANOVA: breeding stage effect $F = 0.63$, $df = 3$, $p > 0.50$) suggesting that sequential breeding stage individuals came from PRD samples. The lack of FMR differences between breeding stages supports my earlier contention that it was not neccessary to correct for body size differences when comparing between stages. As expected, male FMR was significantly longer than female FMR (2-way ANOVA: sex effect $F = 4.30$, $df = 1$, $p < 0.05$).

3. RESULTS

3.1 Nutrient Reserve Dynamics

3.1.1 Prereproductive

3.1.1.1 Males

No relationship between TBP and capture date within the PRD period was found (r^2 =0.079, df = 6, $p > 0.50$). The lack of storage could be misleading because the span of capture dates for TBP was only 10 days. PRD LDW data, on the other hand, spanned 30 days and should have been more revealing than TBP in spite of the confounding interaction of ASH. Again, no relationship between LDW and capture date was found (r^2 =0.050, df = 35, $p > 0.05$). TBP declined significantly between PRD and PRL periods (Table 1). While most muscle and organ weights declined, it was unfortunate that neither the mineral nor fat content of the individual muscles or organs was determined. It was therefore impossible to determine if 1 muscle or organ was contributing to the TBP decline proportionately more than another muscle or organ. However, by using TCARC intead of TBP, detection of the percent contribution made by each tissue towards the overall prereproductive weight change was possible. These latter results are preferable to the former comparison because both the component and TCARC contain protein, fat and minerals whereas if TBP was used the components would contain protein, fat and minerals and TBP would just contain protein. TCARC decreased in weight by 0.42 g

TABLE 1. Changes in the nutrient reserves of male house sparrows over the breeding season.

Variable (g)[a]	Category: Prereproductive	p[b]	Prelaying	p	Laying	p	Postlaying
Body Weight	27.1 ± 1.6 (37)	NS	26.6 ± 1.5 (75)	NS	26.7 ± 1.5 (30)	NS	26.6 ± 0.2 (50)
Total Body Protein	7.62 ± 0.16 (8)	*	7.29 ± 0.07 (35)	NS	7.21 ± 0.10 (18)	NS	7.16 ± 0.11 (15)
Breast Muscle	1.75 ± 0.02 (35)	*	1.68 ± 0.02 (70)	NS	1.67 ± 0.03 (29)	NS	1.62 ± 0.02 (49)
Leg Muscle	0.59 ± 0.01 (37)	NS	0.58 ± 0.01 (74)	NS	0.60 ± 0.01 (27)	NS	0.60 ± 0.01 (49)
Gizzard	0.25 ± 0.01 (38)	***	0.21 ± 0.00 (78)	NS	0.21 ± 0.01 (30)	NS	0.22 ± 0.01 (50)
Liver	0.33 ± 0.01 (38)	***	0.27 ± 0.01 (77)	NS	0.27 ± 0.01 (30)	NS	0.28 ± 0.01 (51)
Carcass	6.87 ± 0.09 (34)	**	6.60 ± 0.05 (66)	NS	6.82 ± 0.11 (27)	NS	6.60 ± 0.05 (47)
Total Body Fat	1.16 ± 0.06 (30)	**	1.03 ± 0.03 (73)	NS	1.03 ± 0.05 (30)	NS	1.01 ± 0.04 (48)
Leg Bone	0.182 ± 0.003 (35)	NS	0.185 ± 0.002 (71)	NS	0.187 ± 0.003 (27)	NS	0.185 ± 0.002 (48)
Sternum	0.089 ± 0.002 (26)	NS	0.091 ± 0.001 (53)	NS	0.092 ± 0.002 (21)	NS	0.090 ± 0.001 (34)

[a] Data are $\bar{x}$ ± 1 SE with sample size in parentheses.

[b] Probability from t-tests that means in adjacent columns are different by chance; * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, NS = $p > 0.05$.

(4.2%) between the PRD and PRL periods of which BM comprised 16.7%, LM- 2.4%, GZ- 9.5%, LV- 14.3% and CARC- 64.3%. Schifferli was apparently not correct in his assumption that BM weight fluctuations were representative of total weight and other tissue weight fluctuations. His conclusion may have resulted from using carcasses assigned to month of capture rather than reproductive stage. The large contribution of CARC suggests that less "essential" muscles, e.g. non-flight muscles, non-feeding muscles, were comprising a large proportion of the TCARC fluctuations.

TBF did not vary significantly with capture date during the PRD period ($r^2 = 0.005$, df = 36, $p > 0.50$). Between the PRD and PRL periods, TBF declined significantly (Table 1).

TBC was significantly heavier in 1982 than 1983 over the breeding season ($t = 8.97$, df = 16, $p < 0.001$). The exact cause of this difference can never be accurately assessed because different methods of calcium determination were used between years. Hereafter TBC will be examined by year.

TBC weights did not differ between WINTER and PRD nor between PRD and PRL in either year (Table 2). Further, in neither year was the span of capture dates during the PRD period sufficient to permit examination of the relationship of TBC to capture date (1982 span, 1 day; 1983 span, 3 days). The lack of differences in TBC between the WINTER and PRD, and PRD and PRL periods suggests that no long term storage was taking place..

No evidence of medullary bone formation was noted during the PRD period as neither LEG nor STERN weights increased during that time ($r^2 = 0.007$, df = 33, $p > 0.10$; $r^2 = 0.007$, df = 24, $p > 0.05$,

TABLE 2. Changes in total body calcium (g) by sex and by year.

Sex	Year	Category: Winter	p[a]	Prereproductive	p	Prelaying	p	Laying	p	Postlaying
Male	1982	0.227 ± 0.030 (4)	NS	0.275 ± 0.018 (5)	NS	0.262 ± 0.025 (4)	NS	0.282 ± 0.024 (5)	NS	0.244 ± 0.018 (5)
Female	1982	0.256 ± 0.011 (5)	NS	0.245 ± 0.192 (4)	NS	0.301 ± 0.023 (4)	NS	0.326 ± 0.021 (4)	NS	0.260 ± 0.030 (5)
Male	1983	0.173 ± 0.012 (6)	NS	0.145 ± 0.005 (8)	NS	0.148 ± 0.011 (10)	NS	0.147 ± 0.007 (6)	NS	0.133 ± 0.008 (9)
Female	1983	0.121 ± 0.006 (6)	NS	0.153 ± 0.015 (10)	NS	0.164 ± 0.007 (12)	NS	0.159 ± 0.005 (21)	NS	0.145 ± 0.010 (11)

[a]As in Table 1

respectively). In a small sample (n=3) of LEG bones from PRD through POST periods, none was found to contain medullary bone (S. L. Cumbaa, pers. comm.). Neither LEG nor STERN weight changed between the PRD and PRL periods (Table 1).

3.1.1.2 Females

The span of capture dates for female TBP was 39 days which was a sufficient period to examine changes in TBP relative to capture date. TBP declined significantly over the PRD period ($r^2 = 0.137$, df = 36, $p < 0.05$). The sign of the slope was opposite to that predicted. Contrary to the situation for males, TBP did not differ between the PRD and PRL periods (Table 3).

Between the PRD and PRL periods, muscle and organ weights did not change except for a 4% decline in GZ and a 5% increase in LM (Table 3). As with males, BM did not reflect accurately the CARC change nor changes in the weights of other tissues.

TBF remained constant over the PRD period ($r^2 = 0.000$, df = 91, $p > 0.50$) and between the PRD and PRL periods.

Female TBC was also significantly heavier in 1982 than 1983 ($t = -9.73$, df = 13, $p < 0.01$). In neither year did WINTER TBC differ from PRD TBC, nor did PRD TBC differ from PRL TBC (Table 2). In both 1982 and 1983, increases in TBC were apparent before the LAY period, but those changes did not occur between any 2 adjacent stages. During 1982, TBC increased significantly between the PRD and LAY periods ($t = -2.83$, df = 5, $p < 0.05$) while in 1983, TBC increased significantly between the WINTER and PRL stages ($t = -4.55$, df = 15, $p < 0.001$).

TABLE 3. Changes in the nutrient reserves of female house sparrows over the prereproductive period.

Variable (g)[a]	Category: Prereproductive	p[a]	Category: Prelaying
Body Weight	27.1 ± 0.1 (112)	*	27.6 ± 0.2 (64)
Total Body Protein	7.18 ± 0.06 (44)	NS	7.30 ± 0.07 (35)
Breast Muscle	1.61 ± 0.01 (106)	NS	1.59 ± 0.01 (62)
Leg Muscle	0.59 ± 0.01 (110)	***	0.62 ± 0.01 (63)
Gizzard	0.26 ± 0.00 (113)	*	0.25 ± 0.01 (65)
Liver	0.37 ± 0.01 (112)	NS	0.36 ± 0.01 (62)
Carcass	6.85 ± 0.05 (98)	NS	6.92 ± 0.05 (60)
Total Body Fat	1.36 ± 0.04 (95)	NS	1.30 ± 0.03 (63)
Leg Bone	0.180 ± 0.001 (110)	***	0.193 ± 0.002 (62)
Sternum	0.084 ± 0.001 (70)	**	0.089 ± 0.001 (43)

[a]As in Table 1

Within the PRD period neither LEG nor STERN varied with capture date (r^2 = 0.1%, df = 96, $p > 0.50$; r^2 = 0.1%, df = 60, $p > 0.25$, respectively). Both LEG and STERN increased between PRD and PRL (Table 3). The percentages of bone weight attributable to medullary bone or cortical bone were not quantified. Of a very small sample of LEG bones examined by S. L. Cumbaa (pers. comm.) for medullary bone presence, 1 of 1 PRD LEG bones showed no medullary bone and 1 of 1 PRL LEG bones showed slight medullary bone development.

3.1.1.3 Summary

Male house sparrows stored neither TBP, TBF nor TBC over the PRD period. In fact, TBP and TBF both declined in weight between the PRD and PRL periods while TBC remained constant.

Female TBP declined while TBF remained constant over the PRD period. Between the PRD and PRL period, neither TBP, TBF nor TBC varied although in 1982, TBC increased from PRD to LAY, and in 1983, TBC increased from WINTER and PRL periods.

3.1.2 Reproductive

3.1.2.1 Males

After the PRL period, there were no changes in male nutrient reserves (Table 1).

3.1.2.2 Females

To investigate female nutrient reserve dynamics over the reproductive period, it follows that the various indices in adjacent breeding stages be compared. However, this approach was not appropriate because: 1) the proportion of LAY females collected at the beginning versus the end of LAY can significantly affect results; 2) a female laying, 3 eggs, is not distinguished from a female laying, 6 eggs, and 3) there is no means of calculating endogenous reserve input to specific egg components per egg. Because of these inherent problems, regression analysis including PRL and LAY female nutrient reserves was used. Traditionally, regression analyses of nutrient reserve dynamics have compared an individual's internal nutrient reserve against the DAY of the laying cycle. This approach can determine: 1) the daily nutrient reserve investment into reproductive tissue, 2) the total nutrient reserve investment into reproductive tissue, 3) the relative reliance on endogenous versus exogenous reserves for the production of reproductive tissue and 4) the amount of reserve an individual laying X number of eggs had remaining after terminating egg formation. An important disadvantage of this method is that the x axis is incremented nominally while the amount of reproductive tissue allocated per day varies continuously. A better technique compares a specific internal nutrient reserve, e.g. TBP, against the actual amount of reproductive tissue known to have been allocated by that individual (Alisauskas and Ankney, in press). For example, to determine the amount of protein allocated to reproductive protein, I determined the sum of the protein present in all yolky preovulatory follicles, in the oviduct, and in the albumen and yolk

protein of eggs already laid. One assumption which allows for a more definitive interpretation of the findings is for the endogenous nutrient reserve to decline linearly with increasing reproductive tissue allocation. If nutrient reserves do not decline, one cannot accurately determine the percent of the reproductive tissues being drawn from endogenous reserves.

Thus the new approach determines: 1) the amount of nutrient reserve invested per gram of reproductive tissue; 2) the amount of nutrient reserve invested per egg or per clutch; and 3) the relative reliance on endogenous versus exogenous reserves for reproductive tissue investment. Finally, assuming that house sparrows use endogenous reserves to build eggs (Schifferli 1976, Pinowska 1979), I predicted that the regression slope would be negative. Therefore, 1-tailed tests were used.

Information necessary to construct these models included: 1) the validity of estimating clutch size based on morphological traits of carcasses, 2) the duration of rapid follicular development and 3) variation in egg composition.

To corroborate my technique of determining clutch size based on the number of pre- and postovulatory follicles, estimates of clutch size were compared against actual clutch size as determined from nest box data. No significant difference was found between estimated clutch sizes and actual clutch sizes for 1981 ($t = -0.75$, $df = 7$, $p > 0.50$) or 1982 ($t = -0.95$, $df = 29$, $p > 0.50$). No nest box data were collected in 1983. Average clutch size as determined from nest box findings (Table 4), indicated that there was a significant decline in mean clutch size between 1981 and 1982 ($t = 2.22$, $df = 36$, $p < 0.03$). However there was

TABLE 4. Frequencies of house sparrow clutch sizes based on nest box counts and estimates from ovaries.

	Nest Box Clutch Size				
Year	3	4	5	6	$\bar{x}$±1 SE
1981	2	7	9	4	4.68±0.19
1982	3	9	5	0	4.12±0.17

	Estimated Clutch Size From Ovaries				
Year	3	4	5	6	$\bar{x}$±1 SE
1981	1	3	1	1	4.33±0.42
1982	9	5	2	2	3.83±0.25
1983	3	6	5	1	4.27±0.23

no significant difference between 1981 and 1982 clutch size estimates ($t = 1.02$, $df = 8$, $p > 0.50$). While this result differs from the clutch sizes of nest boxes statistically, both the estimated and acutal clutch sizes follow the same trend, i.e. both declined from 1981 to 1982. Because estimated clutch size was no different from actual clutch size and because both estimated and actual clutch size followed the same trends between years, I think the estimated clutch size method is valid.

Breeding of house sparrows in captivity proved successful. Thirty-nine clutches of 3 or more eggs were laid yielding 141 eggs while 33 incomplete clutches (1 or 2 eggs) yielded 55 eggs. Nests containing 1 or 2 eggs were considered incomplete because of the 98 LAY and EI female carcasses examined, not 1 carcass had an estimated clutch size of 2 or less. Of the 141 eggs collected, only 63 were analyzed because of breakage or poor fixing. No eggs from incomplete clutches were included in the estimation of rapid follicular development rate.

First, it was necessary to determine whether house sparrow yolks exhibited the characteristic alternating light and dark bands (see Conrad and Warren 1939) that indicated nocturnal versus diurnal deposition of yolk material, respectively (Roudybush et al. 1979). Ten eggs from females fed undyed food exhibited alternating yolk bands. Since the bands were present, the follicular development rate could be determined. Based on profiles drawn from both dyed and undyed yolks (Grau 1976), I estimated that rapid follicular development in house sparrows usually lasts 4 days (77% of all eggs) but 3 yolks (5%) had 5 bands and 11 yolks (17%) had 3 bands. Because variability in

follicular development rates can have implications for modeling nutrient use, 3 and 5 banded yolks were investigated to determine whether these rates of follicular development could be built into the models.

A comment on the accuracy of estimating 3 and 5 banded yolks is necessary. While methods of staining were constant for all yolks, not all yolks stained equally. Because of differential band resolution in the yolks, it was possible that the anomalous yolks were simply misidentifications. A review of my notes indicated that no obvious banding or fixing anomalies were noted for the 5 banded yolks, but in 55% of the 3 banded yolks, both the dyed and stained bands were faint. This suggests that misidentification of 5 banded yolks was not likely but that misidentification of at least some 3 banded yolks was. Since improper techniques cannot explain all of the 3 anomalous banded yolks, I investigated the presence of 3 as well as 5 banded patterns exhibited within or among clutches.

No clutch contained either only 3, only 5, or both 3 and 5 banded yolks, i.e. among-female variability was not the cause of differences in rapid follicular development. The next logical relationship to examine was between the presence of an anomalous yolk and sequence within a clutch. Possibly females could have been altering rapid follicular development to correct for environmental variability. Although the small sample size ($n = 6$) prevented statistical testing, no trend was apparent. Finally the presence of anomalous yolks could have been dependent on clutch size, but no such relationship was found ($G = 3.60$, $df = 2$, $p > 0.05$).

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Since the presence of the anomalous yolks could not be explained, I was unable to incorporate the variable rate of follicular development into any models. Even though follicular development was not always constant within females, I used 4 days as the normal development period.

In addition to the estimation of the period of yolk development, dyed yolks were used to investigate the route that ingested fat followed before deposition in the yolk. Knowing that a single concentrated dose of Sudan black B ingested by a laying female would quickly appear as a distinct dark blue-green band (Grau 1976), and also knowing that dark staining yellow versus light staining yellow yolk represented diurnal/nocturnal deposition, respectively (Roudybush et al. 1979), I predicted the following. If a prereproductive female was fed dyed food up until she laid her first egg followed by undyed food until she finished laying, then the following results should have occurred. 1) The first egg should have been dyed with alternating light and dark dyed bands. 2) The following eggs should have only outer bands alternating between undyed diurnal fat and dyed nocturnal fat; the number of alternating bands increasing with egg sequence.

The feeding scheme resulted in the first egg yolk being completely dyed although alternating dyed and undyed bands were not always present. Subsequent egg yolks always had paler peripheries but never did they have alternating yellow and blue/green bands. Peripheral bands of subsequent egg yolks usually had broad paler regions lacking the diurnal/nocturnal bands. However, in these peripheral bands the presence of undyed fat was always indicated by the color changes proceeding from the core to the periphery (blue or

blue/green changing to yellow-green or aquamarine). Thus, fat depots were being dyed as indicated by the sometimes alternating dyed and less dyed bands. Exogenous undyed fat was being incorporated into egg yolks as indicated by the more yellow/orange peripheries, but later egg yolks did not appear to have diurnal/nocturnal banding as no alternating blue/green or yellow bands were noted.

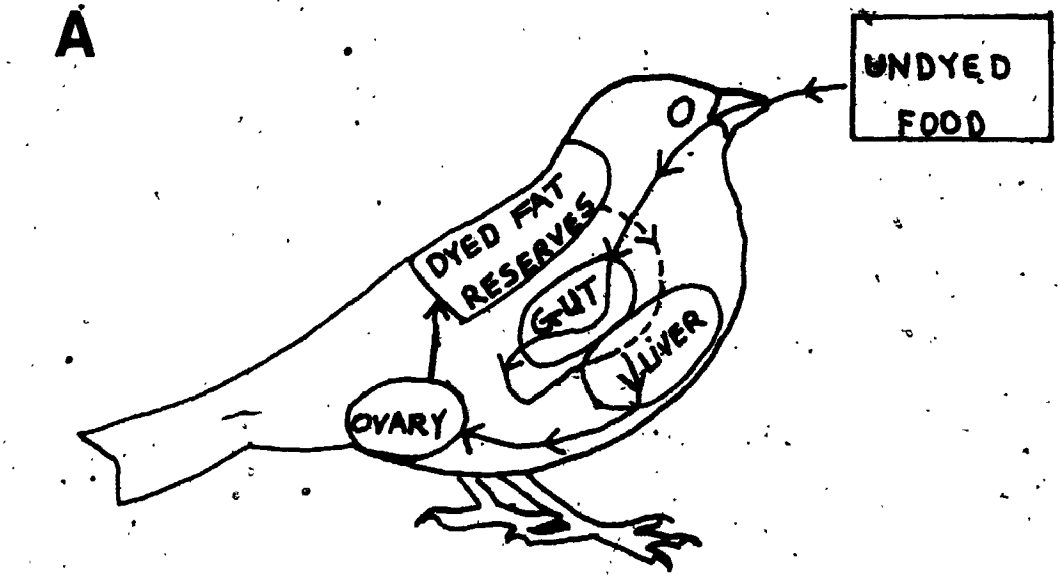
According to these results, undyed fat ingested daily was being mixed with dyed depot fat before being drawn off by the growing follicle (I am assuming that no bleeding of dye in the yolk occurred after fixing). Thus ingested undyed fat was either supplementing dyed fat from depots both during the day and night (that food stored in the crop) (Fig. 2A), or ingested undyed fat was shunted directly to dyed fat depots and diluting those dyed fat depots, and then being routed past the developing follicles.

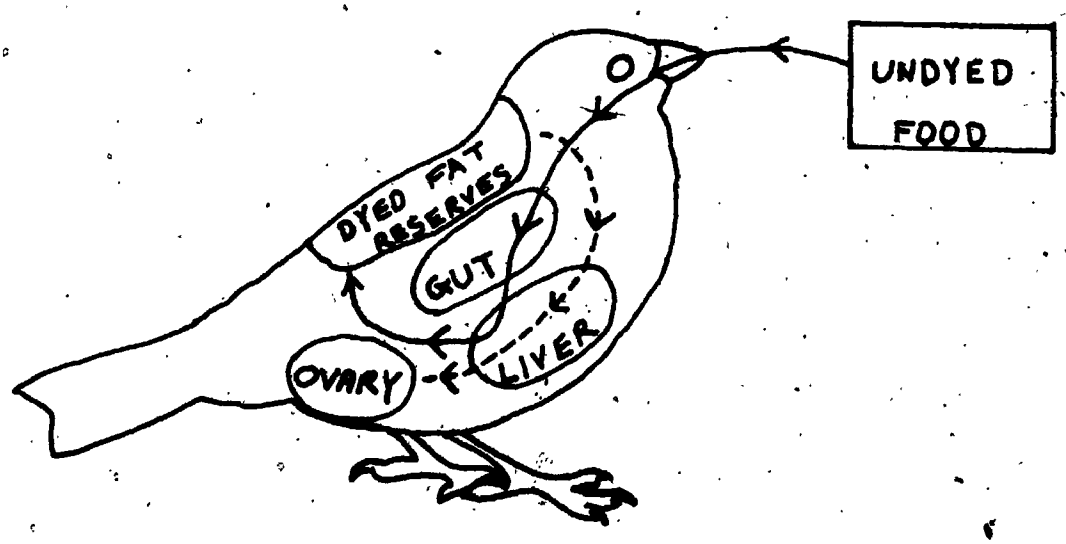
Because the above results were not clear, I thought that I had "overdosed" the females with dye. Possibly so much dye was consumed by a female that any incoming undyed fat was being masked by dyed fat. Therefore I attempted to flush out all traces of stored dyed fat by only feeding undyed feed for 15 days and then restarting the original experimental design. Flushing began on June 15 and ended on June 30. During this time, 15 clutches were begun of which 8 were complete.

Several interesting findings were noted from the 15 clutches. First, the rate at which individual females ridded dyed fat from their depots varied. Two findings suggested this. 1) Four females began clutches within 2 days of each other, the earliest after 5 days of undyed food, had from no dye present (pure yellow yolk) to 2 intensively dyed central bands (blue) with no pure yellow present at

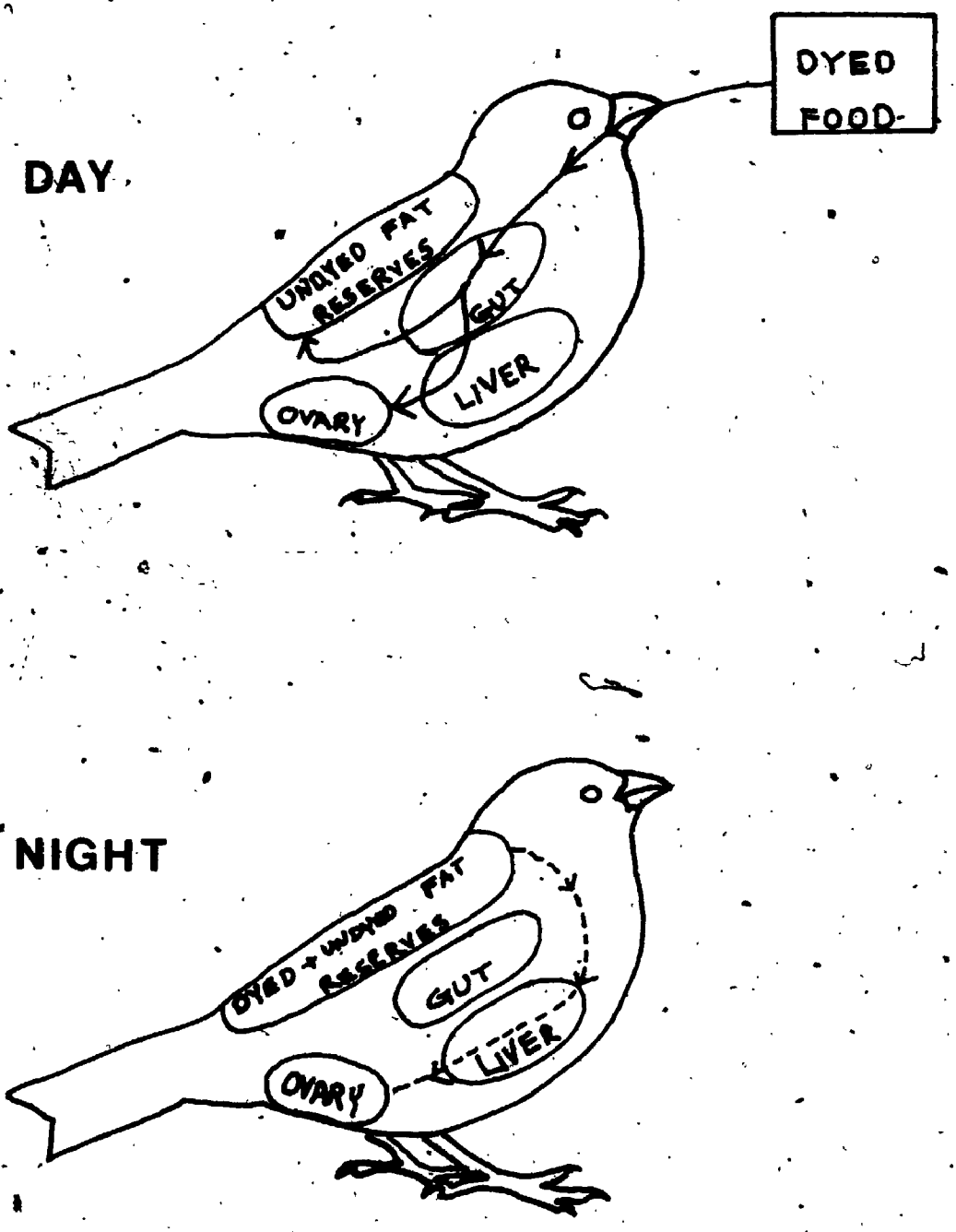
Fig. 2. (A) Possible routes of undyed food from ingestion to deposition in the yolk. (B) Possible routes of dyed food from ingestion to deposition in the yolk; the "day" diagram represents diurnal fat routes; the "night" diagram represents nocturnal fat routes.

A


UNDYED FOOD
DYED FAT RESERVES
GUT
LIVER
OVARY


UNDYED FOOD
DYED FAT RESERVES
GUT
LIVER
OVARY

B


DYED FOOD
DAY
UNDYED FAT RESERVES
GUT
LIVER
OVARY
NIGHT
DYED + UNDYED FAT RESERVES
GUT
LIVER
OVARY

the periphery. 2) The earliest first yolk of pure yellow occurred 7 days after feeding undyed food while 1 female still had dye present in her first yolk after 15 days of flushing. In complete clutches, earlier egg yolks contained more dyed fat, often in alternating dyed and less dyed bands, while sequential egg yolks sometimes contained central-dyed bands with or without alternating bands, and peripheral paler unbanded regions.

After 15 days of flushing, dyed food was readministered. Two complete clutches were started within 2 days of reinitiating the experiment. Instead of removing dyed food from the cages, I allowed the females to complete their clutches consuming dyed food to see if altering the design had any effect. The first clutch (4 eggs), which began on the first day of dyed food administration, had egg yolks 1 and 2 pure yellow. Egg yolk 3 had 1 band of blue fat located at the extreme periphery while egg yolk 4 had 1 band of blue fat also at the extreme periphery, inside of which was an equally wide band of yellow fat again bordered inside by another equally wide band of blue fat; the remaining core was pure yellow. The second clutch (3 eggs), starting 4 days after dyed food was resupplied, had egg yolk 1 identical in banding and color pattern as egg yolk 4 of the first clutch. These 2 eggs were laid on the same day. The second egg yolk had an inner yellow core bordered by a light blue band, bordered by an equally wide dark blue band, bordered by a light blue band, bordered by an narrow dark blue band, bordered by a light blue band. The third egg yolk had a small central yellow core bordered by 3½ alternating bands of equal width light and dark blue bands; the final band was light blue. In every case the blue and yellow bands were distinct and

uniform in color. Had I not read Roudybush et al. (1979), I would have interpreted the alternating blue and yellow band locations (egg yolks 3,4 clutch 1; egg yolk 1 clutch 2) as indicating that daily dyed food was deposited in the yolk at night, not during the day. However Bacon (1981) has shown that radioactively labeled fat, in the arterial system of turkeys, is rapidly deposited in the ovary. Other supportive evidence that the peripheral blue band was not the final band is 1) egg yolk profiles always revealed that lighter yolk material was present on the extreme edge of the peripheral blue band and 2) the sigmoidal growth pattern of growing follicles indicates that little yolk is laid down on the final night before ovulation. For these reasons I believe the apparently peripheral pure blue ring was composed of diurnal fat and a small amount of nocturnal pale blue fat (see below). The yellow band between the equally wide blue bands was most revealing. This band had to have come solely from undyed fat depots at night because all other fat was dyed. However subsequent egg yolks in clutch 2 (egg yolks 2,3) contained no pure yellow bands outside of the central yellow core. Apparently the dyed fat ingested daily was diluting the undyed fat depots until some threshold level was met whereupon nocturnally deposited fat was pale blue instead of the expected yellow.

Thus from these 2 clutches, I concluded that daily ingested fat supplied fat for developing follicles and any daily ingested fat which was not drawn off developing follicles is deposited into fat depots (Fig. 2B). This excess daily fat apparently replaced stored fat within days, i.e. depot fat was turned over quickly but not necessarily depleted quickly.

In summary, rapid follicular development, on average, required 4 days but variation among females in development time was found. Daily ingested fat contributed to diurnal yolk fat needs and also resupplied fat depots. Stored fat was used to meet yolk fat needs at night and was quickly replaced from fat consumed daily.

In all, 98 house sparrow eggs from natural nests were processed: 53 eggs from clutches of unknown final size, 8 eggs from clutches of 3, 19 eggs from clutches of 4 and 18 eggs from clutches of 5. Dry weights of albumen, yolk, shell and total fresh egg weight by sequence in the clutch are presented in Table 5 for clutches of 3, 4, 5 and combined; combined clutches include known-sequence eggs from 3, 4, 5 and clutches of unknown final size. No egg component was found to differ over laying sequence within a specific clutch size (1-way ANOVA). But trends in the yolk and shell weight of 5 egg clutches were noted when the 95% confidence limits for all egg components were examined. In spite of small sample sizes for both (df = 9) yolk increased while shell decreased with laying sequence ($r^2 = 0.488$, $p < 0.02$; $r^2 = 0.378$, $p < 0.05$; respectively).

Having determined the validity of estimating clutch size based on carcass traits, the duration of rapid follicular development and the variation in egg composition, I constructed the following nutrient models.

"Reproductive protein" was defined as the amount of protein present in all yolky follicles, the oviduct and the albumen and yolk protein of eggs already laid. Protein in yolky follicles, ova in the oviduct or laid yolks was determined by multiplying the total weight by 40.91%, the average percent of protein in a house sparrow yolk

TABLE 5. House sparrow egg component weight ± 1 SE by order of laying.

Clutch Size	Component	Egg Order					1-way ANOVA	
		Unknown[a]	1	2	3	4	5	F Ratio	Significance[c]
3	albumen		.19 ± .020 (3)	.21 ± .030 (2)	.20 (1)			0.51	NS
	yolk		.23 ± .020 (3)	.22 ± .018 (2)	.26 ± .005 (2)			0.74	NS
	shell		.174 ± .100 (3)	.184 ± .106 (3)	.182 ± .129 (2)			0.10	NS
	fresh weight		2.75 ± .285 (3)	2.80 ± .32 (3)	2.85 ± .235 (2)			0.02	NS
4	albumen	.23 ± .017 (7)	.18 ± .025 (2)	.24 ± .013 (3)	.23 (1)	.22 ± .012 (6)		1.89	NS
	yolk	.26 ± .012 (7)	.24 ± .025 (2)	.25 ± .022 (3)	.22 (1)	.23 ± .014 (6)		0.39	NS
	shell	.186 ± .006 (7)	.155 ± .011 (2)	.187 ± .005 (3)	.178 (1)	.173 ± .006 (6)		2.43	NS
	fresh weight	2.90 ± .148 (7)	2.50 ± .273 (2)	2.92 ± .186 (3)	2.67 (1)	2.80 ± .128 (6)		0.87	NS

continued...

Clutch Size	Component	Egg Order						1-way ANOVA	
		Unknown[a]	1	2	3	4	5	F Ratio	Significance[c]
5	albumen	.18 ± .015 (7)	.21 ± .000 (2)	.21 ± .005 (2)	.22 ± .009 (3)	.23 ± .015 (2)	.21 ± .025 (2)	0.58	NS
	yolk	.26 ± .006 (7)	.22 ± .015 (2)	.24 ± .010 (2)	.24 ± .017 (3)	.28 ± .015 (2)	.27 ± .005 (2)	2.48	NS
	shell	.169 ± .008 (7)	.195 ± .000 (2)	.176 ± .005 (2)	.181 ± .007 (3)	.169 ± .022 (2)	.155 ± .021 (2)	1.19	NS
	fresh weight	2.48 ± .15 (7)	2.78 ± .000 (2)	2.72 ± .040 (2)	2.72 ± .115 (3)	2.79 ± .134 (2)	2.64 ± .236 (2)	0.19	NS
Combined[b]	albumen	.21 ± .006 (42)	.19 ± .008 (11)	.22 ± .008 (12)	.22 ± .006 (12)	.22 ± .008 (16)	.21 ± .017 (3)	1.66	NS
	yolk	.25 ± .005 (42)	.23 ± .008 (11)	.24 ± .010 (13)	.25 ± .009 (13)	.25 ± .009 (16)	.25 ± .012 (3)	0.90	NS
	shell	.177 ± .005 (42)	.176 ± .006 (11)	.183 ± .004 (13)	.185 ± .004 (13)	.180 ± .004 (16)	.163 ± .045 (3)	1.35	NS
	fresh weight	2.85 ± .052 (42)	2.70 ± .084 (11)	2.89 ± .089 (13)	2.89 ± .075 (13)	2.90 ± .067 (16)	2.72 ± .158 (3)	1.15	NS

[a] This column represents egg component and/or fresh egg weights from a known clutch size but for which the order within the clutch is unknown.

[b] Combined clutch includes clutches of unknown final size plus eggs from 3, 4 and 5 egg clutches.

[c] Probability (from 1-way ANOVA) that means different by chance. NS = $p > 0.05$.

TABLE 6. Mean ± 1 SE weights (mg) of pre- and postovulatory follicles of house sparrows. Numbers in parentheses are sample sizes.

Yolky Preovulatory Follicles				Postovulatory Follicles				
Days before ovulation				Days after ovulation				
-4	-3	-2	-1	1	2	3	4	5
*	14.5 ± 1.68 (84)	60.4 ± 3.81 (50)	166.0 ± 7.10 (38)	3.56 ± 0.138 (56)	1.83 ± 0.105 (55)	0.966 ± 0.081 (53)	0.410 ± 0.057 (49)	0.237 ± 0.062 (27)

*Since only 2 females were found with 4 yolky preovulatory follicles (they were collected after noon), I could not accurately estimate DAY -4 preovulatory follicle weight. The smallest yolky preovulatory follicle found weighed 1 mg.

(Schifferli 1976). If a follicle had been damaged or I could not determine its weight, I substituted the average weight of a comparably developed follicle (Table 6). I assumed that oviduct dry weight was 100% protein. Albumen protein weight was determined from eggs already laid (Table 5).

TBP declined significantly with increasing investment in reproductive protein (Fig. 3). Thus for every gram of protein committed to reproductive protein tissue, 0.149 g of protein came from internal protein reserves; the balance was exogenous. Obviously the input from protein reserves to reproductive protein was low and further the coefficient of determination ($r^2 = 0.035$) was very poor.

To determine if committment of TBP was related to clutch size, 2 analyses were conducted. First the residuals of the TBP versus reproductive protein regression were compared by clutch size. No difference was found between either the residuals of 3 or 4 egg clutches ($t = 1.27$, $df = 14$, $p > 0.2$) nor the residuals of 4 or 5 egg clutches ($t = -1.50$, $df = 8$, $p > 0.15$). Next, the amount of TBP when egg formation was finished was compared against clutch size (clutch sizes of 3,4 and 5 and represented by DAY +2,+3,+4 respectively)(Fig. 4). Terminal TBP was not related to clutch size ($r^2 = 0.023$, $df = 13$, $p > 0.50$). Further, there was no significant difference between the terminal TBP of 3 versus 4 egg females ($t = 0.85$, $df = 6$, $p > 0.50$) nor between 4 versus 5 egg females ($t = -0.41$, $df = 5$, $p > 0.50$).

Finally it was possible to investigate whether TBP committment affected short-term female survivorship. Schifferli reported that approximately 5.4 g of LDW remain in starved house sparrows. By comparing the terminal LDW against the starvation level LDW, short

Fig. 3. Relationship between total body protein of female house sparrows and protein allocated to reproductive tissue. The regression equation is: $Y = 7.31 - 0.149\ X$, se a = 0.08, se b = 0.088, $n = 80$, $r^2 = 0.035$, $p < 0.05$.

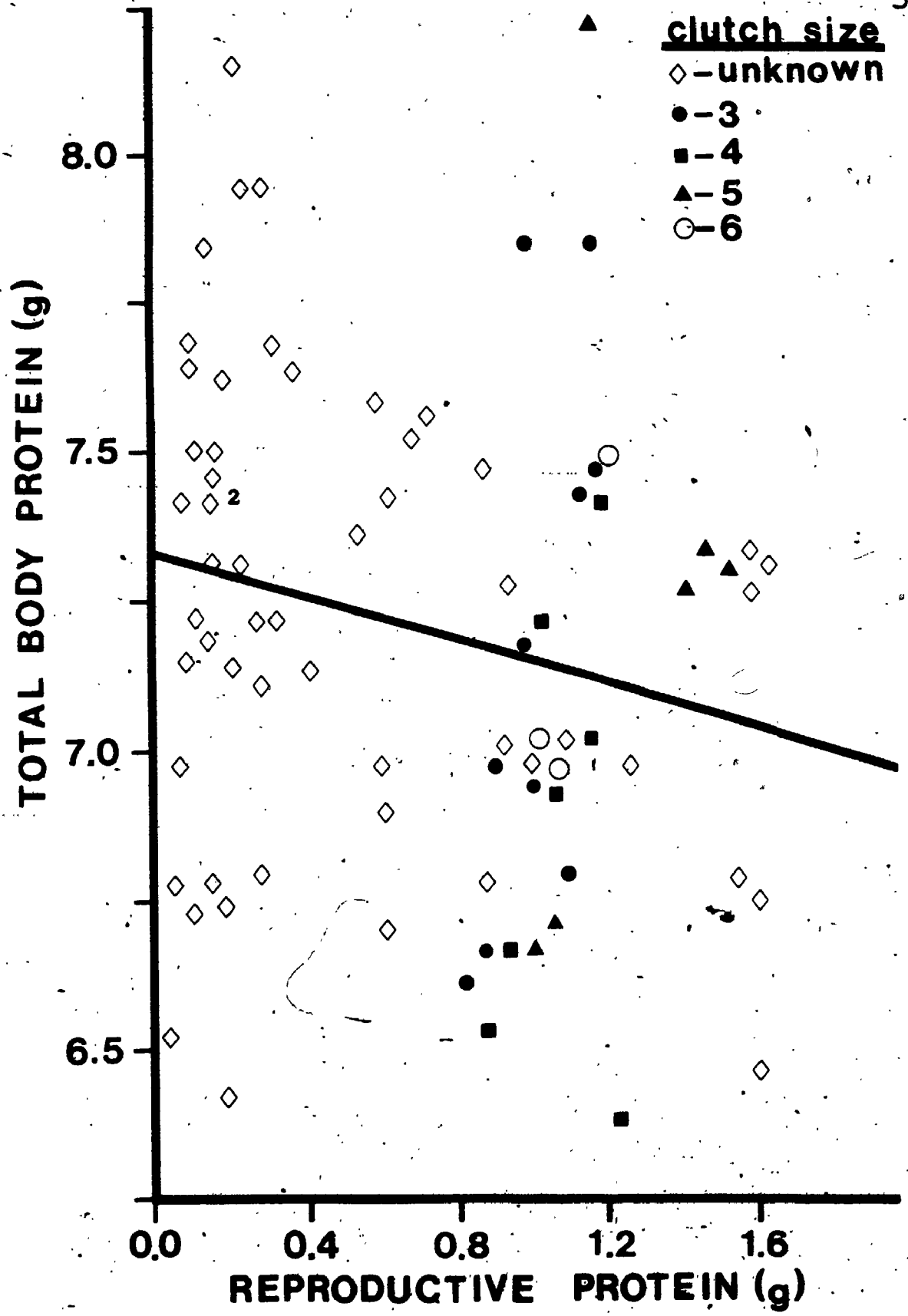
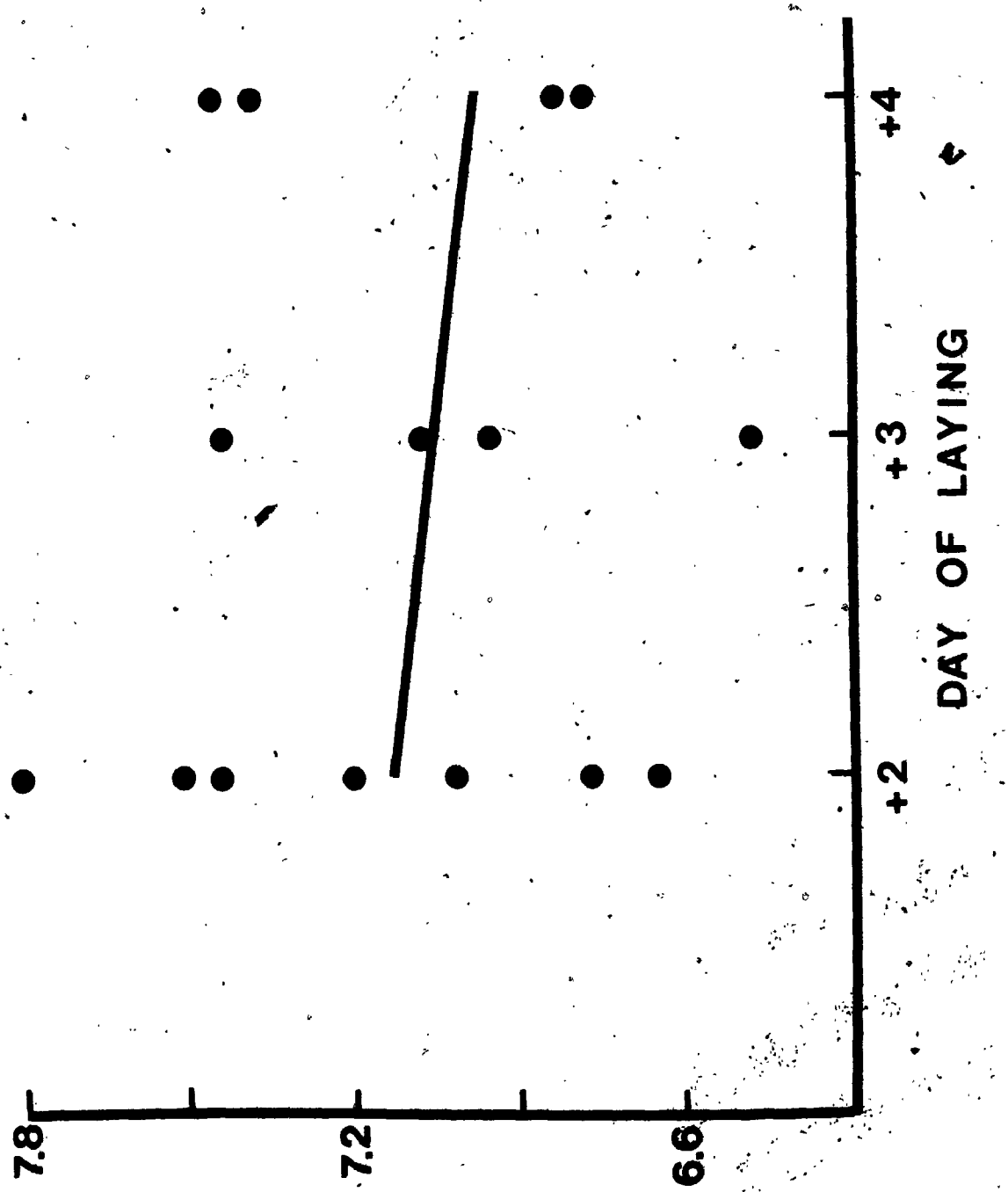

clutch size
◇–unknown
●–3
■–4
▲–5
○–6
8.0
7.5
7.0
6.5
TOTAL BODY PROTEIN (g)
2
0.0
0.4
0.8
1.2
1.6
REPRODUCTIVE PROTEIN (g)

Fig. 4. Relationship between total body protein and the final commitment of reproductive protein to clutches of 3,4 and 5, respectively DAYs +2,+3 and +4. The regression equation is: $Y = 7.30 - 0.067\ X$, se a = 0.35, se b = 0.120, n = 15, $r^2 = 0.002$, $p > 0.50$.


TOTAL BODY PROTEIN (g)
7.8
7.2
6.6
+2
+3
+4
DAY OF LAYING

term female survivorship could be assessed. Comparing LDW versus reproductive protein for this study yielded

$$Y = 8.57 - 0.176\ X, \qquad \text{Eq.5}$$

where Y = LDW and X = reproductive protein (g). The maximum reproductive protein investment was 1.60 g (Fig.3). Solving equation 5 for 1.60 yields an average 8.29 g LDW remaining after egg laying ceased. However, this estimate does contain oviduct protein which probably was recycled into protein reserves (see Section 4.2). The maximum oviduct weight, on average, was 0.4 g (this study). Subtracting maximum oviduct protein from 8.29 yields 7.89 g of LDW which was still approximately 145% over starvation LDW level.

The regression method of Alisauskas and Ankney (in press) was not applicable for modelling the costs of egg fat because the decline in TBF over the reproductive period was not linear (Fig. 5). The findings fit a nonlinear model better; the r^2 increased from 20.6% to 25.2% ($p < 0.001$). Linearity is necessary before I can infer that endogenous reserves were destined for reproductive tissue. While an nth order polynomial equation might have explained the data, I decided, in part based on the *a posteriori* approach, to fit 2 linear regressions through the scatter of points, one before (DAY -3 to DAY 0) and one after (DAY 0 to DAY +4) ovulation of the first egg. Both linear regressions proved significant: DAY -3 to DAY 0- $r^2 = 0.048$, df = 75, $p < 0.05$; DAY 0 to DAY +4- $r^2 = .0.226$, df = 54, $p < 0.001$ (Fig. 5). Thus between DAY -3 and DAY 0 when approximately 50% of clutch fat was

Fig. 5. Relationship between total body fat of female house sparrows and DAY.

The overall equation is: $Y = 1.12 - 0.065\ X$,

se a = 0.03, se b = 0.011,

$n = 125$, $r^2 = 0.206$, $p < 0.001$.

The DAY -3 to DAY 0 regression is: $Y = 1.42 + 0.059\ X$,

se a = 0.07, se b = 0.030,

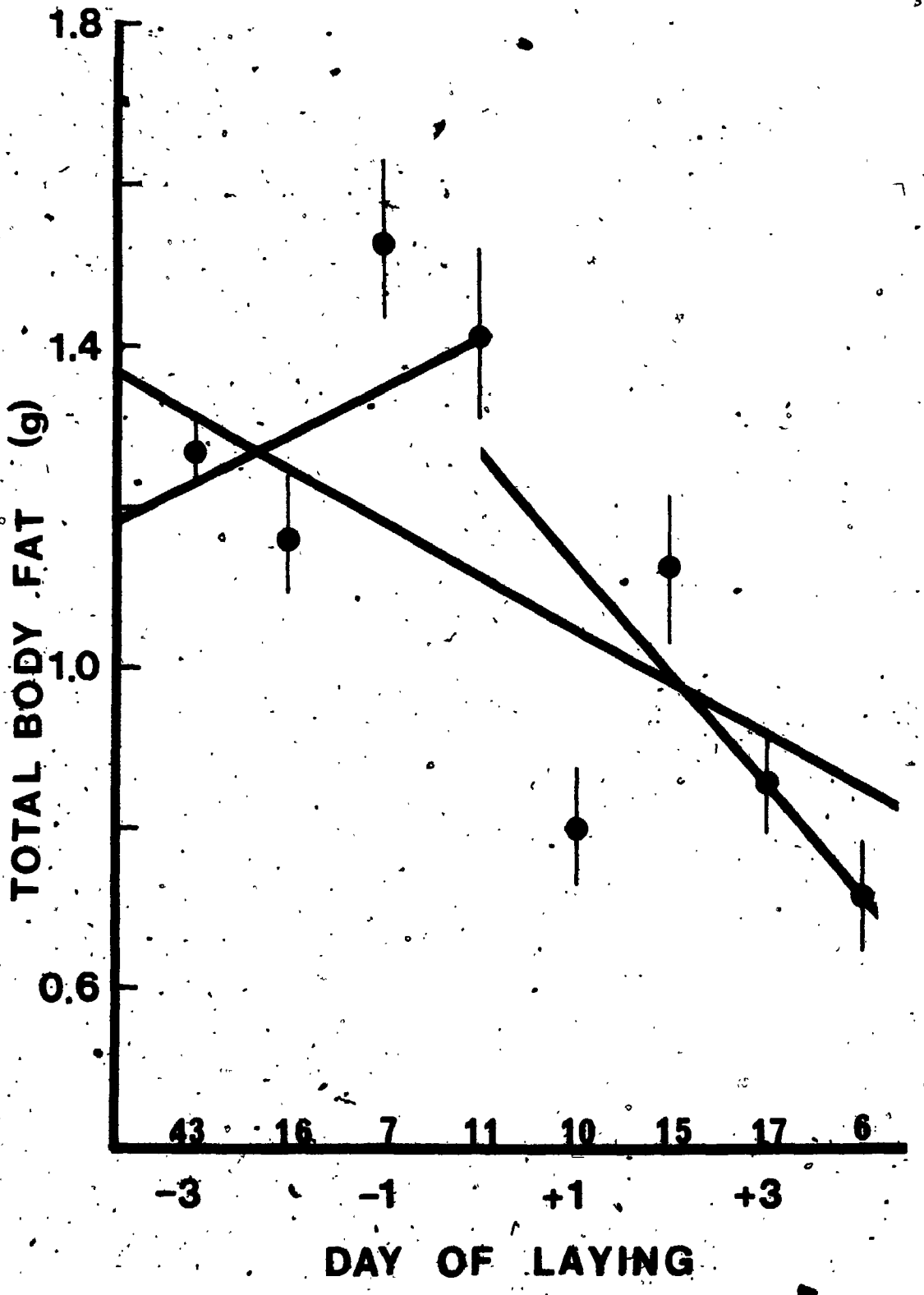
$n = 77$, $r^2 = 0.048$, $p < 0.05$.

The DAY 0 to DAY +4 regression is: $Y = 1.27 - 0.138\ X$,

se a = 0.08, se b = 0.034,

$n = 57$, $r^2 = 0.226$, $p < 0.001$.

Data points are $\bar{x} \pm 1$ se for each respective DAY; sample sizes are below respective points.


1.8
1.4
1.0
0.6
TOTAL BODY FAT (g)
43
16
7
11
10
15
17
6
-3
-1
+1
+3
DAY OF LAYING

deposited (4 egg clutch), TBF increased. Thereafter, TBF declined when the final 50% of clutch fat was deposited and continued to decline through DAY +3 and DAY +4 when no fat for eggs was required. Further, the drop in TBF between DAY 0 and DAY +1 (0.62 g) exceeded the remaining fat needs of the clutch by 103%. Interestingly TBF declined from DAY 0 to DAY +1 but increased between DAY +1 and DAY +2.

Because the amount of fat in an egg is discrete, I could determine the amount of fat committed to clutches of various sizes. When the TBF versus DAY 0 to +4 regression was compared against the actual amount of TBF remaining when a female had stopped laying, I found that the 95% confidence band overlapped or was less than the amount of TBF remaining in 13 of 20 females which had just finished egg formation (Fig. 6).

Residuals from the TBF versus DAY 0 to DAY +4 regression were compared by clutch size to determine if TBF use was dependent on clutch size. No difference was found between residuals of the 3 and 4 egg clutches ($t = 0.80$, $df = 17$, $p > 0.40$) nor between the residuals of 4 and 5 egg clutches ($t = -1.29$, $df = 10$, $p > 0.20$).

When the terminal TBF weights for females laying 3, 4 and 5 eggs were compared against respective clutch size, a significant decline was found ($r^2 = 0.244$, $df = 18$, $p < 0.05$; Fig. 6). With that slope being 0.126, and a house sparow egg having, on average, 0.147 g of fat (this study), an average female producing a clutch of 3, 4 or possibly 5 would stop egg production while she had 86% of the fat necessary to produce an additional egg.

A female laying 3 eggs would require approximately 0.3 more g of fat to continue laying 2 additional eggs. I investigated whether this

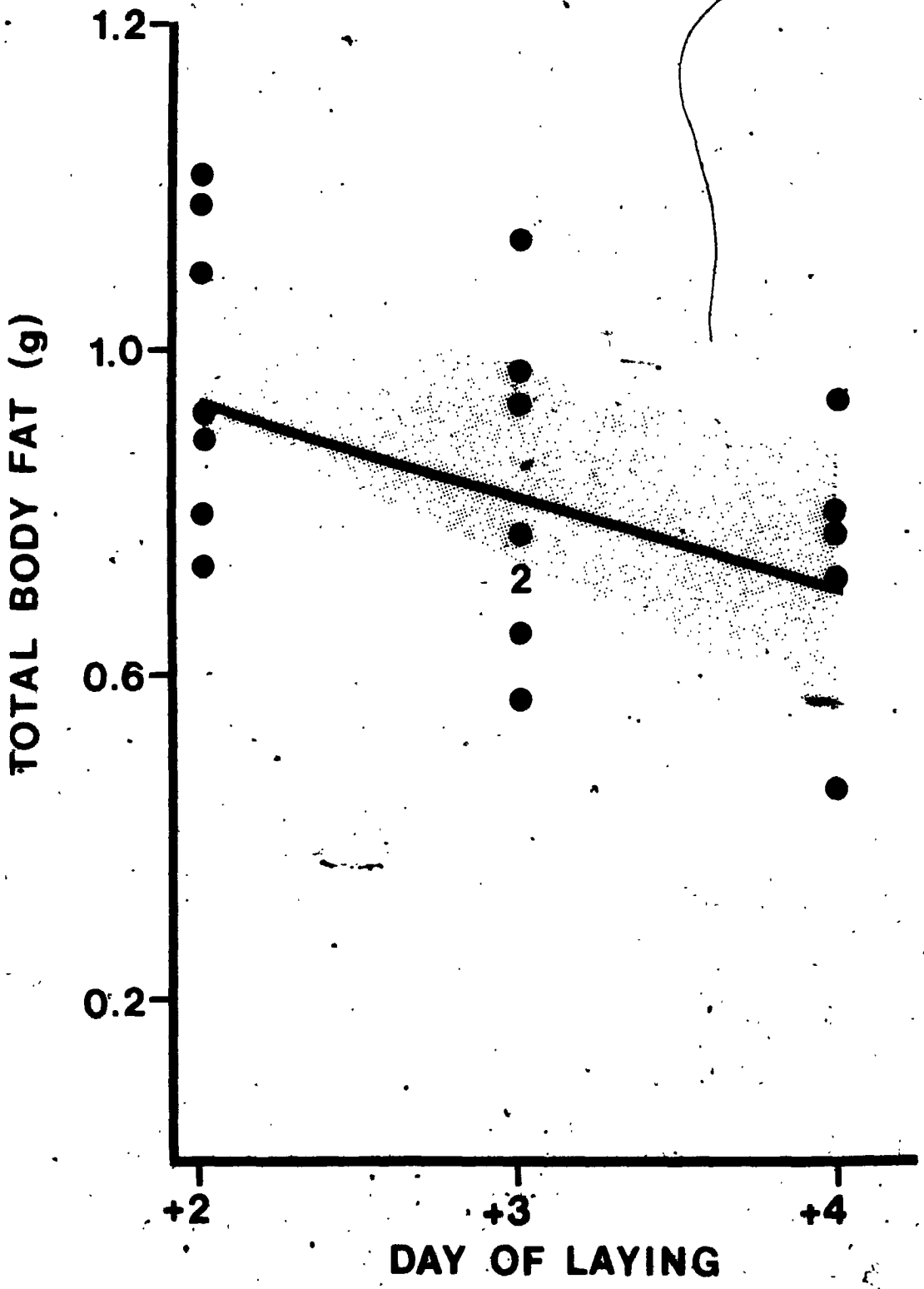
Fig. 6. Relationship between total body fat of female house sparrows for specific clutch sizes of 3,4 and 5, respectively DAYs +2,+3 and +4; and the final committment of reproductive fat to those clutches.

The regression equation is: $Y = 1.09 - 0.126\ X$,

se a = 0.11, se b = 0.052,

$n = 20$, $r^2 = 0.244$, $p < 0.05$.

Superimposed over the terminal total body fat points is the 95% confidence band for the total body fat versus DAY 0 to DAY +4 equation. See Fig. 5 legend for regression equation.


1.2
1.0
0.6
0.2
TOTAL BODY FAT (g)
2
+2
+3
+4
DAY OF LAYING

extra fat loss would lower her survival probability in the short-term. Schifferli (1976) found that the minimum level of TBF in a house sparrow was 0.25 g, the amount remaining after starvation. Fig. 6 clearly demonstrates that the terminal TBFs were on average over 250% greater than 0.25 g. This evidence strongly supports the contention that females were terminating egg formation while sufficient TBF reserves for additional eggs were available.

The above analyses suggest that: 1) TBF was not used exclusively for clutch fat, but also for female energetic needs, 2) the decline in TBF was similar for clutches of different sizes, 3) females stopped committment of TBF to reproductive fat before TBF approached starvation levels, and therefore, 4) females were not being limited by low TBF levels at the termination of their committment to reproductive fat.

Even though TBF did not decline linearly with DAY, the regression of TBF and reproductive fat revealed an interesting pattern.

Reproductive fat for laid eggs was based on the amount of fat per yolk according to egg sequence number (Table 7). TBF declined significantly with increasing reproductive fat commitment (Fig. 7), but there was a conspicuous lack of points below the regression line between approximately 0.1 and 0.4 g of reproductive fat.

Reproductive calcium was determined by summing the amount of calcium necessary to produce each sequential eggshell as determined by the number of postovulatory follicles present (Table 7). Because of the annual variability in calcium content and because the 1982 sample was small, I opted to use only the 1983 data in the following analyses.

TABLE 7. Changes in house sparrow egg components (dry weight) with respect to laying sequence; based on combined egg data (see Table 5).

	Order in Clutch			
Component (g)	1	2	3	4
Protein[a]	0.284	0.318	0.322	0.322
Fat[b]	0.136	0.142	0.148	0.148
Eggshell Calcium[c]	0.067	0.070	0.070	0.068

[a]Protein per egg was determined by multiplying 0.4091, the percent of yolk which is lean dry weight (Schifferli, 1976), times yolk weight (Table 5: combined data) plus albumen weight and DAY +4 oviduct weight (Table 8).

[b]Fat per egg was determined by multiplying 0.5909, the percent of yolk which is fat (Schifferli, 1976), times yolk weight (Table 5: combined data).

[c]Eggshell calcium was determined by multiplying 0.38, the percent of eggshell which is calcium assuming the eggshell is wholly calcium carbonate, times eggshell weight (Table 5: combined data).

Fig. 7. Relationship between total body fat of female house sparrows and fat allocated to reproductive fat.

The regression equation is: $Y = 1.31 - 0.697\ X$,

se a = 0.04, se b = 0.107,

$n = 125$, $r^2 = 0.263$, $p < 0.001$.

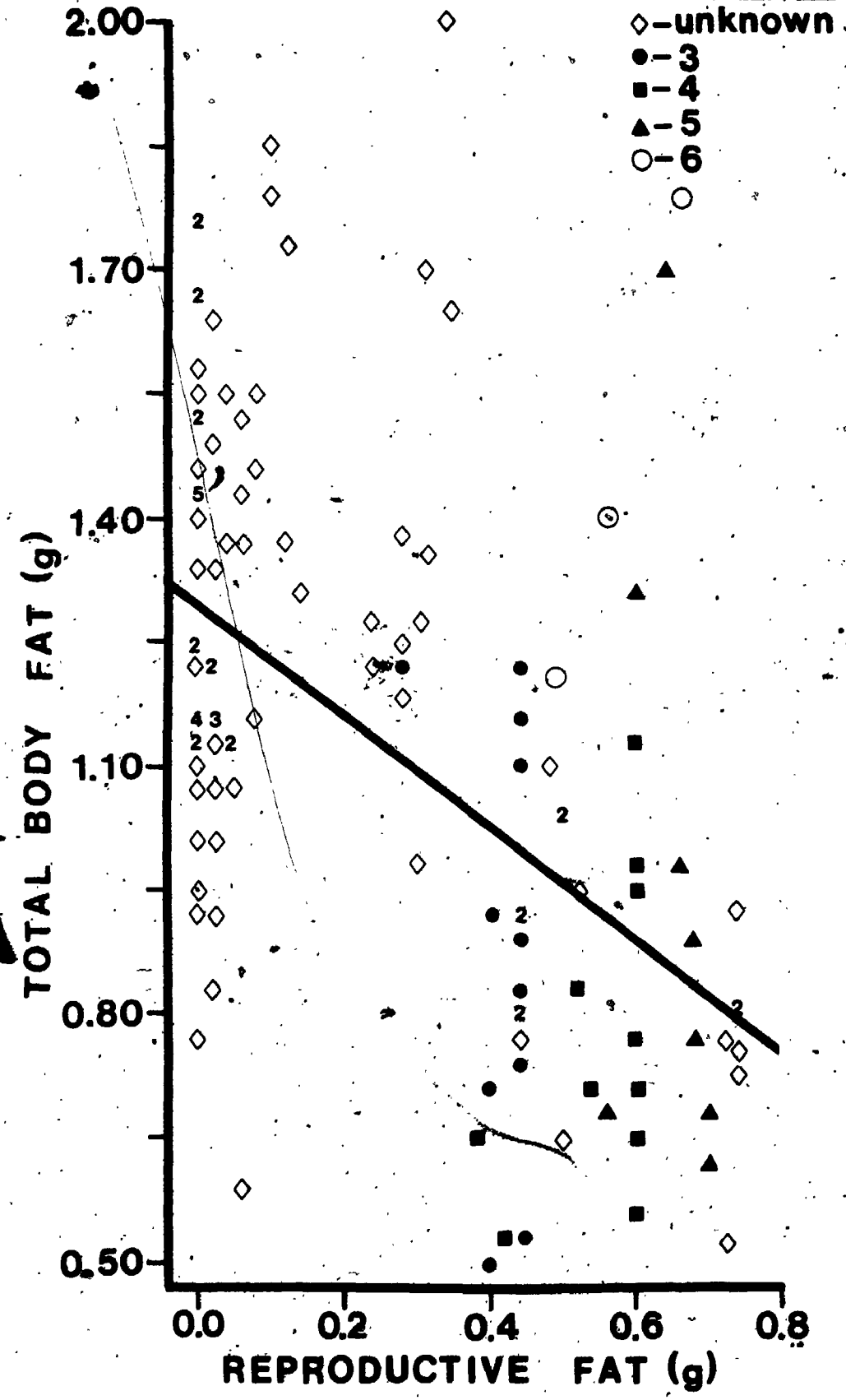
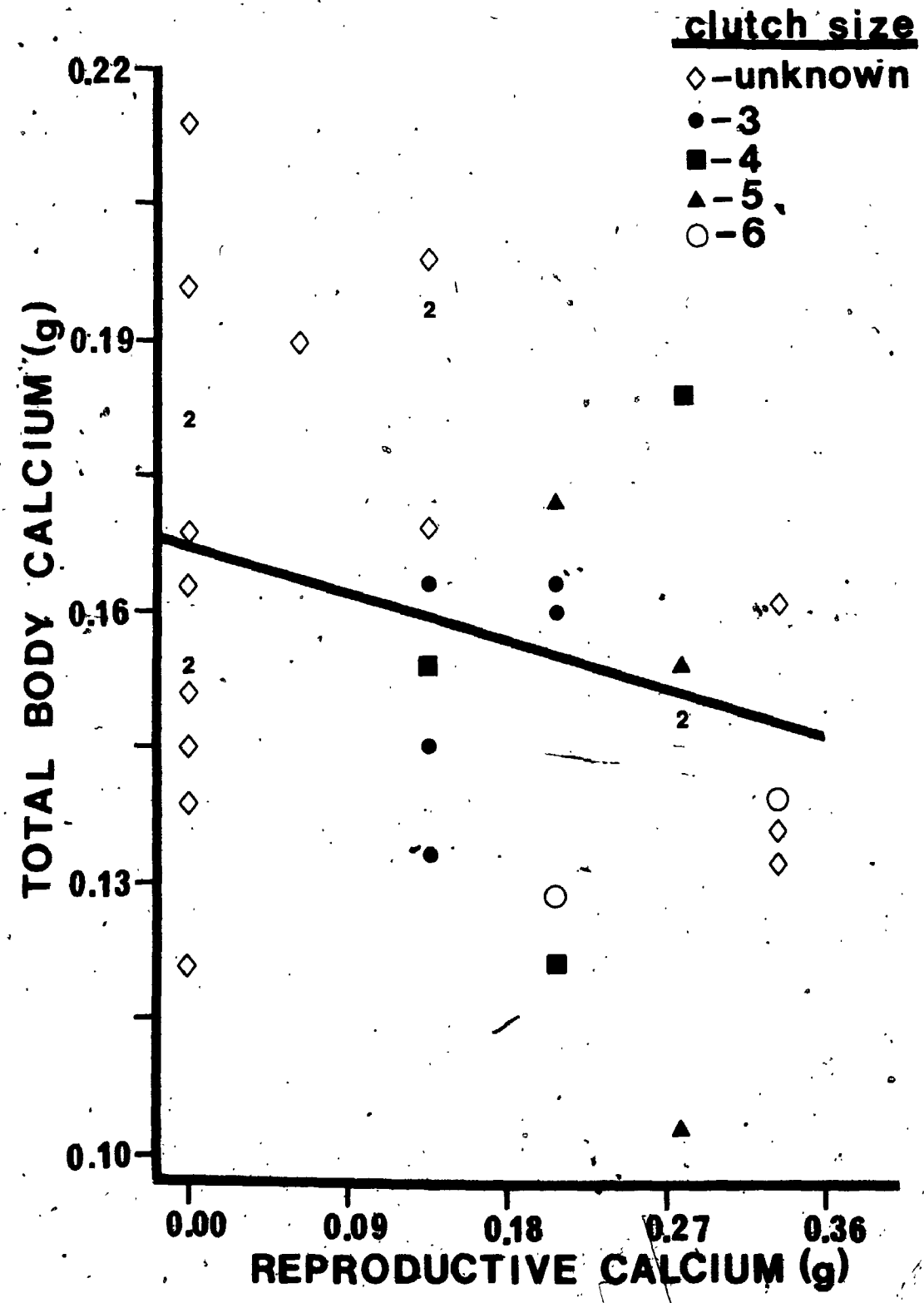

clutch size
◇–unknown
●–3
■–4
▲–5
○–6
2.00
1.70
1.40
1.10
0.80
0.50
TOTAL BODY FAT (g)
0.0
0.2
0.4
0.6
0.8
REPRODUCTIVE FAT (g)

Fig. 8. Relationship between total body calcium of female house sparrows and calcium allocated to reproductive calcium. The regression equation is: $Y = 0.168 - 0.066\ X$, se a = 0.006, se b = 0.034, $n = 35$, $r^2 = 0.104$, $p < 0.05$.


clutch size
◇-unknown
●-3
■-4
▲-5
○-6
TOTAL BODY CALCIUM (g)
0.22
0.19
0.16
0.13
0.10
0.00
0.09
0.18
0.27
0.36
REPRODUCTIVE CALCIUM (g)

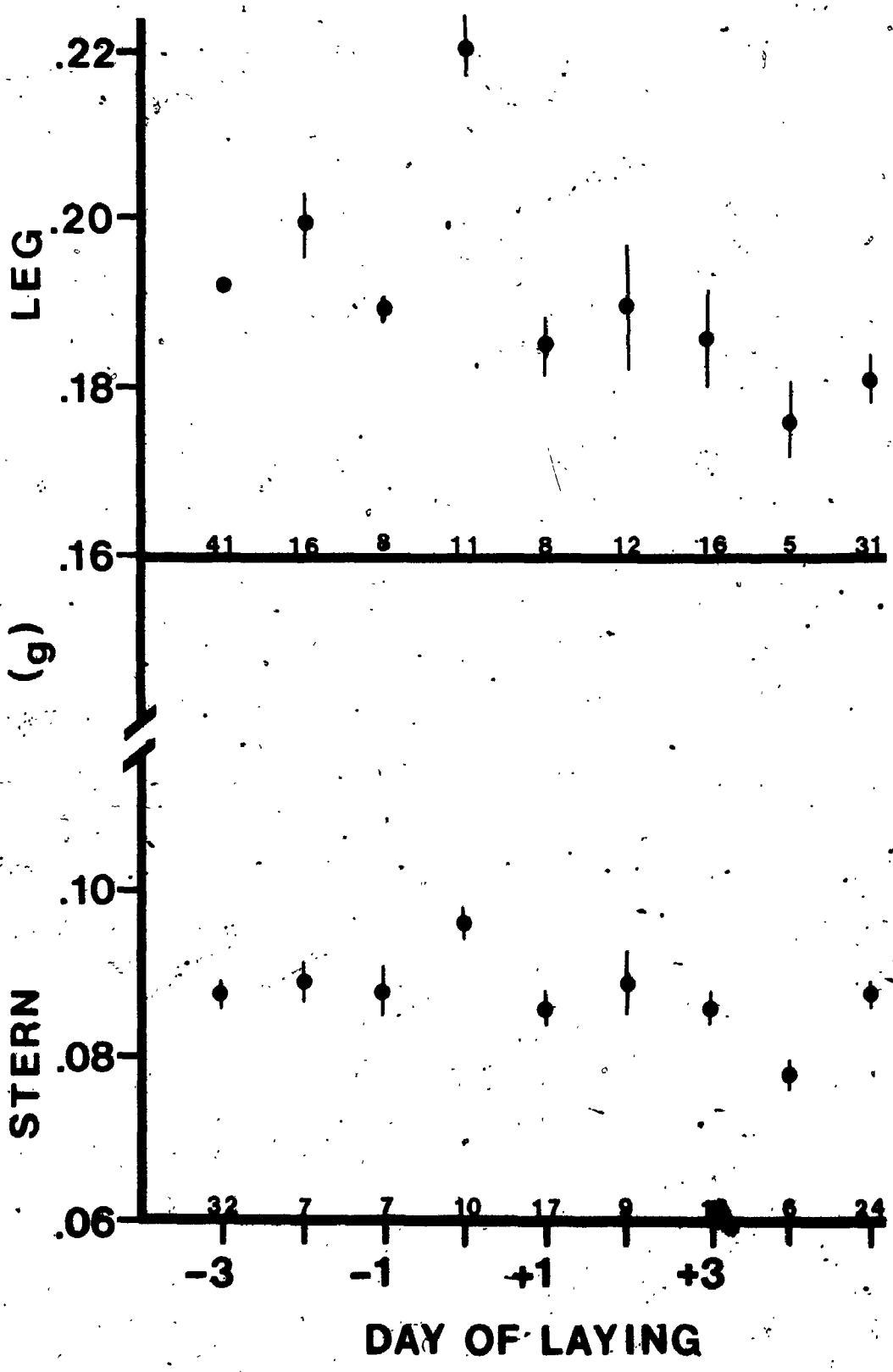
TBC declined significantly with increasing commitment to reproductive calcium (Fig. 8). For every gram of calcium committed to reproductive calcium, 0.066 g of calcium came from internal calcium reserves. The coefficient of determination ($r^2 = 0.100$) was higher than the coefficient of determination for TBP versus reproductive protein but was still quite low.

While the amount of calcium committed per clutch was discrete, insufficient sample sizes prevented comparing trends in TBC according to clutch size.

Both LEG and STERN declined significantly with increasing committment to eggshells ($r^2 = 0.038$, $b = -0.04$, $df = 115$, $p < 0.05$; $r^2 = 0.054$, $b = -0.02$, $df = 89$, $p < 0.01$, respectively). For every gram of calcium committed to eggshells, LEG and STERN declined by 0.038 g and 0.020 g, respectively. Coefficients of determination for LEG and STERN were low. Interestingly, when the first eggshells demands were to be met (DAY 0), both LEG and STERN increased drastically (Fig. 9). This departure from the regression on DAY 0 was true of both LEG and STERN but was not the result of collecting females with large body sizes on that DAY. The FMRs of females on DAY 0 were not significantly different from LAY FMRs ($t = 0.58$, $df = 9$, $p > 0.50$). When these departing points were excluded, the relationship remained significant (LEG: $r^2 = 0.036$, $b = -0.03$, $df = 105$, $p < 0.05$; STERN: $r^2 = 0.048$, $b = -0.02$, $df = 78$, $p < 0.05$).

3.1.2.3 Summary

Fig. 9. Decline in LEG and STERN versus DAY. Note the deviation on DAY 0 for both LEG and STERN. Data are in $\bar{x} \pm 1$ se; sample sizes are below respective points.


LEG (g)
.22
.20
.18
.16
41
16
8
11
8
12
16
5
31
STERN
.10
.08
.06
32
7
7
10
17
9
6
24
-3
-1
+1
+3
DAY OF LAYING

TBP declined significantly with increasing commitment to reproductive protein, but both the coefficient of detemination and slope were low. Females laying different sized clutches did not use protein reserves at different rates. At maximum commitment to reproductive protein, the average female still maintained a TBP level 145% above the starvation level.

TBF declined curvilinearly over the reproductive period. Females terminating yolk formation had TBF levels consistent with the DAY 0 to DAY +4 regression slope. Females laying 3 eggs had significantly more TBF remaining then did females laying 4 or 5 eggs. Even females laying 5 eggs still had over 250% more TBF than at the starvation level.

TBC declined significantly with increasing reproductive calcium commitment. The coefficient of determination and slope were low. Medullary bone indices also declined significantly with increasing reproductive calcium commitment. A peculiar peak in medullary bone indices on DAY 0 followed by a significant drop in weight suggested that much of the stored calcium was spent on the first eggshell.

3.2 Daily Energy Budget for Egg Laying Females

Daily energy costs for reproductive tissue development were determined for a 4 egg clutch, the modal clutch size.

As determined above, not all of the nutrients necessary for egg development were derived from endogenous nutrients. Therefore conversion efficiencies for endogenous versus exogenous nutrients had to be determined. The conversion efficiency of most nutrient reserves into egg components is unknown but it is undoubtedly greater than 77%,

the conversion efficiency of daily dietary intake into reproductive tissue (Brody 1945). The conversion efficiency of protein into egg material is 55% (Scott et al. 1976), but to use a 55% protein conversion efficiency would mean that fat would have a 99% conversion efficiency. I am assuming that protein and fat are the 2 main components of daily intake. Undoubtedly fat does not have a 99% conversion efficiency, so as a compromise, I used the 77% conversion efficiency for both fat and protein. I assume the conversion efficiency of internal nutrient reserves into reproductive tissue is 100%. The following conversion equation was used to correct for daily versus internal nutrient reserve use:

$$C = E [(R)/Pr + (1 - R)/Pd] \qquad \text{Eq. 6}$$

where C = cost to female (kJ) in producing 1 g of egg nutrient, E = energy equivalent of egg nutrient (kJ/g), R = proportion of egg nutrients supplied by female reserves, (1 - R) = proportion of egg nutrients supplied directly by the diet, Pr = efficiency for converting nutrient reserves to egg nutrients (100%) and Pd = efficiency for converting dietary nutrients to egg nutrients (77%)(Alisauskas 1982).

Knowing that 1 g of stored protein is equal to 23.86 kJ/g (Kleiber 1961), then the equation can be solved; for example, to produce 1 g of egg protein, a female would expend 23.86 (0.15 + 0.85 / 0.77) = 29.92 kJ.

Because TBF did not decline linearly with DAY, it was impossible to objectively determine how much clutch fat came from endogenous versus exogenous sources. I do know that some egg fat came from endogenous sources as the yolk/dye experiments demonstrated. Since TBF increased during the PRD period, I can probably assume that most endogenous fat was stored very briefly. If most endogenous fat was briefly stored then the 77% conversion efficiency probably is appropriate to use for all clutch fat since endogenous clutch fat was either derived that day or at most several days before. If 1 g of fat is equal to 37.67 kJ/g (Ricklefs 1974: 160), a female would expend 37.67 (1 / 0.77) = 48.92 kJ to produce 1 g of egg fat.

Daily energy costs were estimated by multiplying daily nutrient allocation by the appropriate correction factor.

Oviduct protein (Table 8) was estimated from females of known clutch size 4 and unknown clutch sized females before DAY 1. DAY -4 oviduct weight was extrapolated using PRD, DAYs -3, -2, -1 and +1. The oviduct probably does not enlarge as quickly as the difference between the PRD and DAY -4 weight suggests but no other means of determining DAY -4 oviduct weight could be devised. Oviduct weight declined after DAY -1. The destination of the lost protein is important in the energetics of egg formation.

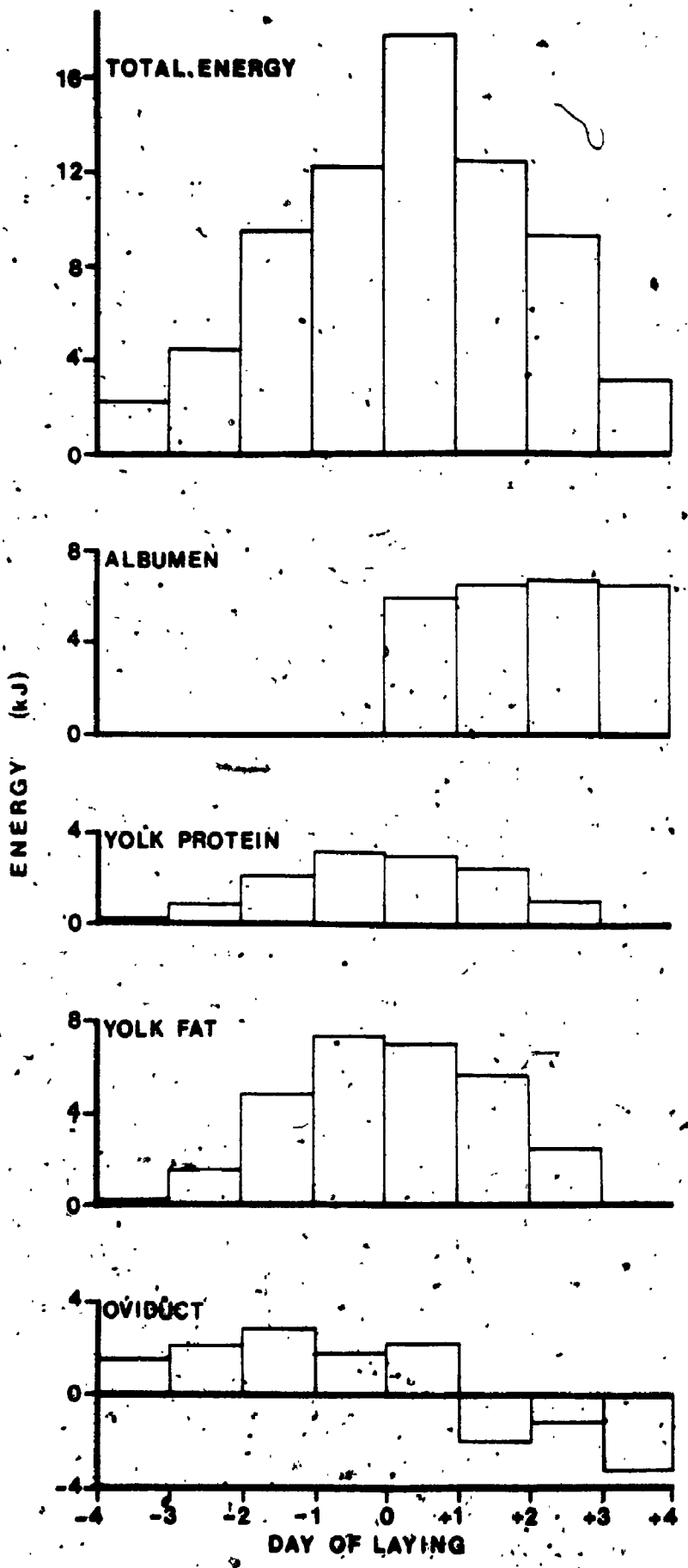
Yolk protein demand grew quickly until DAY -1 when it plateaued and then dropped between DAYs +1 and +2 (Fig. 10). Albumen protein demand was instantaneous and great, exceeding fat energy demands on DAYs 0, +1, +2 and +3, and ended abruptly. Yolk fat demand resembled the yolk protein demand curve except that the fat demand always exceeded protein demand by at least 100%.

TABLE 8. Actual and estimated mean dry oviduct weights of female house sparrows during the reproductive period.

	DAY										
Oviduct weight (g)	PRD	-4	-3	-2	-1	0	1	2	3	4	EI
Actual weight	.006	-	.120	.186	.276	-	.399	.333	.297	-	.100
Estimated weight[a]	-	.064	-	-	-	.333	-	-	-	.190	-

[a] Derived from regression of actual weights. DAY -4 weight determined using oviduct weights from PRD, DAYs -3, -2, and -1; DAY 0 weight determined using oviduct weights from DAYs -3, -2, -1 and +1; and DAY +4 weight determined using oviduct weights from DAYs +1, +2, +3 and EI. See text for definition of "PRD" and "EI".

Fig. 10. Daily energy budget of female house sparrows over the reproductive period. The budget is broken down by major egg components: albumen, yolk protein, yolk fat, and by oviduct energy costs.


TOTAL ENERGY
16
12
8
4
0
ALBUMEN
8
4
0
YOLK PROTEIN
4
0
YOLK FAT
8
4
0
OVIDUCT
4
0
-4
ENERGY (kJ)
-4 -3 -2 -1 0 +1 +2 +3 +4
DAY OF LAYING

The total energy budget curve resembled a normal curve with maximum demand occurring on DAY 0. The influence of reabsorbed oviduct protein was great on DAYs +1, +2 and +3, without which the females total energy budget would have been more sigmoid.

An average LAY female weighed approximately 29.5g. Since wet weights of the reproductive tissues were no recorded, I assumed that the reproductive tissues were 80% water (R. Alisauskus, pers. comm.) Using Aschoff and Pohl (1970) daily standard metabolic rate (SMR) equation for passerines, I estimated an average LAY female expended 37.2 kJ/day. Maximum daily costs of egg production occurred on DAY 0 at 17.92 kJ/day. Forty-eight percent of SMR was the maximum amount expended on the daily reproductive costs. The maximum daily reproductive costs of different sized clutches would not vary greatly ($<10\%$).

The total energy required to produce an average clutch of 4 eggs was 0.50 kJ. Reproductive fat made up 1.2% of the total energy while reproductive protein made up 8.8%. Reproductive protein can be subdivided into oviduct (5.4%), albumen (36.0%) and yolk protein (17.4%).

This energy budget did not include the energy necessary to acquire, convert and assimilate calcium into eggshell. I know of no approximate means of doing so and therefore the above budget should be considered as being conservative.

3.1.3 Postreproductive

3.1.3.1 Males

TABLE 9. Changes in the nutrient reserves of female house sparrows over the postreproductive period.

Variable (g)[a]	Category: Laying	p[a]	Early Incubation	p	Late Incubation/ Nestling
Body Weight	27.3 ± 0.2 (61)	NS	27.6 ± 0.3 (35)	NS	27.2 ± 0.2 (73)
Total Body Protein	7.12 ± 0.06 (46)	NS	7.18 ± 0.12 (19)	NS	7.07 ± 0.05 (41)
Breast Muscle	1.49 ± 0.02 (58)	NS	1.52 ± 0.03 (33)	NS	1.53 ± 0.02 (65)
Leg Muscle	0.58 ± 0.01 (59)	NS	0.59 ± 0.01 (33)	NS	0.59 ± 0.01 (70)
Gizzard	0.24 ± 0.01 (61)	NS	0.25 ± 0.01 (35)	NS	0.25 ± 0.00 (73)
Liver	0.36 ± 0.01 (58)	NS	0.36 ± 0.01 (35)	NS	0.34 ± 0.01 (69)
Carcass	6.55 ± 0.07 (54)	NS	6.65 ± 0.11 (29)	NS	6.73 ± 0.06 (61)
Total Body Fat	0.99 ± 0.05 (61)	NS	1.12 ± 0.06 (37)	*	1.26 ± 0.04 (73)
Leg Bone	0.193 ± 0.003 (54)	*	0.181 ± 0.004 (31)	NS	0.177 ± 0.002 (70)
Sternum	0.087 ± 0.001 (47)	NS	0.086 ± 0.003 (24)	NS	0.083 ± 0.001 (49)
Total Body Calcium	0.159 ± 0.055 (21)	NS	0.145 ± 0.010 (11)		

[a] As in Table 1

All weights remained constant between the LAY and POST periods (Tables 1,2).

3.1.3.2 Females

TBP, TBC, muscles and organs all remained constant between the LAY and LI/N periods (Table 9). Only LEG declined significantly between LAY and EI periods ($t = 2.33$, $df = 83$, $p < 0.05$).

Only TBF increased significantly between EI and LI/N ($t = -2.01$, $df = 108$, $p < 0.05$). All other indices remained constant between those periods; no LI/N TBC values were determined.

3.1.3.3 Summary

Male nutrient reserves remained constant after the LAY period. Female TBP, muscles and organs remained constant after the LAY period. TBF increased between the EI and LI/N periods. LEG decreased significantly between LAY and EI.

3.3 Food Habits

3.3.1 Intake of Animal versus Plant Matter

No samples included category 5, 100% animal, and only 14 of 563 samples contained less than 5% plant material (category 4); 13 of these were females. Because so few samples were classified as category 4, I decided to combine categories 3 and 4. This left 3 categories;

100% plant, <5% animal and >5% animal. Category 2, <5% animal, was extremely sensitive to the presence of animal material, usually only a single piece of an animal was observed when a stomach content was scored as category 2. So sensitive was category 2 to animal matter that I thought, a posteriori, that categories 1 and 2 were equivalent. I therefore combined categories 1 and 2 leaving 2 final categories; < 5% animal and >5% animal. Use of these 2 categories reveals the percent of each sex which are consuming animal matter; the index indicates nothing about the composition of the diet.

In spite of rather consistent laying phenologies between years, emergence phenologies of preferred animal food did not necessarily follow laying patterns. No data were collected on either preferred animal foods nor on the emergence phenologies of those foods. To investigate if year had an effect on animal food emergence, a 4-way R x C contingency table was executed using year, breeding stage, sex and food score. A highly significant 4-way interaction was found ($G = -10555$, $df = 4$, $p < 0.001$). Next, year was removed from the contingency table whereupon no interactions occurred in any year (Table 10). These results suggest that animal emergence phenologies were different between years, and therefore animal/plant food habits were investigated within each year.

In every year, the proportion of males and females with animal matter in their diet was dependent on the breeding stage. During 1981 and 1982; the proportion of sparrows with animal matter increased between the PRL and LAY periods while in 1983, animal intake increased between the PRD and PRL periods suggesting that preferred animal food emerged earlier in 1983 than in 1981 or 1982. Once house sparrows

TABLE 10. Results of 3-way RXC contingency tables comparing breeding stage, sex and food score by year.

Comparison		df	1981[a]	1982[a]	1983[a]
Breeding Stage	X Sex	3	14.08**	17.13***	11.83**
Breeding Stage	X Food Score	3	10.37*	22.86***	18.29***
PRD Food Score	X PRL Food Score	1	0.29	0.03	11.87***
PRL Food Score	X LAY Food Score	1	5.70*	7.30**	1.59
LAY Food Score	X POST Food Score	1	1.70	0.02	0.54
Food Score	X Sex	1	4.11*	7.56**	11.63***
PRD Female Food Score	X PRD Male Food Score	1	0.59	2.01	0.99
PRL Female Food Score	X PRL Male Food Score	1	1.57	2.82	7.12**
LAY Female Food Score	X LAY Male Food Score	1	1.72	0.65	5.78*
POST Female Food Score	X POST Male Food Score	1	3.35	2.10	1.59
Breeding Stage	X Food Score X Sex Interaction	3	-3.10	0.02	4.34
Breeding Stage	X Food Score X Sex Independence	10	31.66***	47.57***	46.09***

[a] G-scores

* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

switched from predominantly seeds to seeds and animal matter, they continued to consume both seeds and animal matter for the remaining breeding stages.

Intake of animal matter was also dependent on sex during every year. More females consumed animal matter than males did over the entire breeding season. Breeding stage by sex differences were only noted in 1983 when more females consumed animal matter during both the PRL and LAY periods.

Thus the proportion of males and females consuming animal matter reflected seasonal availability, but more females consumed animal matter throughout the breeding season.

3.3.2 Calciferous Matter Intake

Because molluscs emerge at different times from year to year and molluscs comprised much of the calcium intake by house sparrows, between year differences in mollusc emergences were tested also using a 4-way R x C contingency table. Factors included were year, breeding stage, sex and calcium intake score. A highly significant 4-way interaction was found ($G = 2491$, $df = 4$, $p < 0.001$). Removing year from the contingency table yielded no 3-way interactions (Table 11) suggesting that snails were emerging at different times of the year between years of the study. Calciferous material intake was therefore investigated by each year.

The proportion of males and females with calciferous material was dependent on the breeding stage. During 1981, the use of calciferous materials by both sexes started out relatively high and remained high

TABLE 11. Results of 3-way RXC contingency tables comparing breeding stage, sex and calcium score by year.

Comparison		df	1981[a]	1982[a]	1983[a]
Breeding Stage	X Sex	3	9.76**	28.01***	23.14***
Breeding Stage	X Calcium Score	3	8.31*	21.75***	39.24***
PRD Calcium Score	X PRL Calcium Score	1	0.07	0.00	0.98
PRL Calcium Score	X LAY Calcium Score	1	2.06	8.43**	16.02***
LAY Calcium Score	X POST Calcium Score	1	7.40**	5.02**	11.21***
Calcium Score	X Sex	1	19.98***	16.92***	29.81***
PRD Female Calcium Score	X PRD Male Calcium Score	1	2.12	0.20	5.06**
PRL Female Calcium Score	X PRL Male Calcium Score	1	12.48***	6.63**	7.51**
LAY Female Calcium Score	X LAY Male Calcium Score	1	6.29*	22.31***	10.33***
POST Female Calcium Score	X POST Male Calcium Score	1	3.79	3.36	6.65**
Breeding Stage	X Food Score X Sex interaction	3	3.14	6.52	-0.27
Breeding Stage	X Food Score X Sex independence	10	41.19***	73.17***	65.31***

[a]G-scores
* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

until the POST period when use declined significantly. During 1982 and 1983 the proportion of sparrows with calciferous materials began low, significantly increased between the PRL and LAY periods and then declined significantly between the LAY and POST periods.

The proportion of calciferous matter in the diet was also dependent on sex during every year. More females consumed calciferous material than did males throughout the breeding season. By breeding stages, in 1981 and 1982, more females consumed calciferous material during the PRL and LAY periods, while in 1983 more females consumed calciferous material during all breeding stages.

Because the proportion of females with calciferous material was always greater than males, it seems logical to conclude that the combined sexes trends were reflecting female intake.

The between and within season calcium intake by females is highly suggestive that females were responding to a calcium appetite.

4. DISCUSSION

4.1 Nutrient Reserve Dynamics

4.1.1 Prereproductive

4.1.1.1 Males

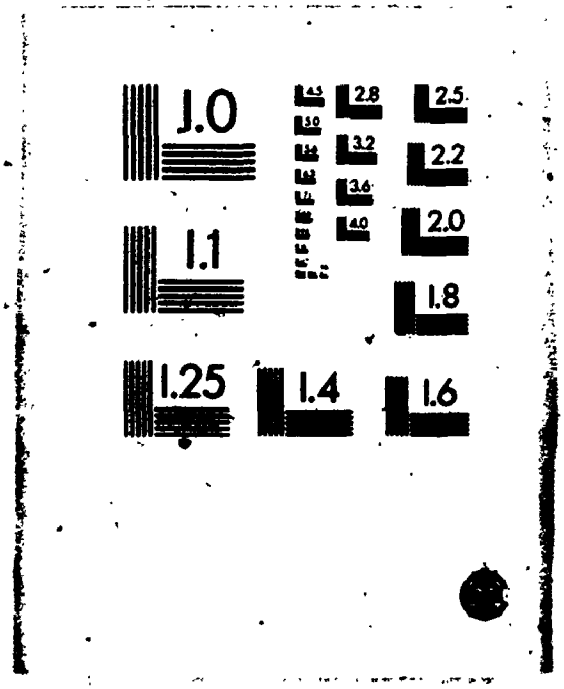
No relationship between protein, or fat, and capture date during the PRD period was noted. Schifferli (1976) also found no significant change in male LDW or TBF during the period of mate attraction and nest defense; his time period corresponds to my PRD period. Likewise, Blem (1980) was unable to demonstrate a significant monthly change in the LDW of male house sparrows between November and March. Further, Anderson (1978) and O'Connor (1973) could find no significant difference in the mean body weight of house sparrows between winter and spring; body weight reflects LDW positively (Schifferli 1976).

In the grey-backed camaroptera, TBP slowly builds during the prenesting period (Fogden and Fogden 1979), a situation different from that of the house sparrow. A comparison of the 2 species should be done cautiously though, because the grey-backed camaroptera will often breed aseasonally (Fogden and Fogden 1979) whereas the house sparrow rarely does so (see Young 1962, Naik and Mistry 1973).

Between the PRD and PRL periods, all protein and fat indices, except LM, declined in weight significantly. This result was surprising considering that no gradual protein or fat weight losses occurred during the PRD period. Possible explanations for these weight

2 2

OF / DE



losses are: 1) breeding behavior peaked during the PRL period, 2) certain amino acids, essential for sperm production, were necessary during the PRD period or 3) climatic stress eased during the PRL period.

In all 3 years males began courtship activities, e.g. singing, nest-site display, by mid-February. These activities peaked in early April when rape flights were common (April 17, 1981, April 9, 1982 but no records were available for 1983). Anecdotal evidence from Threadgold (1960) who found that the spermatogenetic cycle of house sparrows in London, Ontario peaked about mid-April confirms that rape flights were coincident with average peak spermatogenic activity. The peak spermatogenetic phase was defined by Threadgold (1960) as the period when males became capable of producing viable sperm. The PRL period, as determined using Caughley and Caughley's (1974) method, for males began on April 29, 1981, April 13, 1982 and April 26, 1983. While the trend in rape flight activity is similar to the estimated PRL periods between 1981 and 1982, the variability within each year makes any conclusions tenuous.

Fogden and Fogden (1979) speculated that protein decline during the prenesting period of the male grey-backed camaroptera may have resulted from certain amino acid deficiencies. They hypothesized that sperm production required certain amino acids which were scarce in the daily diet but which were present in protein reserves. To free those amino acids, the individual had to catabolize protein stores. While the production and maintenance of sperm by birds is considered energetically negligible (King 1973), it is nevertheless interesting to note that in 1982 and 1983, house sparrow testes weights increased

between the PRD and PRL periods ($t = -4.44$, $df = 25$, $p < 0.001$). No weights of PRD testes from 1981 were available. So as sperm production increased, TBP declined. This result supports the contention of Fogden and Fogden (1979).

Changes in male weight also could have resulted from changing climatic regimes (see Kendeigh et al. 1969). Mackowicz et al. (1970), Davis (1955) and Seel (1968) all found that house sparrows began egg laying when ambient temperatures had reached a level permitting a positive energy balance. Specifically, Mackowicz et al. (1970) found that egg laying began only after weekly temperatures increased to an average of 7-10° C; this temperature range incorporates both Davis's (1955) threshold ambient temperature (7.5° C) and essentially Seel's (1968) threshold ambient temperature range (8.3 - 10.6° C). When the week preceding the first reproductively active female for each year was examined for Mackowicz et al.'s (1970) critical temperature threshold, the 1981 findings were supportive. However, in 1981, 1982 and 1983 critical temperatures were attained 3 weeks before, 3 weeks after and 1 week after any breeding activity by females, respectively. Thus the average weekly temperature preceding first female breeding activity was not consistently related to weight changes in males. The lack of a consistent relationship supports Blem's (1980) hypothesis that house sparrows in northern areas are probably dependent on man to reduce limiting climatic pressures.

Of the 3 hypotheses proposed to explain the weight changes in males between the PRD and PRL periods, the hypothesis based on amino acid requirements was the most consistent hypothesis with the protein findings. I suspect that the decline in fat was caused by the increase

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in ambient temperature, decreasing night-length and increasing food availability (see Ankney and Scott 1980). Why TBF in males did not decline gradually over the PRD period but instead dropped abruptly between the PRD and PRL periods is not understood.

Because male birds are not known to store calcium for reproductive purposes (Simkiss 1967), stable levels of calcium during prereproduction were expected.

4.1.1.2 Females

Protein storage did not occur during the PRD period. Instead TBP, BM and GZ (BM; $t = -1.73$, $df = 33$, $p < 0.05$; GZ; $t = -2.76$, $df = 36$, $p < 0.05$) all declined significantly during the PRD period. Changes in TBP and BM should be interpreted with caution as both regressions had high variability and low slopes. In spite of the statistical changes, biological explanations for these declines are tenuous since no significant difference in either TBP or BM occurred between the PRD and PRL periods. I believe that GZ declined over the prereproductive period because of the seasonal shift from a high fiber diet (seeds) to a lower fiber diet (seeds plus insects) (Miller 1975, Drobney 1984, Ankney unpubl. data). The only protein index to increase in weight between the PRD and PRL periods was LM.

My finding, that TBP did not accumulate during the prereproductive period, agrees with the results of Pinowska (1979) and Blem (1980). Pinowska (1979) found no significant difference in LDW

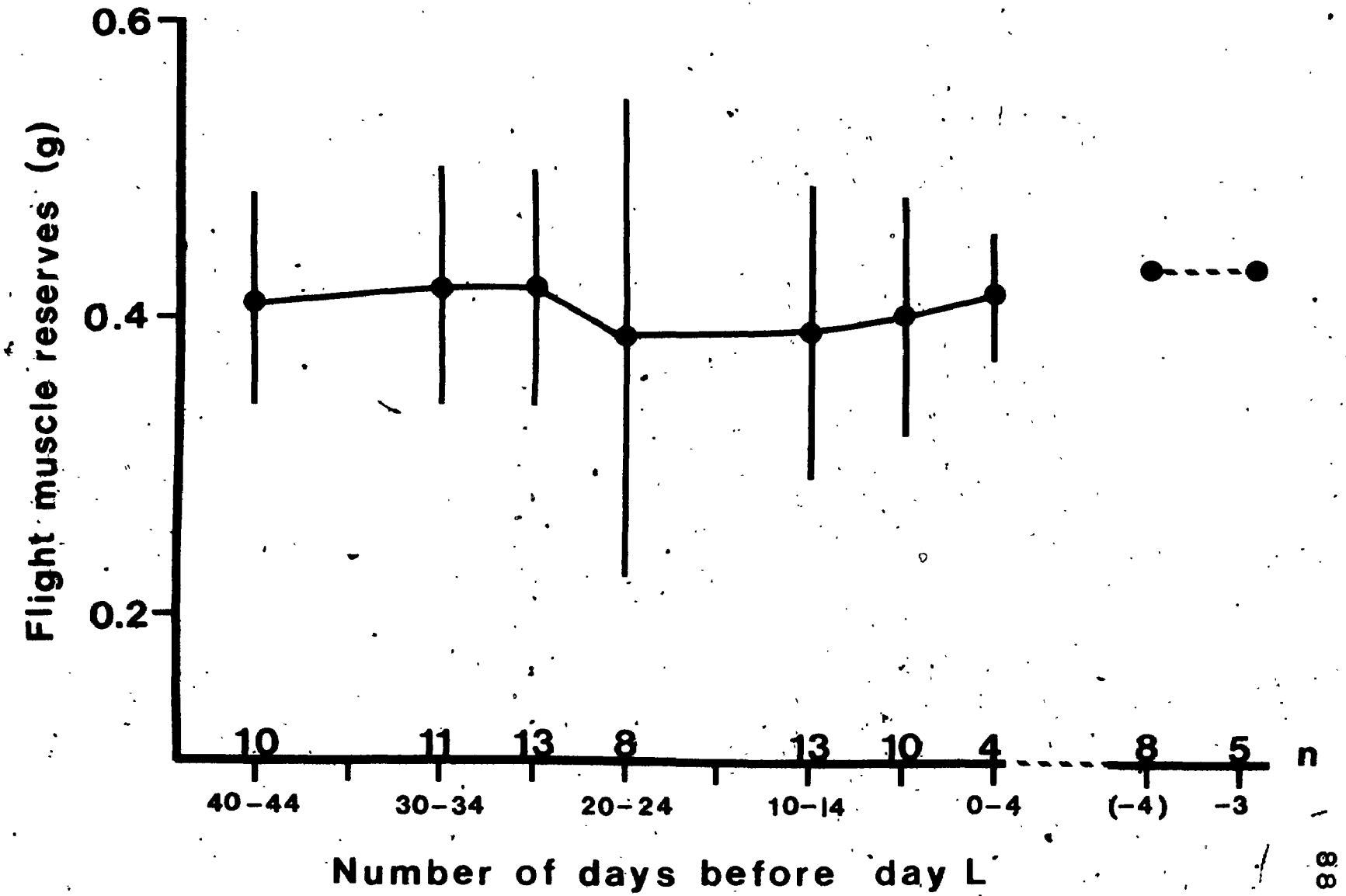
between prebreeders and breeders whereas Blem (1980) noted no significant monthly decline in LDW between November and March.

Schifferli (1976) reported a slow but steady increase in his index of protein over the prebreeding period. His contention, though, was not tested statistically and further the data (Fig. 1L) did not support this. By doubling the standard deviations presented therein, one can approximate the 95% confidence limits (Zar 1974) which reveals that there are no significant trends in the protein index. If true, Schifferli's (1976) data supports Pinowska's (1979) and Blem's (1980) data. Consequently, there is no evidence that protein increases before rapid follicular development in female house sparrows.

Only 2 temperate breeding passerines reportedly build protein reserves before breeding. The reports, for starling (Sturnus vulgaris) (P. Ward cited in Fogden and Fogden 1979) and reed warbler (Acrocephalus scirpaceus) (as in Fogden and Fogden 1979), cannot be assessed as neither report contains sufficient information to determine the timing of protein accumulation before breeding.

Examples of protein accumulation before rapid follicular development are known for tropical passerines including the yellow-vented bulbul (Pycnonotus guiavier) (Ward 1969), the red-billed quelea (Jones and Ward 1976) and the grey-backed camaroptera (Fogden and Fogden 1979). Both the yellow-vented bulbul and the grey-backed camaroptera exhibited seasonal accumulations of protein coincident with the annual flush of insects. In the red-billed quelea, protein was accumulated by the females before arrival at breeding sites; females accumulated 5 times more protein reserve than males before breeding (Jones and Ward 1976). In no report were the protein reserves

Fig. 11. Reproduction of Schifferli's (1976) Fig. 2.14, "Flight muscle reserves of the female, in relation to the start of laying in the population. Means (± 1 s.d.); sample sizes are shown. Note: day 0: median date of laying in the population. day (-4): females collected shortly before starting to form yolks. day -3: females collected three days before ovulating the first egg; the means of day -3 and day (-4) do not differ significantly."


0.6
0.4
0.2
Flight muscle reserves (g)
10
11
13
8
13
10
4
8
5
n
40-44
30-34
20-24
10-14
0-4
(-4)
-3
Number of days before day L

of prebreeders directly compared with the protein reserves of prelayers or layers.

The lack of either a decline in TBF during the PRD period or between the PRD and PRL periods differs from Schifferli (1976) who found that TBF declined significantly between the winter and PRD period and then increased significantly, several days, before the PRL period. However, there was no significant difference in TBF between Schifferli's (1976) winter and PRL weights. He argued that TBF was accumulated just before rapid follicular development because had females slowly accumulated TBF, the transportation costs involved in carrying the stored fat would have negated the benefits of storage. Pinowska (1979) did not discuss the differences in TBF between prebreeders and breeders although she did present data for those periods. In 6 of 7 reported breeding cycles, TBF declined from prebreeding to breeding. Admittedly her measures of variance (although she did not state exactly what these represented, sd or se) were quite large.

The red-billed quelea female did not accumulate TBF before rapid follicular development began (Jones and Ward 1976).

During the prereproductive period, the incidence of animal food in the diet did not differ between the sexes. Why the mean TBP and TBF of males declined while the mean TBP and TBF of females remained constant when the same proportion of individuals was consuming animal matter is not understood.

Unlike the dynamics of protein and fat during prereproduction, female TBC did increase between the WINTER and PRL periods. Although this finding corresponds to the long term calcium increases noted in

young chickens (Classen and Scott 1982), Ojanen et al. (1975) observed that house sparrow TBC remained constant over the year. Comparisons of my findings with Ojanen et al. (1975) are difficult because 1) they provided no information on the sex of the specimens their monthly TBC evaluations were based on, and 2) any changes in TBC resulting from reproductive causes could have been masked by their inclusion of individuals from various reproductive stages.

Only in 1983 did more PRD females than PRD males consume calciferous material. Thus, usually the incidence of calciferous material in the diet was equivalent between the sexes during the prereproductive period. The intake of calciferous materials, by both sexes combined, did not differ between the PRD and PRL periods in any year. Since the incidence of calciferous material intake was constant over the prereproductive period, the only means of accumulating calcium over the long term had to have occurred through physiological changes in the females. In domestic fowl, calcium can be accumulated on a constant diet by increasing calcium absorption across the gut and/or decreasing calcium excretion (Hurwitz 1978).

Because medullary bone is found only in female birds immediately before egg laying (Hurwitz 1978), the long term calcium increases indicate that cortical bone was being stored first. Medullary bone indices, LEG and STERN, increased once the female began rapid follicular development.

Murton and Westwood (1977:191) appropriately stated in reference to the nutrient requirements of egg production that, "it does seem certain critical nutrient requirements for the egg may be accumulated

and stored in advance of egg formation but the capacity to do this is probably limited."

Ward (1969), Fogden and Fogden (1979), Jones and Ward (1976) and Pinowska (1979) all hypothesized that the initiation of breeding in female passerines was cued proximately by the accumulation of sufficient reserves, especially protein. Their hypothesis was supported by the more general observation that by providing supplemental food to prebreeding passerines, the subsequent laying date could be advanced (see Klomp 1970). Examples of altered laying dates include Yom-Tov (1974) who advanced the laying date of the crow (Corvus corone) by 5 days while Kallander (1974) advanced the laying date of the great tit (Parus major) between 3 and 7 days, depending on the age of the female. The hypothesis that nutrient reserves were accumulated to a certain threshold level before the initiation of breeding was not upheld by the house sparrow population I studied. Neither TBP nor TBF increased during the PRD period nor between the PRD and PRL periods. Although TBC did accumulate over the prereproductive period, the poor relationship between TBC and calcium requirements during reproduction (see Section 4.1.2.2) suggests that stored calcium had little to do with breeding initiation.

Possibly the presence of essential amino acids, instead of TBP, cued females to begin breeding (Fogden and Fogden 1979). While this hypothesis is possible I had no means of testing it. Circumstantial evidence from the brown-headed cowbird, which can on average produce 40 eggs per female per season (Scott and Ankney 1980), suggests that daily diet is sufficient in all essential amino acids. If daily diet was not sufficient then how could a brown-headed cowbird continue to

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lay so many eggs for such an extended time period without exhausting her stores of essential amino acids?

Since neither protein, fat nor calcium reserves appear responsible for proximately cueing female house sparrows to breed then what was? As discussed in Section 4.1.1.1, average weekly ambient temperature did not consistently correlate with first female breeding activity, nor would I have expected it. First breeding females are those that nest in heated buildings, not those nesting in non-heated buildings or in trees (Pinowska 1979, pers. observ.). House sparrows, especially early breeders, seem independent of ambient temperatures because they rely on man to alter both energy balances and food supplies (Lowther 1977, Murphy 1978). Since neither protein nor fat were accumulated before the PRL period, the food supplies of man apparently do not result in early breeding females attaining a minimum nutrient reserve threshold before later breeding females. Instead, I agree with Schluter (1984) that food reserves do not, per se, cue female passerines to initiate breeding but instead cue the females to future food resource levels. It is based on these future food resource levels that the females 'decide' when to initiate egg production (see Lack 1947, 1948).

4.1.2 Reproductive

4.1.2.1 Males

No index of protein, fat or calcium varied over the reproductive period which agrees with Schifferli's (1976) findings and Fogden and Fogden's (1979) findings on reed warblers.

My findings confirm that males make an ideal control against which to compare female nutrient reserve trends, because nutrient and energy costs during the reproductive period were constant for males.

More male house sparrows consumed animal matter during the reproductive period, probably reflecting the greater abundance of insects and the scarcity of seeds (Wiens and Johnston 1972) rather than a protein appetite.

Consumption of snail shell and eggshell by males was constant over the breeding season. I agree with Ankney and Scott's (1980) hypothesis that intake of calciferous material by males probably results more from incidental consumption than a specific calcium appetite. Schifferli (1976) did not find evidence of snail shell consumption by males but his sample size was small (n = 5).

The only reported case of a male calcium appetite is in band-tailed pigeons where the male aids in feeding the young "pigeon milk", a substance requiring large amounts of calcium (March and Sadleir 1975). Male band-tailed pigeons were found to significantly increase their intake of calciferous material during the nestling stage but never was there evidence of calcium storage (March and Sadleir 1975).

4.1.2.2 Females

While TBP declined over the reproductive period, the contribution of TBP to the gross protein demands of clutch formation was very small. Considering that 96% of the variation in TBP over the reproductive period was unexplained in conjunction with the small TBP decline, I believe that individual females must have been meeting reproductive protein demands exogenously. This conclusion agrees with Pinowska (1979) who found that LDW did not decline over the reproductive period. She did however observe a seasonal decline in LDW which she attributed to repeated egg production and/or costs associated with caring for young.

Schifferli (1976) noted a 57% decline in his index of flight muscle protein over the reproductive period. This reduction (based on a clutch size of 4) was believed to have been an important contribution to the protein requirements of egg formation, both in terms of meeting total protein costs and in terms of specific amino acid needs. The importance of the flight muscle protein in meeting total egg protein demands is questioned as Schifferli's (1976) overall reduction in flight muscle protein index amounted to 0.17 g over 7 days. While investigating overnight energy requirements of house sparrows captured during the fall and spring, Jones (1980) found that BM declined by an average 0.14 g nightly of which 0.04 g were glycogen. Admittedly comparing the decline in BM observed by Jones (1980) against the decline in BM observed by Schifferli (1976) is not exactly equivalent because she collected her birds when overnight requirements were slightly higher (fall and spring), not during the breeding season. However if house sparrows are using 0.10 g of protein

daily then the purported importance of 0.17 g of LDW over 7 days in meeting egg protein demands is questionable.

The only other extensively studied temperate passerine is the brown-headed cowbird which does not rely on protein reserves to build eggs (Ankney and Scott 1980).

The reed warbler (Fogden and Fogden 1979) loses protein during egg laying in a manner comparable to that of the grey-backed camaroptera (see below), although the pattern of protein loss on DAYS -1 to +3 is unknown. Fogden and Fogden (1979) extrapolated the pattern in the grey-backed camaroptera to the reed warbler and stated that protein loss did not appreciably contribute towards total egg protein needs but may have been important for providing specific amino acids not common in the diet. Anecdotal evidence from the blue tit (Parus major) (C. M. Perrins cited in Schifferli 1976) suggests that no protein is lost over egg laying. The rate and extent of protein loss by this species is unknown.

Of the tropical species investigated, all lost protein over egg laying: chestnut-breasted finch (Lonchura castaneothorax), (C. M. Perrins cited in Schifferli 1976), red-billed quelea (Jones and Ward 1976) and grey-backed camaroptera (Fogden and Fogden 1979). As explained in Section 1, the protein loss in the red-billed quelea is regulated by exogenous protein intake immediately before and during laying. Thus the size of the protein reserve immediately before and during egg production in combination with exogenous protein intake during the same time period was believed to proximately control clutch size (Jones and Ward 1976). Daily intake of protein was important in controlling the clutch size of the red-billed quelea too as evidenced

by the extremely high rate of follicular atresia, i.e. when a female was unable to offset the decline in protein reserves by ingesting protein concurrently, she aborted a follicle(s). As many as 75% of red-billed quelea females starting 4 follicles lose 1 follicle to atresia. In the house sparrow, atresia occurs in less than 2% of females (Schifferli 1976, this study).

In the grey-backed camaroptera (Fogden and Fogden 1979), the protein reserves lose 0.06 g over 7 days which accounts for 15% of the protein in a 3 egg clutch. Note the similarity in percent protein contribution towards the protein requirements of the clutch between the grey-backed camaroptera and the house sparrow in this study. As in reed warblers, the 15% loss may have represented tissue catabolism to meet specific amino acid requirements which were probably uncommon in exogenous protein sources.

Both Schifferli (1976) and I investigated the use of protein reserves according to clutch size. Neither of us found that the use of protein differed among females laying different numbers of eggs.

I found that TBP was not related to clutch size when a female had finished forming her eggs. The slope of terminal TBP versus clutch size was not significantly different from 0. In no reported case has there been evidence that egg laying was terminated by house sparrows because of insufficient protein reserves available or because of the risk of endangering the immediate well-being of the female.

After a female red-billed quelea had finished egg laying, flight muscle protein was not related to clutch size (Jones and Ward 1976). Jones and Ward (1976) interpreted this relationship as demonstrating that a minimum protein level stopped egg formation. My findings cannot

be interpreted similarly because TBP loss over the reproductive period was minor compared to the loss in red-billed queleas (depending on the subspecies monitored, either a 44% or 61% flight muscle loss, Jones and Ward 1976). Females also ceased egg formation while they still exceeded the starvation level of protein by 28% (Jones and Ward 1976).

Neither Schifferli (1976) nor I found that the flight muscle protein index or LDW, respectively; approached the level of starvation when egg laying was terminated. Again, Pinowska (1979) found no change in LDW over laying.

Although the proportion of females with animal food in their guts increased from roughly 20% during the PRD period to roughly 60% during the LAY period (unpubl. data), there was no significant difference between the proportion of males and females with animal food in their diet during the LAY period. Realizing the low use of endogenous protein for reproductive tissues, I would have predicted, a posteriori, that more LAY females would have consumed animal matter than males. My dietary analysis was not designed to test these differences. Pinowska (1975) determined the percent of animal matter in the crop and "stomach" contents of egg laying females to be 59%. Considering that Pinowska's (1975) technique, as was mine, was biased against finding insects (Swanson and Bartonek 1970), then Pinowska's 59% estimate should be considered conservative. Whether an intake of 60% insects meets all the protein needs for house sparrow reproduction on a daily basis is unknown.

Explanations for protein decline over the reproductive period are: 1) increased protein demands of egg formation (Jones and Ward 1976, Schifferli 1976), 2) inadequate intake of specific amino acids

(Jones and Ward 1976, Schifferli 1976, Fogden and Fogden 1979), 3) reduction in feeding time to avoid breaking the developing eggshell (Fogden and Fogden 1979) and 4) to allow for more time to search for calciferous materials (Fogden 1972, Jones and Ward 1976)

The total reproductive protein requirements of house sparrows are greater than the total reproductive fat requirements (Fig. 10), yet the decline in TBP is small compared to the decline in TBF. As discussed above, the high individual varability in use of TBP in combination with the overall low use suggests that the total reproductive protein needs can be met exogenously. The remaining TBP loss, 15%, may represent tissue catabolism to provide essential amino acids uncommon in exogenous protein sources (see Section 4.1.1.2). Research into this possibility is needed.

Fogden and Fogden (1979) were unable to collect any grey-backed camaroptera females between DAY -1 and DAY +3 which they attributed to the altered behavior of females developing eggshells. Supposedly, females during egg laying have to remain sedentary during the initial period of eggshell formation to avoid damaging the eggshell. Schifferli (1976) investigated Fogden and Fogden's (1979) hypothesis by examining eggshells of captured house sparrows for cracks (Schifferli received a manuscript of Fogden and Fogden's 1979 paper before he completed his Ph.D. research). If developing eggshells were more prone to breakage earlier in the day then, because of handling during the capture, those eggshells should have had more cracks. Schifferli (1976) found that the eggshell was not vulnerable to breakage until after sunset when the female had finished feeding. This finding does not prove Fogden and Fogden's (1979) contention incorrect

though because eggshell development rates are species-specific, e.g. blue tits have a completely developed eggshell by roosting time (Perrins 1979) whereas the house sparrow eggshell continues to develop until 2 h before laying at sunrise (Schifferli 1976). Also, in the brown-headed cowbird, which has a hard shelled egg by roosting time (C. D. Ankney, pers. comm.), repeated handling of live-trapped birds caught late in the day did not result in damaged eggshells (see Scott and Ankney 1983). Further, since individual female brown-headed cowbirds repeatedly came back to baited traps during egg laying, then eggshell breakage does not appear to be a factor modifying feeding behavior. Perrins (1979) also commented that when female blue tits were laying eggs, females went to roost with their crops full of a variety of food and calciferous materials. This anecdotal evidence again suggests that egg laying females do not lose the entire day of feeding for fear of damaging the developing eggshell. It seems unlikely that female passerines use TBP to avoid breaking the developing eggshell, especially for the house sparrow.

A gradual reduction in TBP because of restricted foraging time seems unlikely based on the evidence from estimates of daily energy expenditure in the willow flycatcher; nest building females spend, on average, 51.8% of their daytime perched, 2.3% flying and 45.9% at their nest (Ettinger and King 1980). Apparently the willow flycatcher female has ample time during the nest construction phase (includes egg laying) to meet all foraging requirements. Thus the willow flycatcher example was believed to support Wilson's hypothetical "principle of stringency" which suggests, "... that time and energy budgets have evolved to accomodate episodes of extra energy or time demand such as

increased expenditure in foraging when seasonal food supplies are poor, when young are being fed, or when unpredictable events such as cold weather, rain, or snow cover reduce the food supply." (cited in Ettinger and King 1980:543). If the house sparrow uses the principle of stringency, the increased exogenous nutrient needs of egg laying are probably not causing endogenous reserve losses.

Schifferli (1976), Pinowska (1979) and I all found TBF to decline between DAY -3 and DAY +3, but the patterns of decline were different. Schifferli (1976) found TBF to decline continuously from DAY -3 through DAY +4 (4 egg clutch); the loss amounting to a 65% decline in TBF. Pinowska (1979) found TBF to increase between DAY -4 and DAY -1 by approximately 5% and then between DAY -1 and DAY +3, TBF fell linearly by 27%. I found TBF increased between DAY -3 and DAY 0 by 11% and then declined between DAY 0 and DAY +4 by 50%. The most striking difference between Schifferli's (1976) pattern, and Pinowska's (1979) and mine, is that Pinowska (1979) and I found TBF to increase when almost 50% of the clutch fat was deposited (based on the follicular development of the population I studied). The subsequent decline in TBF occurred when not only the remaining 50% of clutch fat was deposited but also when all albumen and shell materials were being deposited (DAY 0 through DAY +3).

Not all temperate passerines lose TBF over the reproductive period. C. M. Perrins (cited in Schifferli 1976) said that the blue tit did not lose TBF over the egg laying period. However over the reproductive period, TBF in the blue tit is expected to be stable because the blue tit's clutch may sometimes exceed its body weight by 50%. Attempting to store and use TBF for clutch fat demands would be

pointless in a bird of such small body size producing so much reproductive material. Meeting the extreme reproductive demands by the blue tit requires the strategy of courtship feeding throughout the breeding season (Perrins 1979). The brown-headed cowbird does not lose TBF during the reproductive period either (Ankney and Scott 1980). As in the blue tit, the brown-headed cowbird produces so much reproductive material that storing and utilizing TBF would be futile.

The curvilinear fat decline was usually observed in tropical species too. Fogden and Fogden (1979) found the grey-backed camaroptera to increase TBF by approximately 86% while 54% of clutch fat was being deposited (DAY -4 to DAY -1). Between DAY -1 and DAY +3, TBF fell 51% but the exact shape of the decline is unknown since no females were captured between these dates. The red-billed quelea arrived at the breeding colony with approximately 1.2 g of TBF which increased 13% by DAY -1 whereupon TBF fell 39% by DAY +2 (Jones and Ward 1976). When allocating fat to the clutch, some red-billed queleas depleted TBF reserves so far that they starved to death that night (Jones and Ward 1976). C. M. Perrins (cited in Schifferli 1976) said that the chestnut-breasted finch did not lose TBF over the reproductive period; no data were provided.

In addition to the curvilinear loss of TBF over the reproductive period, the maximum loss of TBF usually exceeded the total amount of fat in a clutch of 4 eggs. Schifferli (1976) found TBF loss exceeded clutch fat requirements by 75%. Pinowska (1979) noted that the loss of TBF was short of egg fat needs by 52% (using Schifferli's (1976) fat content of 0.52 g/ 4 eggs). Yet later in the same paper, Pinowska (1979) stated that with an increase in clutch size of 1 egg, the

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average female loaded 0.833 g TBF; this amount of fat exceeds the total needs of the clutch by 60%. I cannot explain this discrepency. I found that TBF loss exceeded clutch fat requirements by 46%.

Fogden and Fogden (1979) found TBF loss in the grey-backed camaroptera exceeded the fat requirements of the clutch by approximately 100% (3 egg clutch). TBF loss in the red-billed quelea exceeded the fat requirements of the clutch by 30% (4 egg clutch, Jones and Ward 1976).

The similarity of Pinowska's (1979), Fogden and Fogden's (1979), Jones and Ward (1976) and my results suggest that the observed curvilinear pattern of TBF decline over the reproductive period is more common than the linear decline exhibited by the house sparrow population monitored by Schifferli (1976). If true, then the observed TBF increase while approximately 50% of clutch fat was being deposited in conjunction with the excessive TBF loss over the reproductive period indicates that TBF reserves are not accumulated to provide fat for just developing follicles.

To determine if females laying different numbers of eggs were either differentially storing fat before egg laying or using fat at a rate dependent on clutch size, Schifferli (1976) compared the average residuals of his TBF versus DAY regression with females of known clutch size against one another. Females laying 3 egg clutches were found to have significantly lower residuals than did either females laying 4 or 5 egg clutches. Females laying 4 egg clutches did not differ from females laying 5 egg clutches. Thus females laying 3 eggs either stored less fat to begin with or they used that fat more quickly than did either females laying 4 or 5 eggs (Schifferli 1976).

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In a comparable analysis to Schifferli's (1976), I found females laying different numbers of eggs did not use TBF at different rates. Because of the curvilinear fat decline, I cannot remark on initial TBF stores but after DAY 0, clutch size had no effect on TBF use. Pinowska (1979) examined DAY 0 to the appropriate DAY TBF changes in females laying 3, 4, 5 and 6 egg clutches. She found that only for females laying 6 egg clutches did TBF decline significantly. While this information does not directly correspond to Schifferli's (1976) or my analysis, Pinowska (1979) did show that upon terminating a clutch, albeit no variation estimates were given, females laying 3 eggs had lower TBF weights than females laying 4, 5 or 6 egg clutches. These findings support Schifferli's (1976) analysis that 3 egg females use TBF more quickly than 4, 5 or 6 egg females. My findings show that females laying 3 eggs finish yolk formation with significantly more TBF than either females laying 4 or 5 eggs. No difference in TBF upon finishing yolk formation was found between females laying 4 or 5 eggs. The negative slope through the TBF weights after the formation of 3, 4 or 5 yolks suggested that the females I examined were terminating egg production for reasons other than the depletion of TBF.

The red-billed quelea used fat during egg laying at a rate dependent on clutch size (Jones and Ward 1976).

Further, Schifferli (1976) and I found that females finishing egg formation had enough TBF to build 1 more egg without endangering themselves. Thus, TBF cannot be determining the clutch size of house sparrows.

Upon finishing egg production, female red-billed queleas producing different numbers of eggs showed no difference in remaining TBF (Jones and Ward 1976).

Hypotheses suggested to explain the TBF decline are: 1) to meet clutch fat requirements (Schifferli 1976, Pinowska 1979), 2) to reduce the female's foraging time during egg laying to avoid breaking the developing eggshell (Fogden and Fogden 1979), 3) to allow the female to spend more time searching for high-protein food (Jones and Ward 1976) and 4) to allow the female to spend more time searching for calciferous materials (Schifferli 1976, Fogden and Fogden 1979).

Both hypotheses 1 and 2 have already been shown not to explain adequately the changes in TBF for the house sparrow.

Reproductively active female passerines, including the house sparrow, have often been found to alter their diet to include both more high-protein foods and/or calciferous materials (Pinowska 1975, Jones and Ward 1976, Schifferli 1976). Quantification of the impact of altered food habits on total foraging time during the reproductive period revealed that mockingbirds (Biedenweg 1983) and willow flycatchers (Ettinger and King 1980) do not vary total foraging time during the reproductive period from foraging time during the prereproductive period. If house sparrows are similar in their time energy budgets to either mockingbirds or willow flycatchers, then switching from granivory to omnivory would decrease the amount of time available for intake of seeds. A reduction in seed intake would be deletarious to fat reserves because it is from seeds that fats can be readily built (Ricklefs 1974). I cannot assess if the increased intake of insects compensated for the reduced intake of seeds.

Of the 4 hypotheses, the switch in foraging patterns to include more high-protein foods and more calciferous materials best explains the TBF decline.

Concerning the observation that females tend not to occur below the TBF versus reproductive fat regression line after becoming reproductively active, 2 alternative explanations exist: either females with low TBF quit breeding early or they continued breeding but increased their TBF levels.

The former explanation is not supported by the rarity of large (>2.5 mg) atretics (<1%, this study). If females had quit breeding after they had developed some yolky preovulatory follicles, then these large follicles should have been recognized as large atretics. Admittedly, I found atretics difficult to recognize (see Kern 1972), but Schifferli (1976) also mentioned that atretics were rare (<2%). Schifferli (1976) believed the lack of atretics proved that once follicles began to enlarge in a female, she would lay all eggs "planned". Although all planned eggs were eventually laid, Schifferli (1976) noted that the eggs were not always laid daily. He found that 11% of the females he monitored in 1973 interrupted daily laying during cold spells. Interrupted laying because of weather in house sparrows has also been reported by Seel (1968). In laying white-crowned sparrows (Zonotrichia leucophrys), Kern (1972) found that follicular atresia of yolky follicles was uncommon.

The other alternative, that females continued to breed but increased TBF, has 2 possible explanations. 1) Females with low TBF accumulated TBF quickly. The ability of passerines to deposit fat quickly during hyperphagia has been demonstrated often (Odum et al.

1964, EL-Wailly 1966, Kendeigh et al. 1977). Further, both Pinowska (1979) and I have shown (see above) that house sparrows can accumulate fat while building eggs. A tactic that females with low TBF could have used to accumulate fat, other than hyperphagia, would be to alter the follicular development rate. By slowing down the development rate of a follicle(s), a female may have the ability to divert fat which would have gone into those follicles to reserves. The yolk/dye experiments which demonstrated variability in follicular development within clutches supports this. 2) Low TBF females beginning rapid follicular development could have halted follicular development until reserves were accumulated. Although experimental proof of this is not known, others (Warren and Scott 1935, Grau 1982) have alluded to this possibility. Since female house sparrows can interrupt egg laying in response to inclement weather (Schifferli 1976, Seel 1968), then it is not unreasonable for females to interrupt rapid follicular development because of low TBF levels.

Of the 2 alternatives, I believe the data support the second, that females continued breeding while accumulating TBF.

Just as the interpretation of the TBP decline over the reproductive period was difficult to explain, so too is the interpretation of TBC. A significant decline in TBC over the reproductive period was noted, yet the variability in calcium use was very high (90% unexplained) while the average calcium use was very low; only 6.6% of the calcium needs for a clutch of 4 was drawn from reserves. Clearly, the female meets her needs exogenously. Schifferli (1976) also found that his index of TBC (lean dry weight of the entire skeleton) did not change over the reproductive period. He found that

approximately 0.20 g of skeleton were stored before follicular development (n = 4). If skeleton is mostly calcium carbonate, then approximately 0.08 g of calcium was stored. I found that 0.04 g of calcium was stored between the WINTER and PRL period. If the calcium dynamics for the chicken are an appropriate model for the house sparrow, then between 0.07 and 0.14 g of calcium (4 egg clutch) should come from the skeleton (Comar and Driggers 1949, Mueller et al. 1964). Accordingly, it seems that house sparrow females may store enough calcium to produce 1 eggshell.

LEG and STERN also declined over the reproductive period but these indices also had high variability and low average use. Both LEG and STERN increased between the PRL and LAY period suggesting storage of medullary bone. If this increase was only medullary bone rather than cortical bone, then both LEG and STERN should have remained constant until after the last eggshell was formed, and then dropped (see Simkiss 1967). This did not happen in either LEG or STERN. Both indices declined gradually from DAY -3 to +4 with the exception of DAY 0. Although both LEG and STERN were not different in weight between DAY -3 and -1, there was a sharp increase in weight on DAY 0 (Fig. 9). This peak is probably not the result of marrow fat fluctuations (see Ojanen et al. 1975). Both Raveling et al. (1978) and C. D. Ankney (cited in Hutchinson and Owen 1984) stated that marrow fat declines or remains constant, respectively, in geese over the egg laying period. Such peaks have not been reported for domestic fowl (Simkiss 1967, Hurwitz 1978) where medullary bone slowly accumulates before egg laying (up to 2 weeks)(Simkiss 1967). However, the difference between the PRD LEG and STERN, and DAY 0 LEG and STERN is 22 and 14%,

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respectively. In the chicken, 22% of the femur and 15% of the sternum is comprised of medullary bone at the beginning of laying (Simkiss 1967). The similarity in these values leads me to believe that the DAY 0 peak does represent medullary bone formation. Why the house sparrow waits till DAY 0 to form so much medullary bone is not understood.

The significant drop between DAY 0 and DAY +1 in both indices cannot represent medullary bone loss, if medullary bone is used for the same function as in domestic fowl. In domestic fowl, medullary bone is the only source of calcium labile enough, on the 24 h basis, to meet the demands of the shell gland (Simkiss 1967). Therefore, fowl cannot produce eggshells without medullary bone. Since medullary bone in fowl remains constant in weight throughout the egg laying period, when it is weighed at the same time daily (Simkiss 1967), the fluctuation in LEC and STERN after DAY 0 could only have been caused by cortical bone loss. Thus, the average female appears to use the calcium stored in cortical bone for the first egg, and thereafter relies on exogenous sources.

Whether female passerines can consume sufficient calcium daily to meet eggshell requirements is unknown, but the frequency of calciferous material in the gut contents of breeding passerines suggests that exogenous calcium is important in meeting eggshell needs: house sparrow, snail shell (Kalmbach 1940), snail shell, mortar and eggshell (Summers-Smith 1963), snail shell (Schifferli 1976); red crossbill, bones (Payne 1972); barn swallow, eggshell (Burkli 1974); blue tit, snail shell (C. M. Perrins cited in Schifferli 1976); red-billed quelea, calciferous grit (Jones 1976); and brown-headed cowbird, snail shell (Ankney and Scott 1980). Evidence from fowl

indicates that diurnal intake of calcium is insufficient to meet the daily calcium demands of reproduction (Simkiss 1967, Hurwitz 1978). But the applicability of this model is questioned because the timing of eggshell formation is species specific. If the calcium dynamics of the chicken are appropriate for passerines, then of the passerines studied, I would have predicted that at least the brown-headed cowbird would store calcium. Calcium storage does not occur in the brown-headed cowbird (Ankney and Scott (1980). They concluded that brown-headed cowbirds require medullary bone to meet the logistical needs of eggshell production but that clutch formation is not terminated because of a calcium deficiency.

The house sparrow does store calcium both in cortical and medullary bone before and during rapid follicular development. The necessity of both reserves is unquestioned for if daily intake was sufficient, then why store calcium? Calcium reserves are most likely important in rapidly meeting the calcium needs of developing eggshells and in meeting nocturnal needs. Exogenous calcium probably meets diurnal eggshell needs and helps offset nocturnal calcium deficits.

4.2 Daily Energy Budget of Egg Laying Females

To the best of my knowledge, this is the only daily energy budget constructed for egg laying passerines. Similar budgets have been constructed for an anseriform (Drobney 1980), a gruiform (Alisauskas 1982) and a sphenisciform (Grau 1982).

Of all the subcomponent budgets the energy budget of the oviduct was, to me, the most surprising. The negative budget during DAYs +1 to

+3 suggests that the oviduct acts as a storage organ which both Murton and Westwood (1977) and L. A. Astheimer (pers. comm.) have suggested. According to Murton and Westwood (1977:97) the, "oviduct (especially the magnum) becomes charged with albumen granules during hypertrophy." while L. A. Astheimer states that, "the gross anatomical studies suggest such storage (albumen storage) occurs in the oviduct...". This anecdotal evidence differs from Schifferli's (1976) hypothesis that the oviduct acts strictly as a device to lay down albumen and shell, and to expel the egg. He also thought that after egg laying the oviduct is resorbed quickly to reduce body weight and not to offset any negative protein balance caused by egg production. I believe that after egg laying, the oviduct is quickly resorbed to offset any negative protein balance caused by egg production and to reduce body weight. Reduction in body weight, though, cannot be an important function because the oviduct does not weigh much (5% of total body fresh weight) and there is little need to reduce transportation costs when the female will not be flying much anyway (she begins incubating after laying).

Both yolk fat and yolk protein budgets resembled normal curves, both peaking on DAY -1, with yolk fat demanding more energy per day then yolk protein.

The most energy demanding egg component on a per day basis was albumen. Albumen was the only egg component in which the energy demand began and finished abruptly.

The total energy budget peaked on DAY 0 coincident with first albumen and calcium depositon but after follicular fat and follicular protein had peaked. The drop in TBF between DAY 0 and DAY 1 suggests

that females accumulated fat to meet the energy requirements of DAY 0. Thus by storing TBF, the female could devote much of her limited foraging time to meeting the abrupt and great demands of albumen and eggshell production.

Peak total energy equaled 50% of SMR which is intermediate in the range calculated by King (1973) for altricial Passeriformes (45 - 58%). As pointed out earlier, all estimates of reproductive tissue costs should be considered conservative because they do not include eggshell production costs.

Even though reproduction adds at most a 50% energy demand onto house sparrows SMR, the house sparrow could have used many alternative tactics to lower reproductive costs, e.g. lengthen the rate of follicular development, alter clutch size, sequentially vary egg size, or rely on endogenous reserves to a greater extent. Some of these tactics were observed in the population I studied (variable follicular development rate and possibly the varying of egg composition with sequence), while other tactics were observed between populations (altered clutch size- clutch size varies with latitude (Pinowska 1979), and rely on endogenous reserves to a greater extent- TBF use by the population Schifferli (1976) monitored). The use of some or all of these tactics can be interpreted in 2 ways, either the tactics were used to reduce daily demands or the tactics were used to increase hatchling variability. I doubt the former because compared to the added reproductive costs to BMR of anseriforms (156-239%, King 1973), house sparrow costs are negligible. As to the latter explanation, O'Connor (1977) showed that the house sparrow exhibits the predicted traits of a brood reductionist which include large variation in egg

size, hatching asynchrony, large initial variation in sibling body size, and variable growth rate dependent on hatchling size. Many of these traits are accentuated through differential egg composition (Howe 1978, Ankney 1980). Thus, I believe that instead of having difficulty producing eggs, the house sparrow produces eggs variable in composition to accomplish a specific purpose, brood reduction.

Additional supportive evidence for my contention that acquisition of nutrients/energy does not limit egg production is in Table 12. By comparing the relative costs of egg laying to other periods, one can see that in all cases the nestling/fledgling stages surpass the energetic costs of egg laying. If the production of eggs is so costly, then how could the female survive the higher energetic demands of the nestling/fledgling stages?

4.3 Yolk/Dye Experiments

Schifferli (1976) and I both estimated that house sparrows require, on average, 4 days to form a yolk. While I used lipophilic dyes to determine this period, Schifferli (1976) made his estimate based on the average growth rate per day of yolky follicles. Pinowska (1979) stated that yolks develop over 6 days based on her supposition that all preovulatory follicles greater than 2.0 mm would eventually ovulate. As explained in Section 2.4, I was unable to confirm Pinowska's (1979) claim.

Rapid follicular development rates have been estimated for other passerines (King 1973). Using data derived from King (1973), Ricklefs (1974) hypothesized that the final weight of an egg determines the

TABLE 12. Estimated daily energy costs (kJ · bird^{-1} · day^{-1}) for each stage of the breeding season. These costs are in excess of basal and thermostatic requirements.

	Breeding Stage						
Species	Unmated	Prenesting	Egg laying	Incubation	Nestling	Fledgling	Reference
House Sparrow[a]			13.4	11.3	32.2		Schifferli 1976
" "			10.9	10.0			Kendeigh 1973
" "					10.0[b]		Weiner 1972
Willow Flycatcher		35.0	30.9	28.8	31.4		Ettinger and King 1980
Mockingbird	15.1	17.0	29.5	10.3	31.5	37.5	Biedenweg 1983

[a]The House Sparrow estimates were based on extrapolated energetic requirements of the various phases versus the estimates for the Willow Flycatcher and Mockingbird which were based on time-activity budgets.

[b]Brooding costs only.

rate of rapid follicular development as heavier eggs take longer to develop. Based on an average fresh egg weight of 2.8 g (this study), house sparrows should need 4 days to build a yolk. This supports Schifferli's (1976) and my estimates for rapid follicular development.

Whereas Ricklefs suggested that final egg weight was the determining factor of rapid follicular development, Murton and Westwood (1977: 194) felt that, "...in species not limited by the potential availability of energy resources, p (the number of days required to form an egg) would most economically be close to the clutch size." This implies the rapid follicular development rate is more closely attuned to daily energy demands rather than to total energy/nutrient requirements. Although both Schifferli (1976) and I found a modal clutch size of 4, p would have been 5 because of the 24 additional hours needed to lay down albumen and the eggshell. Although Murton and Westwood's (1977) estimate is off by 1 day, I do not believe that the daily energy demands of reproduction are an unimportant consideration to the female.

Determination of the route(s) that ingested fat follows before incorporation into the developing follicle using lipophilic dyes should be considered cautiously. Even though L.A. Astheimer (pers. comm.) states that these dyes become bound to fats in the liver, I have no proof of what happens to the dyes after they pass through the liver. This uncertainty is important because whether those dyes remain attached to fats after entering either the ovary or fat depots is critical to any interpretation. In this study, I have assumed that the dye remains attached to the original fat carrier after binding in the liver. Another drawback in using dyes is that the relative

contribution of exogenous versus endogenous fat cannot be quantified. For example, the final blue ring in egg yolk 4, clutch 1, appeared uniformly blue but contained a fluctuating profile, indicative of diurnal/nocturnal inputs. My conclusion regarding that particular ring was based on anecdotal evidence as much as it was based on band color and profile structure. And finally profile structures are not exact by any means and without very accurate and precise dye markers, e.g. single concentrated dye doses (see Grau 1976), interpretations can be subjective.

Keeping these drawbacks in mind, the results still suggest that; 1) daily intake is incorporated into developing follicles diurnally, 2) daily intake replenishes fat reserves quickly (days), 3) stored fat is incorporated into the developing follicle nocturnally, and 4) there is considerable variation among-females in the use of stored fat reserves.

4.1.3 Postreproductive

4.1.3.1 Males

Since no nutrient indices varied between the LAY and POST periods, postreproductive activities apparently require equal amounts of energy and/or nutrients as do reproductive activities. My inability to separate POST males into incubation versus nestling males restricts the scope of my findings.

Schifferli (1976) found his protein index of flight muscle remained constant throughout the postreproductive period, but TBF

increased significantly during the incubation period and then decreased significantly during the nestling period. Schifferli (1976) suggested the increase in incubating male TBF resulted from the much lower effort put into reproduction by the male (estimated female energy costs during incubation = 11.3 vs 2.5 kJ day for males). The decline in TBF of males attending nestlings was attributed to the increased energy expenditure by males caring for nestlings. Fogden and Fogden (1979) noted the same protein and TBF patterns in reed warblers over the incubation and nestling/fledgling stages; flight muscle protein remained constant over the postreproductive period while TBF increased during incubation and then fell during nestling/fledgling. The protein and fat content of red-billed queleas increased throughout the incubation period and then fell during the nestling stage (Jones and Ward 1976).

4.1.3.2 Females

No index of protein changed after LAY, corresponding with Schifferli's (1976) findings. So little protein is required during the postreproductive period that even when Schifferli (1976) widowed an incubating female, her flight muscle protein index remained constant. Pinowska found LDW declined through both the incubation and nestling periods.

The BM of red-billed queleas increased throughout the incubation period (Jones and Ward 1976). After the young red-billed queleas hatched, female BM returned to the BM weight at the end of laying (Jones and Ward 1976).

TBF increased between the EI and LI/N periods while TBP and TBC were constant. Similar results during the incubaion period were noted by both Schifferli (1976) and Pinowska(1979). When Schifferli (1976) widowed a female with nestlings, her rate of TBF decline and total TBF loss were significantly greater than control females; however in no case did the widowed female exhaust her TBF.

TBF in Red-billed queleas recovered after egg laying and by the end of incubation exceeded TBF on DAY -1; TBF then declined throughout the nestling period and sometimes approached the starvation level (Jones and Ward 1976).

By the end of laying all calcium indices were constant with their respective EI levels.

4.4 Conclusions

Many in depth investigations of the bioenergetics of anseriforms during breeding have demonstrated that reliance on nutrient reserves for egg production varies with body size (Ankney 1984) and probably the life history of the species. At one end of the spectrum is the snow goose which completely relies on endogenous nutrient reserves to build eggs (Ankney and MacInnes 1978) while at the other end is the ruddy duck (Oxyura jamaicensis) which completely relies on exogenous nutrients to build eggs (Tome 1983).

Realizing the breadth of nutrient reserve use in anseriforms, I would be naive to expect all passerines to use a single nutrient reserve tactic. Already a spectrum of nutrient reserve use for building eggs has been demonstrated although no passerine relying

solely on endogenous reserves has been discovered. The brown-headed cowbird depends exclusively on exogenous protein, fat and calcium (Ankney and Scott 1980). The closest species examined to the opposite end of the spectrum is the house sparrow population Schifferli (1976) monitored which reportedly stored protein, fat and calcium before rapid follicular development and from which stores the female acquired essential nutrients and energy at critical times.

Based on my understanding of the reports on passerine nutrient dynamics, I have interpreted my findings in the following manner.

Protein and fat in males declined before rapid follicular development in females began, but calcium was stable. The proportion of males with high-protein and calciferous materials in their diet was constant (low) over the prereproductive period.

Protein and fat reserves of females were constant before rapid follicular development, but calcium was accumulated. Calcium in cortical bone was stored over a long period (weeks) whereas the calcium in medullary bone was stored during rapid follicular development. The proportion of females with high-protein foods was constant over the prereproductive period while the proportion of females with calciferous materials increased as follicles began to develop.

All indices of protein, fat and calcium reserves in males remained constant throughout the reproductive and postreproductive periods. The proportion of males that ate high-protein foods increased with the emergence of insects but the proportion of males with calciferous materials was constant (low) throughout breeding.

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Protein reserve use in females was slight during the reproductive period; the possibility remains that amongst the protein reserves catabolized were essential amino acids uncommon in daily intake. Fat reserve use was great and surpassed the fat requirements of the clutch. In addition to being used for the fat requirements of the clutch, fat reserves met the energy demands of protein and calcium acquisition during egg laying. Calcium reserve use was slight but essential in the logistics of eggshell formation. As in males, the proportion of females with high-protein foods followed the seasonal emergence of insects but more females consumed calciferous materials than did males during the reproductive period.

Protein and calcium reserves in females remained constant during the postreproductive period but fat reserves increased. The proportion of females with high-protein foods was constant while the proportion of females with calciferous materials declined from the reproductive high.

Daily reproductive energy costs peaked on the first day of ovulation and were no greater than 50% of BMR on that day. While several energy reducing strategies during egg production were demonstrated by house sparrows, I doubt the tactics were used to reduce energy costs. I believe the tactics were used to increase hatchling variability.

I conclude that, although female house sparrows do use nutrient reserves during egg laying, their clutch size is not controlled thereby.

APPENDIX 1. DAYs on which specific clutch sizes can be determined based on the number of pre- and/or postovulatory follicles present. This scheme pertains only to female house sparrows collected before noon.

	DAY							
	-3	-2	-1	0	+1	+2	+3	+4
	Preovulatory follices →			|	← Postovulatory follices			
Clutch size: unknown								
	x							
	x	x						
	x	x	x					
	x	x	x	x				
	x	x	x	x	x			
					x	x	x	x
						x	x	x
							x	x
								x
Clutch size: 3								
		x	x	x				
			x	x	x			
				x	x	x		
Clutch size: 4								
		x	x	x	x			
			x	x	x	x		
				x	x	x	x	
Clutch size: 5								
		x	x	x	x	x		
			x	x	x	x	x	
Clutch size: 6								
	x	x	x	x	x	x		
		x	x	x	x	x	x	
			x	x	x	x	x	x

LITERATURE CITED

Alisauskas, R. T. 1982. Nutrient reserves and the bioenergetics of reproduction in American coots. Unpublished M.S. University of Western Ontario, London.

Alisauskas, R. T. and C. D. Ankney. Nutrient reserves and the energetics of reproduction in American coots. Auk:in press

Anderson, T. R. 1978. Population studies of European sparrows in North America. Occasional Papers, Museum of Natural History 70: 1-58.

Ankney, C. D. 1980. Egg weight, survival, and growth of lesser snow goose goslings. J. Wildl. Mgmt. 44: 174-182.

Ankney, C. D. 1984: Nutrient reserve dynamics of breeding and molting brant. Auk 101: 361-370.

Ankney, C. D. and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95: 459-471.

Ankney, C. D. and D. M. Scott. 1980. Changes in nutrient reserves and diet of breeding brown-headed cowbirds. Auk 97: 684-696.

Aschoff, J. and H. Pohl. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. J. Ornithol. 111: 38-47.

Bacon, W. L. 1981. Metabolism of lipid labeled very low density lipoprotein from laying turkey hens in laying turkey hens and immature turkeys. Poult. Sci. 60: 1525-1536.

Biedenweg, D. W. 1983. Time and energy budgets of the mockingbird (Mimus polyglottos) during the breeding season. Auk 100: 149-160.

Blem, C. R. 1980. Multiple regression analysis of mid-winter lipid levels in the house sparrow, Passer domesticus. 1136-1142. 17th Intl. Ornithol. Congress, Berlin.

Brody, S. 1945. Bioenergetics and growth. New York, Reinholt Publ. Corp.

Bumpus, H. C. 1899. The elimination of the unfit as illustrated by the introduced sparrow, Passer domesticus. Biol. Lectures, Marine Biol. Lab., Woods Hole: 209-226.

Bürkli, W. 1974. Eischalen als Bestandteil der Rauchschwalbennahrung. Orn. Beob. 71: 172.

Caughley, G. and J. Caughley. 1974. Estimating median date of birth. J. Wildl. Mgmt. 38: 552-556.

Classen, H. L. and T. A. Scott. 1982. Self-selection of calcium during the rearing and early laying periods of white leghorn pullets. Poult. Sci. 61: 2065-2074.

Comar, C. L. and J. C. Driggers. 1949. Secretion of radioactive calcium in the hen's egg. Science 109: 282.

Conrad, R. M. and D. C. Warren. 1939. The alternate white and yellow layers of yolks in hen's ova. Poult. Sci. 18: 220-224.

Davis, E. A., Jr. 1955. Seasonal changes in the energy balance of the English sparrow. Auk 72: 385-411.

Dawson, D. G. 1972. The breeding biology of house sparrows. Unpublished Ph.D. Univ. Oxford, England.

Drobney, R. D. 1980. Reproductive bioenergetics of wood ducks. Auk 97: 480-490.

Drobney, R. D. 1982. Body weight and composition changes and adaptations for breeding in wood ducks. Condor 84: 300-305.

Drobney, R. D. 1984. Effect of diet on visceral morphology of breeding wood ducks. Auk 101: 93-98.

El-Wailly, A. J. 1966. Energy requirements for egg-laying and incubation in the zebra finch. Condor 68: 582-594.

Ettinger, A. D. and J. R. King. 1980. Time and energy budgets of the willow flycatcher (Empidonax traillii) during the breeding season. Auk 97: 533-546.

Fleischer. R. C. and R. F. Johnston. 1982. Natural selection on body size and proportions in house sparrows. Nature 298: 757-749.

Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. Ibis 114: 307-343.

Fogden, M. P. L. and P. M. Fogden. 1979. The role of fat and protein reserves in the annual cycle of the grey-backed camaroptera in Uganda (Aves: Sylvidae). J. Zool., London. 189: 223-258.

Godin, A. J. 1960. A compilation of diagnostic characteristics used in aging and sexing game birds and mammals. Unpublished M.S. Thesis. University of Mass., Amherst.

Grau, C. R. 1976. Ring structure of avian egg yolk. Poult. Sci. 55: 1418-1422.

Grau, C. R. 1982. Egg formation in Fiordland crested penguins (Eudyptes pachyrhynchus). Condor 84: 172-177.

Greenlaw, J. S. 1978. The relation of breeding schedule and clutch size to food supply in the rufous-sided towhee. Condor 80: 24-33.

Howe, H. F. 1978. Initial investment, clutch size and brood reduction in the common grackle (Quiscalus quiscula L.). Ecology 59: 1109-1122.

Hörwitz, S. 1978. Calcium metabolism in birds. Pp. 273-306 in Chemical Zoology, Vol. 10 (M. Florkin and B. T. Schneer, Eds.). New York, Academic Press.

Hutchinson, A. E. and R. B. Owen. 1984. Bone marrow fat in waterfowl. J. Wildl. Mgmt. 48: 585-591.

Jones, M. M. 1980. Nocturnal loss of muscle protein from house sparrows (Passer domesticus). J. Zool., Lond. 192: 33-39.

Jones, P. J. 1976. The utilization of calcareous grit by laying Quelea quelea. Ibis 118: 575-576.

Jones, P. J. and P. Ward. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch size in the red-billed quelea. Quelea quelea. Ibis 118: 547-574.

Johnston, R. F. and R. C. Fleischer. 1981. Overwinter mortality and sexual size dimorphism in the house sparrow. Auk 98: 503-511.

Källander, H. 1974. Advancement of laying of great tits by the provision of food. Ibis 116: 365-367.

Kalmbach, E. R. 1940. Economic status of the English sparrow in the United States. U.S.D.A. Tech. Rept. No. 711: 1-66.

Kendeigh, S. C. 1973. Monthly variations in the energy budget of the house sparrow throughout the year. Pp. 1-43 in Productivity, population dynamics and systematics of granivorous birds (S. C. Kendeigh and J. Pinowski, Eds.). Warszawa, PWN - Polish Scientific Publ.

Kendeigh, S. C., J. E. Kontogiannis, A. Mazac, and R. R. Roth. 1969. Environmental regulation of food intake by birds. Comp. Biochem. Physiol. 31: 941-957.

Kendeigh, S. C., V. R. Dolnik and V. M. Gravrilov. 1977. Avian energetics. Pp. 129-204 in Granivorous birds in ecosystems (J. Pinowski and S. C. Kendeigh, Eds.). Cambridge, Cambridge Univ. Press.

Kern, M. D. 1972. Seasonal changes in the reproductive system of the female white-crowned sparrow, Zonotrichia leucophrys gambelii, in captivity and in the field. Z. Zellforsch. 126: 297-319.

Kerr, D. C., C. D. Ankney and J. S. Millar. 1982. The effects of drying temperature on extraction of petroleum ether soluble fats of small birds and mammals. Can. J. Zool. 60: 470-472.

King, J. R. 1973. Energetics of reproduction in birds. Pp. 78-107 in Breeding biology of birds (D. S. Farner, Ed.). Washington, D.C., Nat. Acad. Sci.

Klomp, H. 1970. The determination of clutch size in birds. A review. Ardea 58: 1-124.

Korschgen, C. E. 1977. Breeding stress of female eiders in Maine. J. Wildl. Mgmt. 41(3): 360-373.

Krapu, G. L. 1981. The role of nutrient reserves in mallard reproduction. Auk 98: 29-38.

Lack, D. 1947-48. The significance of clutch-size. Ibis 89: 302-352; 90: 25-45.

Lowther, P. E. 1977. Selection intensity in North American house sparrows (Passer domesticus). Evolution 31: 649-656.

Lowther, P. E. 1979. Interfarm variation in breeding biology of a Kansas population of house sparrows (Passer domesticus). Unpublished Ph.D. thesis, Univ. of Kansas, Lawrence.

Mackowicz, R., J. Pinowski and M. Wieloch. 1970. Biomass production by house sparrow (Passer d. domesticus L.) and tree sparrows (Passer m. montanus L.) populations in Poland. Ekol. Polska 18: 465-501.

March, G. L. and R. M. F. S. Sadleir. 1975. Studies on the band-tailed pigeon (Columba fasciata) in British Columbia. III Seasonal changes in body weight and calcium distribution. Phys. Zool. 48: 49-56.

Miller, M. R. 1975. Gut morphology of mallards in relation to diet quality. J. Wildl. Mgmt. 39: 168-173.

Milne, H. 1976. Body weights and carcass composition of the common eider. Wildfowl 27: 115-122.

Mueller, W. J., R. Schraer and H. Schraer. 1964. Calcium metabolism and skeletal dynamics of laying pullets. J. Nutr. 86: 20-26.

Murphy, E. C. 1978. Seasonal variation in reproductive output of house sparrows: the determination of clutch size. Ecology 59: 1189-1199.

Murphy, E. C. 1980. Body size of house sparrows: reproductive and survival correlates. Pp. 1155-1161 in Symposium on ecology and systematics of the genus Passer. C. R. Blem (chairman). 17th Intl. Ornithol. Congress. Berlin.

Murton, R. K. and N. J. Westwood. 1977. Avian breeding cycles. Oxford, Clarendon Press.

Naik, R. M. and L. Mistry. 1972. Breeding season and reproductive rate of Passer domesticus (L.) in Baroda, India. Pp. 133-140 in Productivity, population dynamics and systematics of granivorous birds (S. C. Kendeigh and J. Pinowski, Eds.). Warszawa, PWN - Polish Scientific Publ.

North, C. A. 1973. Population dynamics of the house sparrow, Passer domesticus (L.) in Wisconsin, U.S.A. Pp. 195-210 in Productivity, population dynamics and systematics of granivorous birds (S. C. Kendeigh and J. Pinowski, Eds.). Warszawa, PWN - Polish Scientific Publ.

O'Connor, R. J. 1973. Patterns of weight change in the house sparrow, Passer domesticus (L.). Pp. 111-125 in Productivity, population dynamics and systematics of granivorous birds. (S. C. Kendeigh and J. Pinowski, Eds.). Warszawa, Polish Scientific Publ.

O'Connor, R. J. 1977. Growth strategies in nestling passerines. Living Bird 16: 209-238.

Odum, E. P., D. T. Rogers and D. L. Hicks. 1964. Homeostasis of the nonfat components of migrating birds. Science 143: 1037-1039.

Ojanen, M., H. Haarakanges and H. Hyvärinen. 1975. Seasonal changes in bone mineral content and alkaline phosphatase activity in the house sparrow (Passer domesticus L.). Comp. Biochem. Physiol. 50A: 581-585.

Payne, R. B. 1972. Nuts, bones, and a nesting of red crossbills in the Panamint Mountains, California. Condor 74: 485-486.

Perrins, C. M. 1979. British tits. London, William Collins Sons and Co. Ltd.

Peterson, S. R. and R. S. Ellarson. 1979. Changes in oldsquaw carcass weight. Wilson Bull. 91: 288-300.

Pinowska, B. 1975. Food of female house sparrows (Passer domesticus L.) in relation to stages of nestling cycle. Pol. Ecol. Stud. 1: 211-225.

Pinowska, B. 1979. The effect of energy and building resources of females on the production of house sparrow (Passer domesticus (L.)) populations. Ecol. Polska 27: 363-396.

Raveling, D. G. 1979. The annual cycle of body composition of Canada geese with special reference to control of reproduction. Auk 96: 234-252.

Raveling, D. G., M. Sifri and R. B. Knudsen. 1978. Seasonal variation of femur and tibiotarsus constituents in Canada geese. Condor 80: 246-248.

Reinecke, K. J., T. L. Stone and R. B. Owen, Jr. 1982. Seasonal carcass composition and energy balance of female black ducks in Maine. Condor 84: 420-426.

Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pp. 152-279 in Avian energetics (R. A. Paynter, Jr., Ed.). Publ. Nuttall Ornitol. Club. No. 15.

Ricklefs, R. E. 1984. Variation in the size and composition of eggs of the European starling. Condor 86: 1-6.

Romanoff, A. L. and A. J. Romanoff. 1949. The avian egg. New York, John Wiley and Sons.

Roudybush, R. E., C. R. Grau, M. R. Peterson, D. G. Ainley, K. V. Hirsch, A. P. Gilman and S. M. Patten. 1979. Yolk formation in some charadriiform birds. Condor 81: 293-298.

Schifferli, L. 1976. Factors affecting weight and conditions in the house sparrow particularly when breeding. Unpublished Ph.D. Univ. Oxford, Oxford.

Schluter, D. 1984. Feeding correlates of breeding and social organization in two Galapagos finches. Auk 101: 59-68.

Scott, D. M. and C. D. Ankney. 1980. Fecundity of the brown-headed cowbird in southern Ontario. Auk 97: 677-683.

Scott, D. M. and C. D. Ankney. 1983. The laying cycle of brown-headed cowbirds: passerine chickens? Auk 100: 583-592.

Scott, M. L., M. C. Nesheim and R. J. Young. 1976. Nutrition of the chicken, 2nd Ed. Ithaca, New York, M. L. Scott and Associates.

Seel, D. C. 1968. Clutch size, incubation and hatching success in the house sparrow and tree sparrow Passer spp at Oxford. Ibis 110: 270-282.

Selander, R. K. and S. Y. Yang. 1966. The incubation patch of the house sparrow, Passer domesticus Linnaeus. Gen. Comp. Endrocrinol. 6: 325-333.

Siegfried, W. R., A. E. Burger and P. G. H. Frost. 1976. Energy requirements for breeding in the maccoa duck. Ardea 64: 171-191.

Simkiss, K. 1967. Calcium in reproduction physiology. London and New York, Chapman and Hall.

Stobo, W. T. and I. A. McLaren. 1975. The Ipswich sparrow. Halifax, Nova Scotia. Nova Scotian Institute of Science.

Summers-Smith, D. 1963. The house sparrow. London, Collins.

Swanson, G. A. and J. C. Bartonek. 1970. Bias associated with food analysis in gizzards of blue-winged teal. J. Wildl. Mgmt. 34: 739-746.

Threadgold, L. T. 1960. A study of the annual cycle of the house sparrow at various latitudes. Condor 62: 190-201.

Tome, M. W. 1983. The role of endogenous energy in reproduction of female ruddy ducks. Unpublished abstract. Delta Waterfowl Res. Station.

Ward, P. 1969. The annual cycle of the yellow-vented bulbul Pycnontus goiavier in a humid equatorial environment. J. Zool., Lond. 157: 25-45.

Warren, D. C. and H. M. Scott. 1935. The time factor in egg formation. Poult. Sci. 14: 195-207.

Weaver, R. L. 1942. Growth and development of English sparrows. Wilson Bull. 54: 183-191.

Weaver, R. L. 1943. Reproduction in English sparrows. Auk 60: 62-74.

Weiner, J. 1973. Energy requirements of house sparrows, Passer d. domesticus (L.) in southern Poland. Pp. 45-58 in Productivity, population dynamics and systematics of granivorous birds (S. C. Kendeigh and J. Pinowski, Eds.). Warszawa, PWN - Polish Scientific Publ.

Wiens, J. A. and R. F. Johnston. 1977. Adaptive correlates of granivory in birds. Pp. 301-340 in Granivorous birds in ecosystems. (S. C. Kendeigh and J. Pinowski, Eds.). Cambridge, Cambridge Univ. Press.

Will, R. L. 1973. Breeding success, numbers, and movements of house sparrows at McLeansboro, Illinois. Ornithol. Monogr. 14: 60-78.

Wolf, L. L. and F. R. Hainsworth. 1978. Energy: expenditures and intake. Pp. 307-358 in Chemical Zoology, vol. 10 (M. Florkin and B. T. Schneer, Eds.). New York, Academic Press, Inc.

Yom-Tov, Y. 1974. The effect of food and predation on breeding density and success, clutch size and laying date of the crow (Corvus corone L.). J. Anim. Ecol. 43: 479-498.

Young, T. G. 1962. Unseasonal breeding of house sparrows. Scottish Birds 2: 102.

Zar, J. H. 1974. Biostatistical analysis. Englewood Cliffs, N.J., Prentice-Hall, Inc.

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