

CHANGES IN NUTRIENT RESERVES AND DIET OF BREEDING BROWN-HEADED COWBIRDS

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ABSTRACT.—We collected Brown-headed Cowbirds (*Molothrus ater*) in southwestern Ontario in 1976 to determine the relative importance of nutrient reserves and dietary nutrients to laying females; males were used as controls. Lean dry weight and leg and breast muscle weights were used to index protein reserves, ether-extractable fat to index fat reserves, and leg and breast bone weights to index calcium reserves. Gizzard contents were examined to evaluate diet composition. Females neither stored fat or protein before they began egg laying nor utilized fat or protein reserves for egg production. Calcium reserves of females, however, increased before egg laying and were used for egg production. The diets of males and females changed from mainly seeds before egg laying began to mainly insects during the laying season and back to mainly seeds after the laying season. The shift to insects, however, was much more pronounced for females. Additionally, the gizzards of nearly all laying females contained mollusc shells. We conclude that female cowbirds obtain the nutrients for egg production directly from their diet. The relevance of this to the egg-laying pattern of female cowbirds is discussed. *Received 7 May 1979, accepted 12 November 1979.*

EGG production imposes considerable nutritional demands on female birds (King 1973, Ricklefs 1974). Recently, several studies have investigated whether females meet these demands by utilizing body reserves and/or by increasing the quality or quantity of the food that they eat. Laying Pintails (*Anas acuta*) utilize fat reserves and eat a high protein, invertebrate diet (Krapu 1974), laying Red-billed Queleas (*Quelea quelea*) use protein and fat reserves and eat food rich in protein and calcium (Jones 1976, Jones and Ward 1976), and female Lesser Snow Geese (*Chen caerulescens caerulescens*) feed little during egg laying (Ankney 1977) and rely heavily on fat, protein, and calcium reserves for egg production (Ankney and MacInnes 1978).

This paper presents the results of an investigation of the changes in fat, protein, and calcium reserves and in diet of breeding Brown-headed Cowbirds (*Molothrus ater*, hereafter called cowbirds). Cowbirds are an interesting and ideal subject for such a study, because (1) the females' major nutrient demand during reproduction is egg production, as they do not build nests, incubate, or feed young; (2) they lay many eggs during a breeding season (Payne 1973, 1976; Scott and Ankney 1980) and lay several clutches (Payne 1965, Scott 1978); and (3) they are abundant and easily collected.

By collecting cowbirds before, during, and after the egg-laying period and by comparing data from females to those from males, we determined that females rely little, if at all, on body reserves for egg production. They meet the increased nutrient demand directly through their diet.

STUDY AREA AND METHODS

We collected cowbirds within a 50-km radius of London, Ontario in 1976. Nearly all birds were collected by shooting with .410 shotguns using small shot (#s 7½, 8, or 9); the last three samples were netted. To avoid potential bias associated with repeated sampling of a local population (e.g. "new" birds moving into the area or changes in reproductive activity of survivors), we collected in a different area each week (each collection area was >8 km from all other such areas), except for the last three samples,

which were taken from one feedlot. Birds were collected in many different habitats, e.g. plowed fields, pastures, hawthorn scrub (*Crataegus* spp.), river and stream valleys, and along roadsides. Nearly all birds were taken in the morning.

The first weekly sample was collected during 3–5 April, shortly after migrant cowbirds began arriving in this area. Weekly samples were collected until 28 July, except during 18–24 July.

Cowbirds were assigned to three categories—Prelaying, Laying, and Postlaying. We defined these as follows:

Prelaying—females that had not begun to lay, i.e. did not have any discernible postovulatory follicles. We arbitrarily designated Prelaying males as those collected before or on the date when the first Laying female was collected. The dates and sample sizes were: females, 3 April–10 May, $n = 52$; males, 3 April–29 April, $n = 48$.

Laying—females that had either an oviducal egg or discernible postovulatory follicles and a developed oviduct (nearly all had one or more developing yolky ova). Laying males were those collected after the date when the first Laying female was collected but before the date when the first Postlaying female was collected. The dates and sample sizes were: females, 27 April–7 July, $n = 164$; males, 3 May–7 July, $n = 108$.

Postlaying—females that did not have an oviducal egg or any large (>3 mm) yolky ova and had a regressed oviduct. Postlaying males were those collected on or after the date when the first Postlaying female was collected (all had testes that had regressed in size). The dates and sample sizes were: females, 7 July–28 July, $n = 49$; males, 7 July–28 July, $n = 29$.

Each of these three collection periods was split into two equal time periods, and the data from birds in the first half of a period were compared with those from birds in the second half. When such a comparison showed a significant difference ($P < 0.05$) the data were kept separate for further comparison; if no difference was found ($P > 0.05$) the data were combined. Also, we initially separated yearling males from adult males using the criteria of Selander and Giller (1960). In 21 statistical comparisons (3 categories of birds, 7 variables), however, yearlings and adults differed in only 1 ($P < 0.05$). As this would be expected on the basis of chance ($21 \times 0.05 = 1.05$), we combined the data from adult and yearling males. We were unable to distinguish yearling from adult females satisfactorily. This may have increased the variability of the data if these groups differed in the variables investigated.

To examine the relation between size of nutrient reserves and stage in the laying cycle, we established three categories of Laying females:

About to start a clutch—females without an oviducal egg but with at least one developing ovum >5.0 mm in diameter. The largest ovum in about half of these birds was >7.5 mm, indicating ovulation the following day; in the others the largest follicle was 5.0–7.5 mm, indicating ovulation 2 days hence (see Payne 1965, 1973).

Starting a clutch—females with an oviducal egg but only one large postovulatory follicle, i.e. the oviducal egg was the first egg of a clutch.

Finishing a clutch—females with an oviducal egg and no large (>5.0) developing ova, i.e. the oviducal egg was the last egg of a clutch.

Birds were individually tagged and weighed to the nearest 1 g on a 100-g Pesola spring scale immediately after they were collected. Then the ovary and oviduct of a female were removed, the presence or absence of an oviducal egg was recorded, and these organs, including any oviducal egg, were placed in 10% formalin. The birds were then stored in deep-freeze. Subsequent dissections were done as follows. A bird was split open laterally and the esophagus, proventriculus, and gizzard were removed and their contents stored in 70% ethanol for later examination. The breast muscles (*pectoralis*, *supracoracoideus*, and *coracobrachialis*) and all those leg muscles having either their origin or insertion on the femur or tibiotarsus were unilaterally excised and weighed to the nearest 0.001 g on a Sartorius electric balance accurate to 0.0001 g. The sternum was then completely cleaned of muscle. Muscles, digestive tract, bones, and the remainder of the carcass including feathers were placed in a small aluminium pan, dried to constant weight in an oven for at least 24 h at 95°C, and then weighed, to the nearest 0.01 g, in total. This weight was termed the Carcass Dry Weight. After drying, the cleaned leg bone (femur and tibiotarsus) and the sternum were individually weighed to the nearest 0.001 g; we did not attempt to apply any correction for potential differences in size of leg bones and sterna, because sample sizes were large and assumed to be random. The remainder of the dried material was ground in a Wiley mill two or three times until it was a homogeneous powder. We used an approximately 1-g aliquot of this from each bird for fat extraction. Extractions were done for 12 h with a Goldfish extractor using petroleum ether. We calculated for each bird:

TABLE 1. Changes in nutrient reserves of female cowbirds.

Variable (g) ^b	Category ^a						
	Prelaying			Laying			
	1st half	<i>P</i>	2nd half	<i>P</i>	1st half	2nd half	
Body Weight	38.7 ± 0.6 (26)	*	40.2 ± 0.4 (26)	***	42.0 ± 0.2 (164)	***	40.5 ± 0.3 (49)
Lean Dry Weight	11.62 ± 0.11 (50)	NS	11.69 ± 0.07 (75)	NS	*	11.47 ± 0.07 (86)	NS
Breast muscle	4.03 ± 0.05 (52)	NS	4.03 ± 0.05 (52)	NS	3.93 ± 0.03 (159)	***	3.75 ± 0.03 (49)
Leg muscle	1.25 ± 0.02 (52)	NS	1.29 ± 0.02 (74)	NS	**	1.34 ± 0.02 (83)	***
Total Body Fat	2.03 ± 0.12 (50)	***	1.14 ± 0.97 (75)	***	**	0.97 ± 0.03 (86)	***
Leg bone	0.156 ± 0.003 (44)	***	0.156 ± 0.003 (44)	***	0.144 ± 0.001 (146)	*	0.150 ± 0.002 (49)
Breast bone	0.142 ± 0.003 (25)	***	0.160 ± 0.005 (19)	***	0.144 ± 0.002 (67)	***	0.138 ± 0.002 (49)

^a A combined mean value is shown where means from first and second halves of a category were not significantly different. *P* is the probability (from paired *t*-tests) that adjacent means are different by chance; * = *P* < 0.05, ** = *P* < 0.01, *** = *P* < 0.001, NS = *P* > 0.05.

^b Data are $\bar{x} \pm 1$ SE with sample size in parentheses.

$$\text{Total Body Fat} = \frac{\text{weight of fat in aliquot}}{\text{total weight of aliquot}} \times \text{Carcass Dry Weight}$$

and

$$\text{Lean Dry Body Weight} = \text{Carcass Dry Weight} - \text{Body Fat}$$

We used breast muscle and leg muscle weights to index protein reserves, Total Body Fat (TBF) as a measure of fat reserves, and leg bone and sternum weight to index calcium reserves. Lean Dry Body Weight served as an overall index of protein reserves.

Our original intention was to use only esophageal contents for analysis of food habits because of the potential bias against finding animal matter in gizzard contents (Swanson and Bartonek 1970), but few birds had been feeding immediately before they were collected, and thus most did not have food in the esophagus, so we examined the contents of the proventriculus and gizzard also. These were placed in a petri dish, examined under a binocular microscope at 40× magnification, and scored as follows: (1) 100% plant—no trace of insect matter; (2) Plant + trace of insect—nearly all plant material but some evidence of insect (e.g. a leg, a beetle elytron); (3) Both plant and insect—both types of material present in > trace amounts; (4) Insects + trace of plant—nearly all insect material but some evidence of plant (e.g. a seed, seed hull); or (5) 100% insect—no trace of plant material seen.

We used $R \times C$ tests of independence to compare the proportions of birds in these categories versus the birds' category (e.g. Prelying males vs. Prelying females). We then combined the data for the birds in categories 1 and 2 (above) and those in categories 4 and 5 and repeated the tests. In every case the probability value was identical to that of the respective test in the first analysis. Thus, only the results of the tests using three categories of food (called 100% plant, Both plant and insect, and 100% insect) are presented. We realize that this gives only an index to cowbird food habits and that it is probably biased in favor of plant material.

We also recorded the presence or absence of shell in each food sample. Several of these shells were identified as "mollusc shell (probably snail)" by G. Fox, which confirmed our tentative identification.

A sample of male and female leg bones was examined by A. Rick, who analyzed them for the presence of medullary bone.

Sample sizes are not always consistent for several reasons: (1) several birds were lost after being examined in the field, (2) badly damaged organs and bones were excluded from analyses, (3) some food samples were discarded before the decision was made to use gizzard and proventriculus contents, and (4) in several birds the upper digestive tract was empty.

Statistical tests follow Sokal and Rohlf (1969). Throughout the paper means are given \pm the standard error. Weights taken to the nearest 0.001 g were used as such for statistical analyses, but mean values are shown here rounded to the nearest 0.01 g.

RESULTS

CHANGES IN NUTRIENT RESERVES

Females.—The long-term changes in the weights of variables that we used to index nutrient reserves are summarized in Table 1. Much of the changes in body weight can be attributed to changes in ovary and oviduct weights (Payne 1973: 87) and to the presence of an oviducal egg in many Laying females. There was little change in Lean Dry Body Weight during the breeding season. The average weight of a female's protein reserves (breast and leg muscles) did not increase before egg laying began, and egg laying did not result in a long-term decline in the weight of these reserves. Protein reserves declined significantly after the Laying period. Although mean fat reserves (TBF) did not increase during Prelying, they declined during Laying and then increased during Postlaying. The pattern of changes in calcium reserves (sternum and leg bone weights), although somewhat different for the two bones, suggests that there was some calcium storage during Prelying and utilization of skeletal calcium during Laying; leg bone weight increased after Laying, but sternum weight did not. The tentative conclusion that can be made from these

TABLE 2. Comparison of nutrient reserves of Laying females that had an oviducal egg to those of females without an oviducal egg.

Variable (g)	Females with egg	<i>P</i> ^a	Females without egg
	$\bar{x} \pm SE$ (<i>n</i>)		$\bar{x} \pm SE$ (<i>n</i>)
Body Weight	42.4 ± 0.2 (115)	***	41.1 ± 0.4 (44)
Lean Dry Weight	11.66 ± 0.77 (113)	NS	11.53 ± 0.09 (42)
Breast muscle	3.94 ± 0.03 (111)	NS	3.89 ± 0.05 (42)
Leg muscle	1.32 ± 0.01 (109)	NS	1.33 ± 0.02 (42)
Total Body Fat	1.04 ± 0.03 (113)	NS	1.07 ± 0.08 (42)
Leg bone	0.145 ± 0.001 (103)	NS	0.143 ± 0.002 (37)
Breast bone	0.140 ± 0.001 (99)	NS	0.143 ± 0.003 (37)

^a As in Table 1.

data is that, over the entire breeding season, female cowbirds do not utilize body protein, but they may use fat and calcium reserves.

To explore further whether or not females used body reserves for egg production, we compared the Laying females that had an oviducal egg with those that did not have one (Table 2). The only significant difference between them was in body weight, and this resulted from the weight of the oviducal egg, which weighs between 1.0 and 2.8 g depending on its stage of development. These two groups of females are heterogeneous with respect to egg laying, e.g. some with an oviducal egg were starting a clutch and others were finishing one, while some without an egg had just finished a clutch and others were about to start one. Females with an oviducal egg, however, will on average have laid 2.2 eggs, as the average clutch size of cowbirds is 4.4 eggs in southern Ontario (Scott 1978). Thus, any large change in the size of a female's nutrient reserves would be detected by this comparison, especially as sample sizes were large.

We hypothesized that, if females utilized body reserves for egg production, this utilization should be most obvious in a comparison of those starting a clutch with those finishing one, so we compared data from females in the categories "About to start a clutch," "Starting a clutch," and "Finishing a clutch" (Table 3). Clearly, the fat and protein reserves of female cowbirds did not increase while they were between clutches, nor did they use these reserves when laying a clutch, but the size of their calcium reserves increased, via the leg bone, while they were between clutches and declined during egg laying.

Males.—The only change ($P < 0.05$) in mean body weight of males occurred during the Laying period and resulted from declines in TBF and leg muscle (Table 4). Breast and leg muscle weights decreased during the breeding season and reached their lowest value during Postlaying. TBF did not change between Prelaying and Laying but decreased during Laying and increased after Laying. Inexplicably, mean leg bone and sternum weights fell during Laying, although they did not increase after that.

TABLE 3. The relation between stages in the laying cycle and nutrient reserves of female cowbirds.

Variable (g)	Stage				
	Starting clutch		Finishing clutch		About to start clutch
	$\bar{x} \pm SE$ (n)	P^a	$\bar{x} \pm SE$ (n)	P^a	$\bar{x} \pm SE$ (n)
Body Weight	42.4 \pm 0.6 (13)	NS	42.4 \pm 0.5 (15)	NS	41.7 \pm 0.4 (33)
Lean Dry Weight	11.69 \pm 0.2 (13)	NS	11.48 \pm 0.2 (14)	NS	11.67 \pm 0.1 (32)
Breast muscle	3.89 \pm 0.16 (12)	NS	3.92 \pm 0.08 (14)	NS	3.94 \pm 0.05 (32)
Leg muscle	1.29 \pm 0.06 (12)	NS	1.26 \pm 0.03 (14)	NS	1.34 \pm 0.02 (32)
Total Body Fat	1.01 \pm 0.09 (13)	NS	1.14 \pm 0.08 (14)	NS	1.16 \pm 0.1 (32)
Leg bone	0.147 \pm 0.002 (11)	*	0.135 \pm 0.003 (14)	*	0.145 \pm 0.002 (29)
Breast bone	0.142 \pm 0.004 (11)	NS	0.138 \pm 0.006 (14)	NS	0.142 \pm 0.004 (28)

* As in Table 1.

CHANGES IN DIET

The diets of males and females changed from mainly plant matter during Prelaying to predominantly insects during Laying and back to mainly plant during Postlaying (Fig. 1). Diet composition was not independent of period of the breeding season (males: $G = 29.73$, $df = 4$, $P < 0.005$; females: $G = 87.82$, $df = 4$, $P < 0.005$). Similar analyses, however, showed that the diets of males and females differed only during Laying (Prelaying: $G = 1.32$, $df = 2$, $P > 0.5$; Laying: $G = 49.19$, $df = 2$, $P < 0.005$; Postlaying: $G = 5.35$, $df = 2$, $P > 0.05$). This difference resulted because the increased insect consumption was much more pronounced in females (Fig. 1).

Another marked change in the diet of cowbirds occurred during the breeding season; the ingestion of mollusc shell, especially by females, increased during Laying (Fig. 2). The ingestion of shell was not independent of period during the breeding season (males: $G = 9.62$, $df = 2$, $P < 0.01$; females: $G = 161.06$, $df = 2$, $P << 0.005$). The proportion of females with mollusc shell in their gizzards, however, was greater than that of males during Prelaying ($G = 10.43$, $df = 1$, $P < 0.005$) and Laying ($G = 162.38$, $df = 1$, $P << 0.005$) but not during Postlaying ($G = 1.29$, $df = 1$, $P > 0.1$).

DISCUSSION

Changes before and during egg-laying period.—Using leg and breast muscle weights as indices, we did not detect either long-term decreases in female protein reserves (i.e. over the entire egg-laying season) or short-term decreases (i.e. between birds starting a clutch and those finishing one). This differs greatly from what happens in Red-billed Queleas (Jones and Ward 1976) and Lesser Snow Geese (Ankney and MacInnes 1978). Females of these species rely very much on protein reserves for egg production, and clutch size is at least partly determined by the amount of a Prelaying female's protein reserves. Lesser Snow Geese feed little immediately

TABLE 4. Changes in nutrient reserves of male cowbirds.

Variable (g) ^b	Category ^a						
	Prelaying	P	Laying			Postlaying	
			1st half	P	2nd half		
Body Weight	51.3 ± 0.4 (48)	NS	52.1 ± 0.4 (52)	**	50.2 ± 0.3 (55)	NS	51.3 ± 0.6 (29)
Lean Dry Weight	15.78 ± 0.19 (46)	NS		15.37 ± 0.11 (108)	**		14.61 ± 0.25 (29)
Breast muscle	5.35 ± 0.7 (46)	**		5.10 ± 0.11 (108)	**		4.78 ± 0.06 (29)
Leg muscle	2.06 ± 0.03 (46)	NS	2.15 ± 0.03 (51)	**	1.99 ± 0.04 (55)	***	1.67 ± 0.03 (29)
Total Body Fat	2.75 ± 0.15 (46)	NS	2.52 ± 0.17 (52)	***	1.73 ± 0.09 (56)	**	2.44 ± 0.25 (29)
Leg bone	0.201 ± 0.003 (44)	NS	0.202 ± 0.003 (49)	*	0.194 ± 0.002 (49)	NS	0.199 ± 0.004 (28)
Breast bone	0.194 ± 0.003 (42)	**	0.209 ± 0.003 (47)	***	0.187 ± 0.002 (53)	NS	0.187 ± 0.004 (29)

^a As in Table 1.^b Data are $\bar{x} \pm SE$ with sample sizes in parentheses.

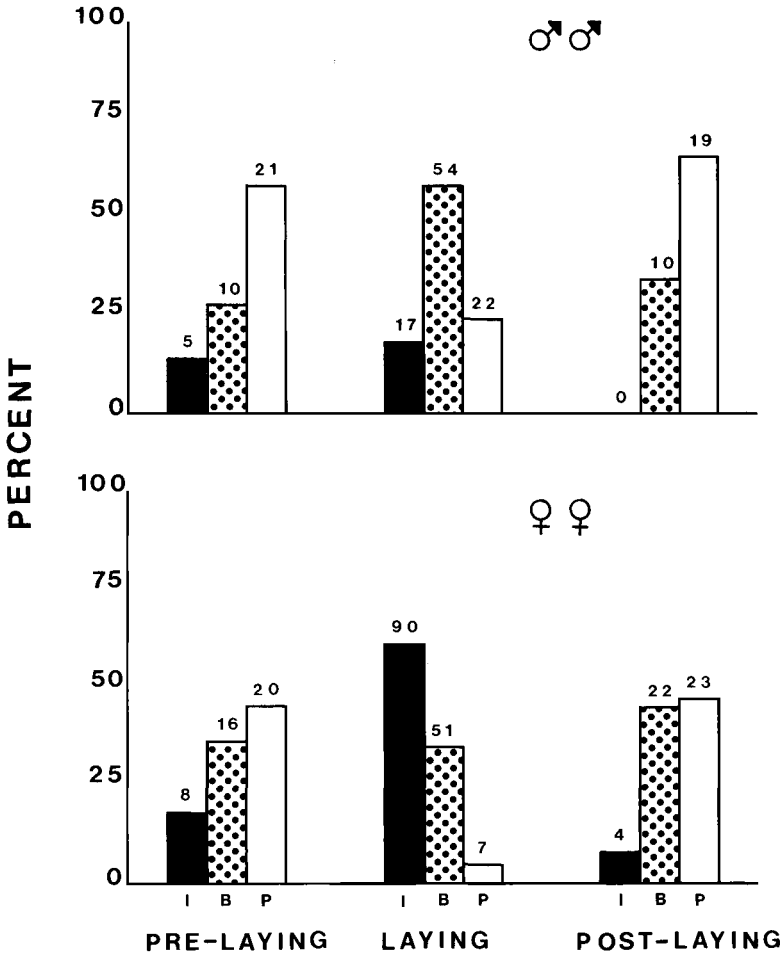


Fig. 1. Diet of breeding cowbirds. I = 100% insect; B = Both plant and insect; P = 100% plant. Sample sizes shown above columns.

before and during egg laying and so must rely on body reserves (Ankney 1977). Red-billed Queleas feed before and during laying and consume some insects (Jones and Ward 1976). This consumption, however, never exceeded 25% on a dry weight basis and, based on percent occurrence, was only about 60% in both Prelaying and Laying females (Jones and Ward 1976: 560-561). But the proportion of Prelaying female cowbirds with insects was 55%, and this increased to 95% in Laying females (percentages calculated from data in Fig. 1). We did not determine dry weight of plant and insect matter but note that 61% of Laying females contained only insects. These data are even more striking when one considers that our index of diet was biased toward finding seeds. Thus, we conclude that female cowbirds, which are mainly vegetarian before and after the Laying period, obtain sufficient protein for egg production by greatly increasing their consumption of insects. This is very similar to observations on female Pintails (Krapu 1974).

The diet composition of male cowbirds, which do not have the nutrient demands

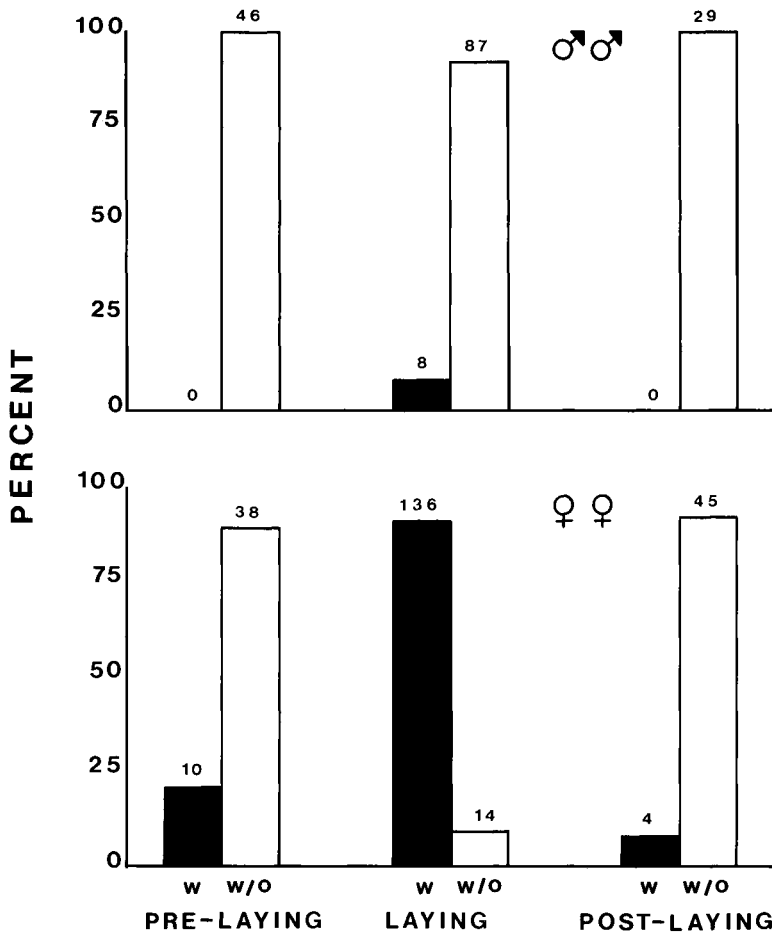


Fig. 2. Calcium ingestion by breeding cowbirds. W = with mollusc shell in gizzard; W/O = without mollusc shell in gizzard. Sample sizes shown above columns.

of egg production, should reflect the daily nutrient requirements of a nonlaying bird and, at least partially, food availability. Thus, the diet of males is useful for evaluating whether insect consumption by Laying females reflected selectivity or simply increased insect availability (insects were undoubtedly more abundant in the Laying period than during the Prelaying period). Males and females usually feed together, and there were no differences in diet of Prelaying or Postlaying males and females. Although the insect consumption by both sexes increased during Laying, however, this increase was much greater for females. Therefore, we think that females were selectively eating insects to obtain protein and perhaps other nutrients.

Recent calculations (King 1973, Ricklefs 1974) show that for small passerines the energy cost of egg laying is about 45% of a female's normal (nonlaying) basal metabolic rate and thus only 13–16% of her normal daily energy requirements. Thus, it was not surprising that the weights of fat reserves did not differ between female cowbirds starting a clutch and those finishing one. Little is known about fat reserves of other female passerines before and after they have laid a clutch of eggs. Jones

and Ward (1976) showed that female Red-billed Queleas deplete their fat reserves considerably when laying eggs. But they determined that 75% of this use was not directly for egg production and thus must have been for the female's maintenance. This, and the high reliance of these birds on protein reserves, suggests that Queleas are unable to obtain sufficient food during egg laying. That may not be surprising, as these birds nest in very dense colonies (the two colonies studied by Jones and Ward contained 20,000 and 200,000 birds) and probably rapidly deplete nearby food resources. King et al. (1965) and Morton et al. (1973) reported that female White-crowned Sparrows (*Zonotrichia leucophrys*), nesting in Alaska and California, respectively, maintained their fat reserves during the egg-laying period (in neither study, however, were females separated into those starting a clutch and those finishing one).

Females of many nonpasserine species use fat reserves when laying eggs, e.g. Blue-winged Teal (*Anas discors*) (Harris 1970), Pintail (Krapu 1974), Ring-neck Pheasant (*Phasianus colchicus*) (Anderson 1972). In anseriforms, however, the female's daily cost of egg production is 52–70% of normal daily energy requirements, and in galliforms it is 21–30% (King 1973).

We do not think that the gradual declines in fat reserves that occurred during the breeding season indicate an accumulation of slight energy deficits for Laying females or for males. Rather, we propose that they reflect a reduced need for cowbirds to maintain large reserves at that time. A major function of fat reserves is to provide energy for an organism when it is unable to obtain sufficient amounts exogenously, e.g. at night, during cold weather, and/or when food supplies are low or unpredictable (Blem 1976). There are several changes that occur during the 3 months (April–June) that comprised our Prelaying and Laying periods: (1) average temperatures increase, (2) nights become shorter, and (3) food supplies (insects and seeds) increase. These changes all decrease the need for cowbirds to maintain large fat reserves. Payne (1973) indexed fat reserves of breeding cowbirds in California by visually scoring fat deposits and stated (p. 91) that "The seasonal changes in body weight and in body fat in the cowbirds do not show clearly that breeding or molting directly exhaust the abilities of the birds to keep up their energy intake for several weeks at a time at the level required for these activities."

The difference that we found between leg bone weights of females starting and finishing clutches suggests that females use calcium reserves for egg production. Medullary bone was present in the leg bones of 4 of 5 Prelaying and 5 of 5 Laying females that were examined (A. Rick pers. comm.); sterna were not examined but probably also contained medullary bone, as it occurs there in other species that have medullary leg bone (Simkiss 1961). Leg bones of 5 males (2 Prelaying and 3 Laying) did not have medullary bone. Of the five Laying females examined, four had an oviducal egg, and the amount of medullary leg bone was less in them than in the female without an oviducal egg.

Nearly all Laying females had mollusc shell in their gizzards. Investigators have only recently begun to examine this aspect of the nutritional requirements of wild birds (see Rothstein 1972, Ricklefs 1974: 194–195), although poultry scientists long ago realized the importance of calcium to the laying chicken (Simkiss 1961). Calcareous grit (e.g. shell, bone, or gravel containing calcium salts) has been found in females of species that apparently do not store medullary bone [e.g. sandpipers (*Calidris* spp.), MacLean 1974], in some that do store it [e.g. House Sparrow (*Passer*

domesticus), Schifferli (cited in Jones 1976); Band-tailed Pigeon (*Columba fasciata*), March and Sadleir 1972], and in some in which it was not determined whether or not medullary bone was stored [e.g. Red Crossbill (*Loxia curvirostra*), Payne 1972a; Golden Plover (*Pluvialis apricaria*), Byrkjedal 1975; Red-billed Quelea, Jones 1976]. This has led to uncertainty (see MacLean 1974, Jones 1976) regarding the importance of medullary bone to wild birds, especially for species in which the female is small and lays many and/or large eggs and could not store enough calcium to lay all of them. Jones (1976: 576) stated that "Even if calcium storage occurs in Red-billed Queleas it cannot contribute much to eggshell formation." We suggest that this uncertainty has arisen from a misinterpretation of the function of medullary bone. Our understanding (from Simkiss 1961, 1967; Taylor 1970; March and Sadleir 1975) is that medullary bone serves as a calcium supply that is readily absorbed into the bloodstream and transferred to the oviduct when the egg shell is being laid down, as the gut is unable to supply calcium rapidly enough to meet the requirements of the shell gland (Taylor 1970: 92). Medullary bone is renewed daily (or over a longer period, depending on the female's laying rate) so that there is sufficient stored calcium for the next egg. Thus, medullary bone is not normally a long-term reserve and probably rarely serves to supply a female with calcium to lay a complete clutch. Further studies of other species will likely show that, whether or not the female stores medullary bone, she also consumes large quantities of calcium during egg laying. We predict that exceptions will be either birds that lay very small clutches and small eggs relative to body size or large birds that feed little during egg laying (as in Lesser Snow Geese, Ankney and MacInnes 1978).

That female cowbirds store medullary bone and consume mollusc shells does not preclude the possibility that they finish a clutch because of a calcium deficiency, but we do not think that this is so. Mean leg bone weight of Laying females with an oviducal egg did not differ from that of Laying females without one. Thus, it seems that only females finishing a clutch have lower stores of medullary bone (see Table 3), but, as they were not going to ovulate the following day, that may be expected (see above).

The proportion of males with mollusc shells in their gizzards also increased during Laying but much less than in females (Fig. 2). This may happen incidentally as they feed with females, which probably seek areas where shell is abundant (e.g. flood plains). Males, however, require some calcium for body maintenance. We cannot explain the changes in leg bone and sternum weights of males that occurred between Prelaying and Laying and during Laying.

Changes after egg laying.—None of the birds collected during the first half of the Postlaying period was molting, but 80% of females and 100% of males collected in the second half were molting. This suggests that the interval between breeding and molt is about 3 weeks in Ontario and is similar to the interval Payne (1973) reported for cowbirds in California. Thus, it is difficult to say whether the differences between Laying and Postlaying birds resulted from cessation of breeding or from preparation for and beginning of molt. The increased seed consumption and greatly reduced consumption of shell at this time suggest that the protein and calcium requirements for molt are less than those for breeding. Leg and breast muscles of males and females declined, however, between Laying and Postlaying. Although this could indicate a protein deficiency, we think that it was more likely related to reduced activity of postbreeding and molting birds. We do not have daily time budgets for

cowbirds, but our impression is that, during Postlaying, cowbirds have become much less active; they spend considerable time, in flocks, sitting in trees or on the ground close to feeding areas such as feedlots or ripening grain. King (1974: 38) generalized that birds are less active during the postnuptial molt than at other times of the annual cycle.

Fat reserves of males and females increased after the Laying period, as they also did in cowbirds in California (Payne 1973). This is apparently not unusual in small passerines with a relatively prolonged molt (Payne 1972b). The increased fat reserves may reflect the increased energy demands for feather formation and thermoregulation of molting cowbirds (Lustick 1970), especially when temperatures drop below the thermoneutral range (35–40°C, Lustick 1970). July temperatures in southern Ontario are normally below that level.

CONCLUDING COMMENTS

Female Brown-headed Cowbirds have a high egg-laying rate in southern Ontario, laying on average about 40 eggs between late April and early July (Scott and Ankney 1980). They do this apparently without relying on fat or protein reserves. Thus, Payne's (1976: 342) suggestion that the clutch size of cowbirds is limited by the amount of protein or fat that a female can store is not supported.

Rothstein (1976: 504) assumed that egg production by cowbirds is energetically so costly that it is maladaptive for them to parasitize "rejecter" species. But King (1973) calculated that egg production by passerines is a relatively slight energetic demand, and our data support this (i.e. females did not use energy reserves for egg production). Therefore, we propose that it is maladaptive for a female cowbird to parasitize a "rejecter" species only if she does so *instead* of parasitizing an "accepter" species. How frequently that occurs is unknown.

If nutrients are not limiting, why do cowbirds not lay an egg every day instead of laying in series? Rothstein (1976: 507) suggested that there are "certain physiological restraints forcing cowbirds to lay eggs in series." Alternatively, we agree with Friedmann's (1929: 184) suggestion that female cowbirds are somewhat indeterminate in laying. We propose that the "clutch size" of a female is directly related to the availability of host nests (both accepters and rejecters). We have found (Scott and Ankney 1980) that the average laying rate of cowbirds does approach an egg per day during late May and early June, when the availability of host nests is likely maximal. This, and observations of captive and wild females (Friedmann 1929: 184, Jones 1941, McGeen and McGeen 1968), suggest that many females are laying an egg a day for extended periods. Clearly needed are more data about laying rates of individual females throughout the breeding season and about the relation between laying rates and availability of host nests. The latter may be particularly difficult to obtain.

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