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CYTOLOGICAL AND CHEMICAL ADAPTATIONS OF FAT DEPOSITION IN MIGRATORY BIRDS

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INTRODUCTION

Over the past three decades, numerous anatomical and physiological adaptations have been investigated as they might relate to energetics of protracted avian flights. Most migratory species experience conspicuous biennial weight increases as the result of fat deposition prior to their flights, with the major fat depots being in subcutaneous and abdominal regions. Control mechanisms for these seasonal cycles of fat deposition have been reviewed recently by Farner et al. (1968) and clearly implicate an adaptive hyperphagia which permits some small birds to complete vernal fat deposition in 6–10 days (King and Farner 1965; Odum and Perkinson 1951). All of these activities certainly maximize energy-rich fat depots at times of greatest energetic demands (protracted flights). Less well understood, however, are events transpiring at the cytological and biochemical levels as birds deposit fat, and the present paper is a contribution toward this understanding.

MATERIALS AND METHODS

Many of the birds utilized for the data introduced here were nocturnal casualties at the WCTV television tower near Tallahassee, Florida. Birds were also obtained from various localities in Florida, chiefly in the environs of Gainesville. For consistency, in most cases of fat analyses only the interfurcular fat pad (claviculo-coracoid of McGreal and Farner 1956) was used. Fat-pad volume was measured by liquid displacement in a graduated insulin syringe. Histological manipulations were initiated with either fresh or frozen adipose tissue; sectioning at 8 μ was followed by routine staining with hematoxylin and eosin. Chemical extractions of the fat began with dehydration in a vacuum oven at 55°C until weight loss was negligible. The dried fat was thoroughly pulverized in a tube-and-pestle homogenizer using chloroform-methanol (2:1) as a solvent. The nonfat, dry components were then separated from the dissolved lipids by double-filtration through Whatman No. 42 filter paper. Subsequent complete solvent evaporation permitted quantification of the purified fat or lipid extract. Triglyceride composition of the extract was determined by the method of Van Handel and Zilversmith (1957).

CYTOLOGICAL CHANGES IN ADIPOSE TISSUE

In 1964, Odum et al. proposed that ". . . fat is added to and used from preexisting tissue spaces [adipocyte vacuoles] without appreciable change in the water content or the nonfat dry weight of the body as a whole." Essentially, this proposition meant that fat bodies of birds can increase in size without an increase in adipocyte number. Subsequent analyses of several species have generally confirmed this "tank theory" (see Hicks 1967; King and Farner 1965; Helms et al. 1967), but among these investigations only Hicks made direct histological studies. His photomicrographs suggested that fat deposition in thrushes is accompanied by only a small increase in nonfat material but a significant increase in cell size.

Subsequent to Hicks' findings, Clark (1970) made extensive histological examinations of fat from a large number of Indigo Buntings (Passerina cyanea) in our Florida laboratories. The results, summarized in part in figures 1 and 2, show that (1) the interfurcular fat pad increased in weight at a constant rate with an increase in volume; (2) no significant variation in adipocyte numbers was detected in fat pads of a very wide range of volumes; (3) adipocyte numbers in a given high power field diminished in a curvilinear fashion as the fat pad volume increased; and (4) the mean adipocyte volume increased in a curvilinear fashion with an increase in fat pad volume.

These data are consistent with the concept of constancy in adipocyte numbers, and suggest a further, important energetic adaptation for a migratory bird. If a bird can "simply" add or remove lipid materials to and from pre-existing cells, it would essentially avoid the high energetic cost of a biennial production of new cells prior to migratory flights. At first, this cytological adaptation appeared to be unique to migratory birds, but the report by Ewing et al. (1970) on bats (genus Myotis) also indicates the probable capacity to fill pre-existing adipocytes without the construction of new cells. Migratory salmon, furthermore, very likely also have a reasonably constant adipocyte number (A. A. Benson, pers. comm.), despite seasonal increases in fat.

CHEMICAL COMPOSITION OF ADIPOSE TISSUE

Qualitative or quantitative composition of adipose tissue for feral birds has been treated by Walker (1964), Rosen (1966), Hicks (1967), King (1967), Hartman and Shorland (1968), Moss and Lough (1968), West and Meng (1968a,b), and Tanhuanpaa and Pulliainen (1969). The Domestic Chicken (Gal-
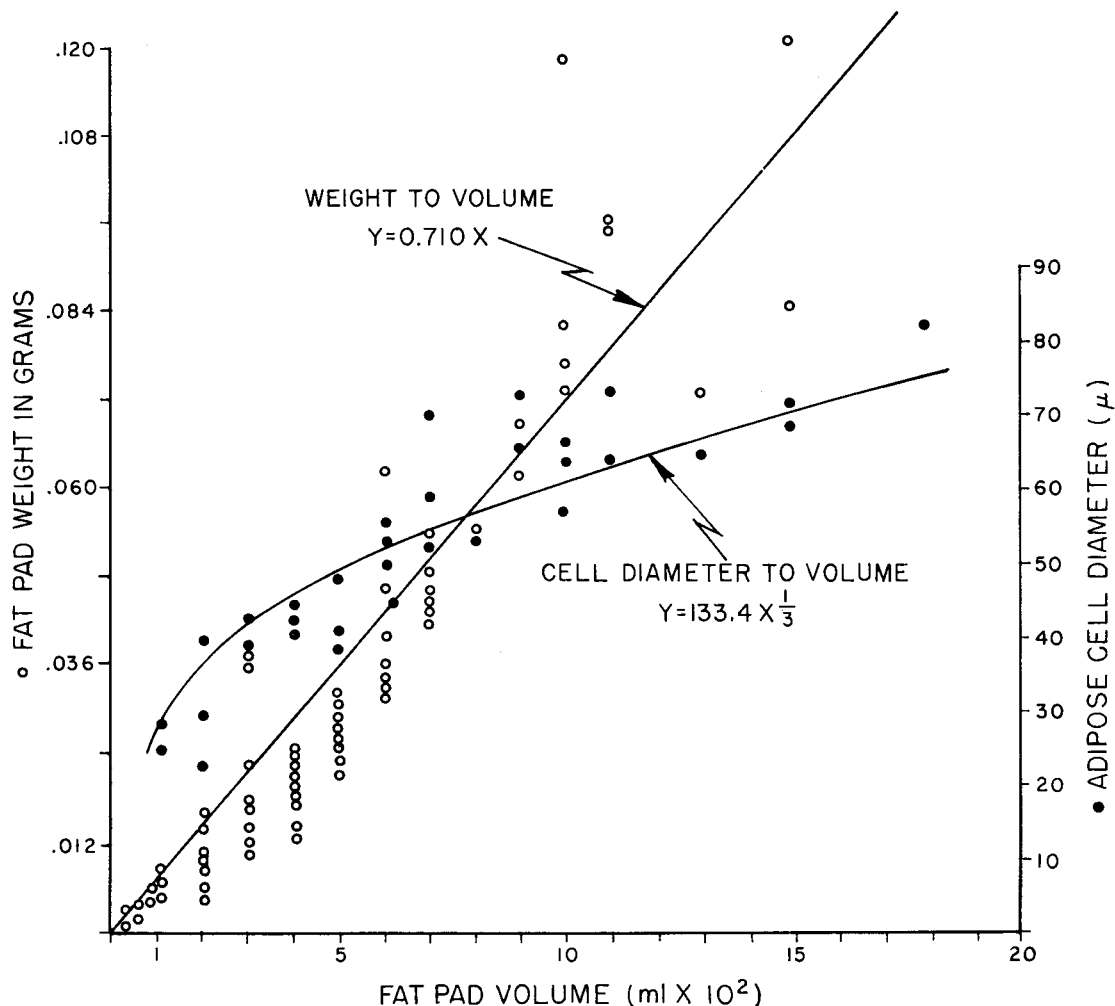
FIGURE 1. Relationship between fat pad volume, fat pad weight, and adipose cell diameter in the Indigo Bunting. Adapted from Clark (1970).

lus gallus) has also been studied in this regard (Mickelberry et al. 1966; Sell et al. 1968). For the feral birds, attention has been focused chiefly on migratory species at the time of maximum vernal fat deposition. To supplement and expand upon the results of these studies, we have recently completed a large number of extractions of adipose tissue, sampling five species of differing migratory propensities and from various seasons. The data summarized in table 1 permit the following conclusions: (1) the fraction of extractable fat ("lipid") is highest in long-distance migrants (*Passerina, Vireo*) in the vernal and autumnal premigratory and intramigratory periods; (2) conversely, the lipid fraction is conspicuously low during the summer months (*Passerina, Vireo, Dendroica, Zonotrichia*); (3) in the nonmigratory House Sparrow (*Passer domesticus*), seasonal variation in fat content of the adipose tissue is less pronounced than in the migratory species cited above; (4) postmigratory individuals of *Passerina*, though still categorized as "moderately fat" birds, have significantly less extractable fat (72%) than during pre- (89%) and intramigratory (85%) periods (this suggests intraflight utilization of lipids); and (5) interestingly, sparrows of the genus *Zonotrichia* wintering in north-

ern areas (e.g., Massachusetts) contain more extractable fat (90%) than those wintering in Florida (63%). Therefore, as a whole, the data in table 1 show that the migratory period is characterized by proportionate increases chiefly in the lipid component of adipose tissue.

The extractable fat or lipid component of the adipose tissue is high in triglycerides at the time of migration, up to 84–98% (table 2). From studies of the triglyceride moiety in domesticated species, a predominance of the unsaturated fatty acids such as oleic ($C_{18:1}$), linoleic ($C_{18:2}$) and linolenic ($C_{18:3}$) has been demonstrated (table 3). The common saturated fatty acids include palmitic ($C_{16:0}$) and stearic ($C_{18:0}$). A survey of the literature on fatty acid composition of adipose tissue in a wide variety of species suggests different patterns between nonmigrants and intramigrants. As seen in table 3, the strongly migratory forms (*Porzana, Dendroica, Vireo, Dolichonyx*) tend to be high in unsaturated fatty acids, and the data for *Acanthis* (West and Meng 1968b) depict a progressive increase in the unsaturated fatty acids with the onset of a migratory period. In addition, Nakamura (1964), basing his conclusions on iodine numbers, reported a shift toward more unsaturated fatty
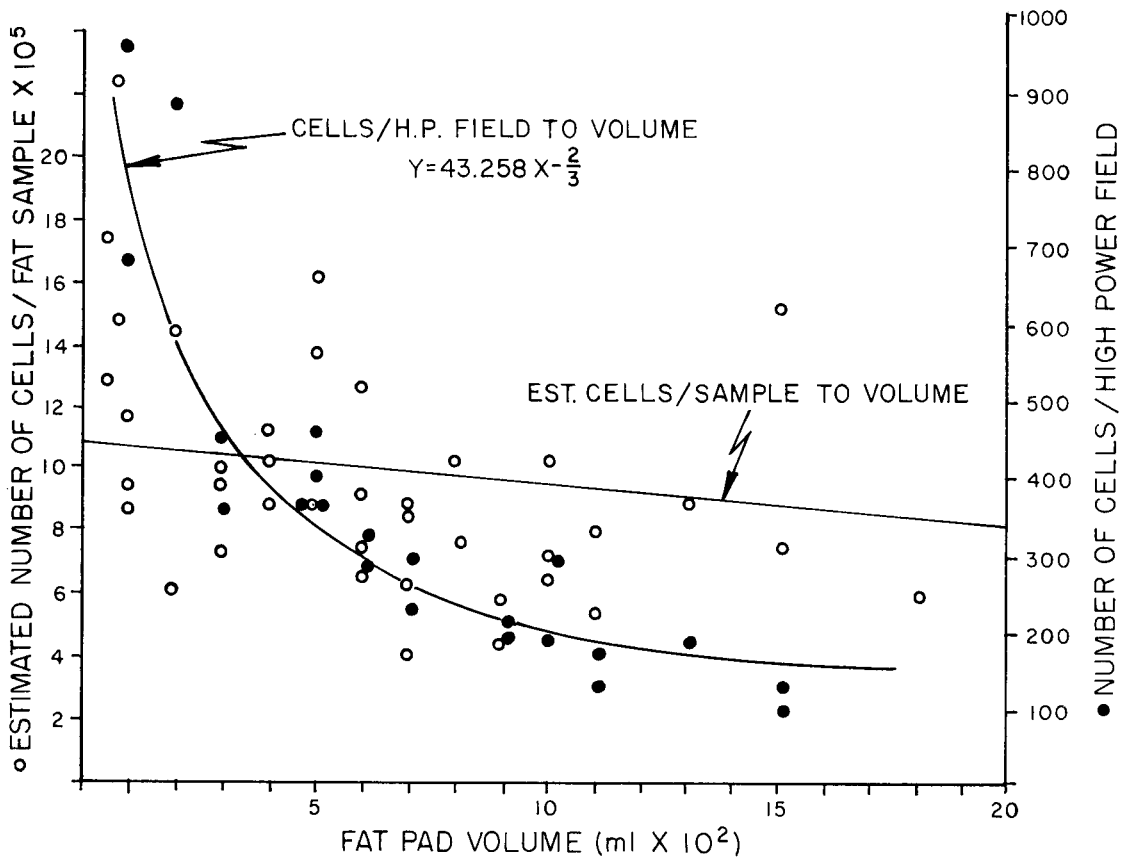
FIGURE 2. Relationship between numbers of adipocytes and fat pad volume in the Indigo Bunting. Adapted from Clark (1970).

TABLE 1. Extracted components from adipose tissue.

Species	Season	Activity status	Locality	Number specimens	Mean fat pad wt.[a] (g)	% water	% nonfat dry residue	% lipid
Indigo Bunting (*Passerina cyanea*)	Spring	Premigrant	Jamaica	(10)	0.195	5.0	5.7	89.4
	Spring	Postmigrant	Florida	(9)	0.145	19.7	8.2	72.0
	Summer	Breeding	Florida	(10)	0.039	35.6	8.9	55.6
	Fall	Migrating	Florida	(14)	0.307	9.8	4.8	85.4
Red-eyed Vireo (*Vireo olivaceus*)	Spring	Migrating	Florida	(19)	0.238	16.8	8.3	74.9
	Summer	Breeding	Florida	(5)	0.022	49.5	20.9	29.5
	Fall	Migrating	Florida	(6)	0.312	14.3	7.7	78.0
Myrtle Warbler (*Dendroica coronata*)	Spring	Premigrant	Florida	(10)	0.214	18.6	7.0	74.4
	Summer	Breeding	Canada	(4)	0.047	34.5	16.1	49.2
	Winter	Wintering	Florida	(7)	0.056	9.1	4.6	86.3
White-throated Sparrow (*Zonotrichia albicollis*)	Spring	Premigrant	Florida	(6)	0.078	32.9	16.3	50.8
	Summer	Breeding	Canada	(11)	0.072	46.4	17.7	35.9
	Fall	Postmigrant	Florida	(7)	0.076	34.3	16.0	49.7
	Winter	Wintering	Florida	(8)	0.101	31.1	6.4	62.5
	Winter	Wintering	Mass.	(4)	0.228	7.6	2.2	90.2
House Sparrow (*Passer domesticus*)	Spring	Breeding	Florida	(8)	0.156	24.4	9.1	66.5
	Winter	Wintering	Florida	(9)	0.121	30.0	9.4	60.6
	Winter	Wintering	Mass.	(10)	0.079	41.1	9.3	49.6

[a] Interfurcular fat pad. This weight gives an indication of the bird's overall obesity, i.e., a *lean* bird's pad = ca. 0.01–0.07 g, *moderately fat* = ca. 0.1 g, *obese* bird = 0.2–0.3 g.

TABLE 2.   Percent triglycerides extracted from adipose tissue.[a]

Month	No. specimens	Species	% Triglycerides
April	2	Indigo Bunting (*Passerina cyanea*)	88.7, 87.2
	1	Myrtle Warbler (*Dendroica coronata*)	92.4
	2	Red-eyed Vireo (*Vireo olivaceus*)	84.9, 98.1
July	1	Myrtle Warbler	63.6
	2	White-throated Sparrow (*Zonotrichia albicollis*)	43.5, 55.9

[a] Interfurcular depots.

acids prior to migration in Grey's Grasshopper Warbler (*Locustella fasciolata*). The adaptive significance of increased unsaturated fatty acids at the time of migration is obscure, but it might be associated with a greater mobility of lipid stores when metabolically needed.

Diet is known to influence depot fat composition, such that a seasonal shift in diet (from one high in saturated fatty acids to one high in unsaturated fatty acids) should evoke a proportionate shift in the adipose tissue composition. Several authors, including Walker (1964), Bower and Helms (1968), West and Meng (1968a,b), earlier made this suggestion for migratory birds, but field and laboratory data are not yet conclusive. To shed some light on temporal features of fatty acid composition, Landau (1970) exposed caged Indigo Buntings to various experimental diets and, in the spring, biopsied the fat depots at 2-week intervals. Some of his data (fig. 3) show that in *all* cases specific fatty acids in adipose tissue reached the dietary level in some 6–8 weeks. Because these birds were not as obese as feral ones at the same season, it seems plausible that the latter might reflect dietary changes in fatty acids more rapidly.

SUMMARY

Morphological and physiological adaptations relating to energy-rich adipose tissue in migratory birds have been elucidated in recent decades. Cytological investigations of fat depots in Indigo Buntings support the hypothesis that increasing obesity is accomplished by an increase in lipid content per adipocyte rather than by an increase in adipocytes. Furthermore, chemical extractions of adipose tissue from a variety of migratory passerine species have revealed generally an inverse correlation between the lipid fraction and either the nonlipid or water fractions.

Triglycerides from the lipid fraction predominate at the time of migration, but not necessarily at other seasons. In most birds that have been studied the triglycerides consist chiefly of unsaturated fatty acids, and some evidence suggests that proportional increases in unsaturated fatty acids in depot fat occur at the time of migration. These increases are probably related to dietary shifts in nature. The studies of caged buntings reveal that a period of 6–8 weeks elapse before alterations in dietary fatty acid levels are clearly and uniformly reflected in the depot fat levels.

TABLE 3.   Fatty acid composition of avian adipose tissue.[a]

Species	% total fatty acids	
	Saturated	Unsaturated
Kiwi (*Apteryx australis*)	24.2	75.8
Quail (*Coturnix coturnix*)	31.3	68.7
Domestic Chicken (*Gallus gallus*)	23.7–33.9	66.1–75.6
Black Grouse (*Lyrurus tetrix*)	22.0–29.1	71.9–78.0
Capercaillie (*Tetrao urogallus*)	16.0–20.7	79.3–84.0
Rock Ptarmigan (*Lagopus mutus*)	33.4	66.6
Willow Ptarmigan (*Lagopus lagopus*)[b]	24.0–31.6	68.4–76.0
Takahe (*Notornis mantelli*)	25.6	74.4
Sora (*Porzana carolina*)	19.0	81.0
Grey's Grasshopper Warbler (*Locustella fasciolata*)[c]	23.0	77.0
Wood Thrush (*Hylocichla mustelina*)[d]	32.3–34.1	65.9–66.1
Wood Thrush (*Dendroica* 2 spp., *Vireo olivaceus*)	16–18	82–88
Bobolink (*Dolichonyx oryzivorus*)	20.0	80.0
Common Redpoll (*Acanthis flammea*)[c,e]	6.5	93.5
	23.9	76.1

[a] Data from Hartman and Shorland (1968), Lovern (1938), McMullin et al. (1968), Moss and Lough (1968), Nakamura (1964), Rosen (1966), Tanhuanpaa and Pulliainen (1969), Walker (1964), West and Meng (1968a,b).
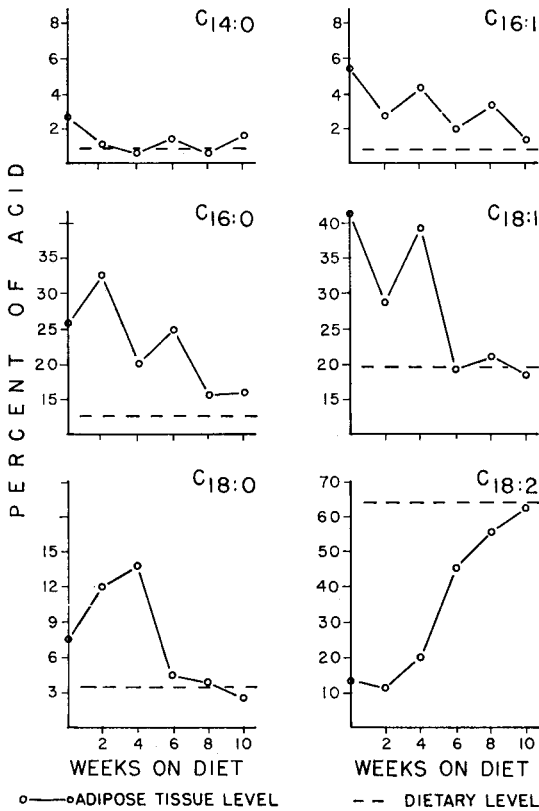[b] Annually.
[c] Spring.
[d] May–Sept.
[e] Summer.

FIGURE 3. Levels of fatty acids in adipose tissue of caged Indigo Buntings. Adapted from Landau (1970).

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DEVELOPMENT OF THERMO-REGULATION IN MALLARD DUCKLINGS

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Numerous investigators have found hypothermia caused by chilling and evaporative cooling in wet young birds. The development of thermoregulation in newly hatched birds was reviewed by Romanoff (1941). Nye (1963) worked with heat loss in the precocial wet, downy young of Mallards (*Anus platyrhynchos*) and Domestic Chickens (*Gallus gallus*) and found the ability to thermoregulate correlated to the water-proofing quality of their down. Ability to thermoregulate in duckling species has been correlated with environmental temperatures by Koskimies and Lahti (1964). They found ducklings of more northern nesting waterfowl able to maintain normal body temperatures for extended periods of time at a low ambient temperature whereas those of more southern nesting species did not.

METHODS AND MATERIALS

Mallard ducklings were taken from automatically controlled incubators immediately after hatching and placed in a temporary brooder. The temperature in the brooder was maintained between 35–40°C. Each duckling was individually marked by a series of web punches.

Each bird was subjected to one or more thermoregulatory experiments. Successive experiments in individual birds were separated by at least 12 hr to allow recovery from previous experiments. The elapsed times from hatching to the beginning of the trial periods were 0, 1, 2, 4, 8, 16, and 24 hr. Each trial consisted of three to five treatments run on different birds of the same age group. Experiments were also conducted on a wet and dry carcass for comparison.

The treatment lasted one-half hour, during which continuous recordings were made of a body and ambient temperature. Body temperature was taken by a thermistor placed down the esophagus and into the gizzard. A small, precooled box was used to confine the bird inside an environmental chamber. Ambient temperature inside the chamber was maintained at 1–2°C throughout the treatments. An Atkins multi-probe switch box (Atkins Technical Inc., Gainesville, Florida) and an Esterline Angus recorder (Esterline Angus Inc., Indianapolis, Indiana) were used to record temperatures.

RESULTS AND DISCUSSION

One-way analysis of variance was used to compare average slopes of various trials. Variances were found homogeneous. Ducklings age 0 and 1 hr; 2 and 4 hr and the dry carcass; and 4, 8, and 16 hr were not found significantly different from each other using Duncan's test for separation. The wet carcass
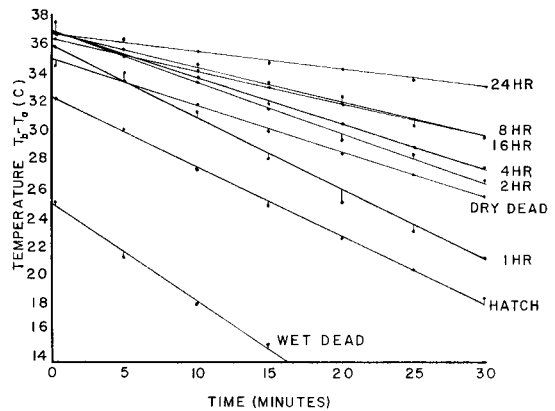

FIGURE 1. Difference between Mallard duckling body temperature and ambient temperature plotted at 5-min intervals. Duckling age in hours appears on the right. Lines represent the expected slope of cooling for that age. Data points are average of trial.

and 24-hr ducklings were significantly different from all other trials. Significance level was 0.90.

Mallard ducklings are near homeothermic 24 hr following hatching (fig. 1). Subsequent tests on 48-hr birds may well show them to maintain even more stable body temperatures during treatment than 24-hr ducklings. When exposed to cold, an initial slight drop in body temperature in young ducklings would be expected as Scott (pers. comm.) found in adult Mallards. It is doubtful downy young could thermoregulate over extended periods. Koskimies and Lahti (1964) stated that thermoregulation in young Mallards breaks down when exposed to low ambient temperatures for periods longer than used in these experiments. In the wild, young are brooded by the female for a large part of the first 24 hr and periodically thereafter. Mallard ducklings need some external heat source until 2 weeks of age (pers. obser.). However, their ability to thermoregulate for short periods without exogenous heat permits them to forage for a few hours without direct or indirect parental care before 2 weeks of age. This is an essential characteristic of the more precocial birds that receive no food from the parent.

The data represented in figure 1 indicate two major periods of change in the ability to maintain body temperature. One period of increased thermoregulatory ability occurs between 1 and 2 hr following hatching and the other between 16 and 24 hr. The ability to maintain temperature was similar between 2 and 4-hr groups and between 4, 8, and 16-hr groups, but changed between and after them. I believe the first period is probably due to increasing insulation values of drying down. The second period is due to physiological change in the individual occurring during this period. One hour after hatching ducklings were damp, insulation values were not yet at a maximum. At 2 hr, ducklings were dry and at 4 hr, the majority of