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Multivariate Analyses of Mid-Winter Fattening in Two Species of Passerine Birds

Michael Harold Shelor

College of Humanities and Sciences
Virginia Commonwealth University

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Director of Thesis

[redacted]

Committee Member

[redacted]

Committee Member

[redacted]

Committee Member

[redacted]

Department Chairman

[redacted]

College Dean

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Date

Multivariate Analyses of Mid-Winter Fattening in Two Species of Passerine Birds

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University

by

Michael Harold Shelor

Director: Dr. Charles R. Blem

Professor of Biology

Virginia Commonwealth University

Richmond, Virginia

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INTRODUCTION

Although the adaptive significance of daily and seasonal fattening of birds has been studied by many investigators (see Odum, 1965; King, 1972; Blem, 1976a), surprisingly little is known about the interactions of proximate and ultimate environmental factors regulating avian lipid levels. An exception is the study by Evans (1969). He found that lipid levels in Yellow Buntings (*Emberiza citrinella*) were more closely correlated with long-term temperature averages than with temperatures of the day of capture, or the days preceeding or following capture. This is an indication that temperature may be more important as an ultimate control of fattening, through natural selection, than as a proximate cue. The relative effects of temperature, photoperiod, and morphological variables on daily lipid levels have not been assessed simultaneously in any species. Mid-winter fattening appears to be a widespread phenomenon in small birds of the temperate zone, but it is well known for only a small number of species (see King, 1972; Blem, 1976a; for reviews). It is known that lipid levels fluctuate and the amounts stored vary with weather conditions, both daily and seasonally. The amplitude of the daily cycle and the magnitude of lipids stored are maximized during mid-winter. Most of the birds have energy reserves for only a few hours of activity in the morning. It has also been found that lipid stores are not greater during favorable weather conditions. This suggests a balance between lipids stored for energy production and energy required for food gathering activities, risks from predation and lethal temperature extremes.

Statistical models of the relationship between environmental variables and the amount of lipid reserve began with research by King and Farner (1966) and Evans (1969). Their results emphasized the importance of climatic variables as both proximate and ultimate factors (also see Vincent and Bedard, 1976). These analyses involved only simple regression techniques or restricted multivariate models involving only a few or single dependent variables. More sophisticated multiple regression techniques and modern computer implementation provide a means of determining the relative importance of several independent variables in the prediction of a dependent variable. This type of analysis is particularly suited to certain aspects of fat deposition in sparrows.

Multiple regression analyses provide two potentially important pieces of information about independent variables. The coefficient of determination (R^2) is an estimate of the amount of variability explained by the multiple regression coefficient (Zar, 1974) and the standard partial regression coefficients indicate that relative importance of independent variables in the prediction of a dependent variable. Such analyses do not insure that all significant variables have been included or even considered, however, such variables may be later added to the model. In this study the relative importance of a wide range of variables will be investigated.

The purpose of the present analysis is threefold: (1) Firstly, an attempt has been made to develop predictive equations which might be used to quantify lipid reserves in passerine birds from measurements of living specimens. Specific points analyzed herein include: (a) how accurately might such equations predict lipid content, and (b) how many birds must be included in the analysis to obtain maximum accuracy. (2) The second emphasis of this study is the identification and comparison of important independent variables and a comparison of the relative importance of morphometric variables with environmental measures. (3) Finally, a comparison will be made of the relative importance of various temperature measures of the day of capture with long-term averages in an attempt to assess the relative selective importance of prolonged temperature regimes.

Estimates of lipid content are useful for field studies of premigratory fat deposition, the energetics of overnight survival, or any life history phenomena where storage and utilization of energy is crucial. Variables will be measured that will provide relatively precise predictions of the fat content of birds. The success of this attempt will be primarily indicated by the coefficient of determination (R^2). Hopefully, models will be generated that will provide a method for studying lipid deposition cycles without tedious fat extraction processess or having to sacrifice large numbers of wild birds.

METHODS

House Sparrows (*Passer domesticus*) and White-throated Sparrows (*Zonotrichia albicollis*) were captured by mist-net throughout the winter (November, 1975 - March, 1976) at several locations in the metropolitan area of Richmond, Virginia. House Sparrows were captured at a livestock yard located in the central portion of the city and in the suburbs of western Henrico County. A few birds were collected from other locations in Hanover County north of Richmond. White-throated Sparrows were collected in suburban west Richmond and western Henrico County. The House Sparrows had access to ample food throughout the winter at feeders and from scattered livestock feed. White-throated Sparrows either foraged naturally in forest edge or visited feeders.

Approximately a three-week collecting cycle was maintained so that birds were captured over the widest possible variety of dates, times and weather conditions. No bird remained in the net longer than five minutes and most were removed and sacrificed by thoracic compression immediately. The time of capture was recorded in total minutes after midnight and each bird was weighed in the field to the nearest 0.1 g on a triple beam balance. Specimens were temporarily stored on ice and transported to the lab in a portable ice chest where they were quickly frozen. They were stored in a freezer until further analysis could be conducted.

Thawed birds were reweighed on an electronic balance to the nearest 0.01 g as a check of field weights. Wing chord was measured to the nearest millimeter and primary feathers were then removed. Tarsometatarus length was measured to the nearest 0.1 mm by means of calipers. Length of the tarsometatarsus was determined to be the distance between the notch formed by the joining of the tibiotarsus and tarsometatarsus distally to the last rigid, undivided scale where the tarsometatarsus joins the phalanges. The culmen of the bill was measured from the external nares to the tip to the nearest 0.1 mm. Fat class, a subjective evaluation of the obesity of the bird based on the amount of furcular and abdomenal fat, was determined visually with the aid of a classification scheme devised by Helms and Drury (1960) and modified slightly in that intermediate classes were recognized (see Table 1).

The birds were then plucked and dissected. Gonad length and width was measured with calipers to the nearest 0.5 mm. Size was determined by multiplying length times width to arrive at a number by which gonad size could be relatively compared. In male birds, three distinct size classes were evident whereas in females only two distinct class could be determined. These were assigned subjective values of 1-3 and 1-2 respectively for analysis. All measurements were made on gonads on the left side of each specimen.

Crop contents were removed, weighed and fresh weights corrected by subtracting the weight of food. Each bird was sectioned and freeze-dried for 72 hours. The dried carcass was reweighed and the dry weight was determined. Each carcass was then ground in a Waring blender in preparation for the fat extraction process.

Lipid content of each bird was determined by Soxhlet extraction with a 5:1 mixture of petroleum ether:chloroform. Extraction time was

24 hours, which, according to preliminary tests, was sufficient to remove all lipid. Aliquots of dried pulverized carcass were weighed before and after extraction and the percentage of fat loss was determined. Lean dry weight was calculated as dry weight minus total fat, where total fat is dry weight X fat content (as a decimal fraction). The lipid index was determined and is defined as lipid (g)/lean dry weight (g).

A wide variety of temporal and environmental variables associated with the collection time of each bird was obtained for future analyses. Temporal data included the Julian date, month, hour (converted to the hour plus decimal fraction), number of hours after sunrise, number of hours before sunset and the total hours of daylight. All times except month and date were recorded to the nearest 0.1 hour. Climatic variables for each collection day included mean dry bulb temperatures, both for year of capture and long-term (35 year) averages, and the daily extremes. Mean wet-bulb temperature and the daily extremes were also recorded. A long-term average for wet-bulb temperature was not available from U. S. climatological data. Also included in the analysis was a repeat of dry bulb, long-term dry bulb, and wet-bulb temperature averages for the day before and the day after capture. The daily means for relative humidity and wind velocity were included. Wind chill factor was determined from the above parameters by the formula derived by Siple and Passell (1945). This formula is:

$$\text{Kcal/m}^2\text{/h} = (10.45 - v + 100\ v)\ (33 - T)$$

where v is wind speed in meters/sec and T is dry bulb temperature in °C. A number of other variables and interactions between variables were also computed and used in the analyses (see Table 1 for a summary of all variables).

All analyses were performed by means of the "Stepwise, Max R" pro-

Table 1. Independent variables included in analyses of mid-winter fattening of the House Sparrow and White-throated Sparrow.

I. Morphological variables

A. Body weight (g)[1]
B. Wing length (mm)
C. Culmen length (mm)
D. Tarsus length (mm)
E. Sex (Male = 1, female = 2)
F. Fat class

II. Temporal variables

A. Julian date[2]
B. Month[3]
C. Hours after sunrise[4]
D. Hours before sunset[4]
E. Eastern standard time[4]
F. Photoperiod (hours of light)[4]

III. Weather variables

A. Dry-bulb temperature[5]
B. Long-term (35-year) average dry-bulb temperature[5]
C. Wet-bulb temperature[5]
D. High and low dry-bulb temperatures
E. High and low wet-bulb temperatures
F. Relative humidity
G. Barometric pressure[5]
H. Precipitation[5]
I. Wind velocity
J. Percentage sunshine
K. Chill factor[6]

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[1] Also body weight expanded to the exponential powers 0.67, 0.72, and 0.75.

[2] Adjusted so that days from November through March are numbered consecutively.

[3] November = 1, December = 2, January = 3, February = 4, March = 5.

[4] Quantified to the nearest 0.1 hour.

[5] Including the day of capture (D), day before capture (DB), and day after capture (DA).

[6] Calculated by method described by Siple and Passel, 1945.

cedure of the Statistical Analysis System (SAS Institute, 1979) as implemented by IBM 370/145 computer. This is a multiple regression procedure which finds the "best" one-variable model first. This is the equation including a single independent variable which produces the maximum R^2 (coefficient of determination). The coefficient of determination indicates the percent of variation attributable to the model (included in the predictive equation). Once the one-variable model is found, the variable which produces the greatest increase in R^2 of the remaining variables is chosen and added to the model. Each of the remaining variables is compared to those already in the model to determine if replacing the variable by one not in the model would result in a larger R^2. The process continues until it is determined that no exchange of variables could increase R^2, and the resulting model is deemed the "best".

RESULTS

One hundred House Sparrows and 99 White-throated Sparrows were collected during mist-netting activities. In addition, a test sample of 21 House Sparrows was collected from November 1976 - March 1977. Sample sizes and sex ratios are summarized in Table 2. Weights and gross carcass composition are summarized in Tables 3 and 4.

House Sparrows. An analysis of variance within and between variables categorized by month and sex revealed that wing length varied significantly with sex (F = 60.4) and with the month of capture (F = 5.9). There was a significant sexual difference in lipid quantity (F = 5.0) and in lipid index (F = 6.3); however, there was no significant monthly difference in either of these variables (see Table 5). There was no significant sexual or monthly difference in body weight or lean dry weight of House Sparrows collected in this study.

A large number of independent variables were used to generate various equations for predicting lipid levels. Many of these variables appeared significant in one or more of the models generated and interactions between some variables proved to be even more important. The most important single variables for the prediction of lipid content in this study are fat class and body weight. Body weight was slightly more influential in the predictions when adjusted to the exponential power of 0.72 as was determined by maximum improvement in the coefficient of determination (R^2). The model best predicting lipid levels

Table 2. Sexes and capture dates of House Sparrows and White-throated Sparrows used in the analyses.

		Males	Females	Total
House Sparrows				
	November, 1975	13	6	19
	December, 1975	17	10	27
	January, 1976	7	3	10
	February, 1976	14	7	21
	March, 1976	11	12	23
	Total	62	38	100
White-throated Sparrows				
	November, 1975	1	1	2
	December, 1975	10	11	21
	January, 1976	17	7	24
	February, 1976	17	14	31
	March, 1976	10	10	20
	April, 1976	1	0	1
	Total	56	43	99

Table 3. Body composition of House Sparrows collected near Richmond, Virginia. All values are means ± one standard error.

Date	Sex	Weight (g)	Fat class	Lean dry weight (g)	Lipid (g)	Lipid index
November, 1975	Male	29.2 ± 0.5	1.9 ± 0.2	7.3 ± 0.1	1.5 ± 0.2	0.20 ± 0.01
December, 1975	Male	28.5 ± 0.4	1.8 ± 0.2	7.0 ± 0.1	1.3 ± 0.1	0.18 ± 0.01
January, 1976	Male	28.1 ± 0.7	1.8 ± 0.3	6.9 ± 0.2	1.4 ± 0.2	0.21 ± 0.02
February, 1976	Male	27.4 ± 0.4	2.0 ± 0.2	6.8 ± 0.1	1.4 ± 0.1	0.20 ± 0.01
March, 1976	Male	28.0 ± 0.4	1.9 ± 0.2	6.9 ± 0.1	1.4 ± 0.1	0.19 ± 0.01
November, 1975	Female	26.1 ± 0.5	2.1 ± 0.2	6.5 ± 0.1	1.5 ± 0.1	0.22 ± 0.01
December, 1975	Female	28.0 ± 0.6	2.1 ± 0.2	6.9 ± 0.2	1.5 ± 0.1	0.22 ± 0.02
January, 1976	Female	28.2 ± 1.1	2.2 ± 0.2	6.8 ± 0.3	1.5 ± 0.1	0.22 ± 0.02
February, 1976	Female	28.8 ± 0.5	1.9 ± 0.3	7.2 ± 0.3	1.5 ± 0.1	0.19 ± 0.02
March, 1976	Female	27.8 ± 0.5	1.9 ± 0.2	6.8 ± 0.1	1.5 ± 0.1	0.23 ± 0.01

Table 4. Body composition of White-throated Sparrows collected near Richmond, Virginia. All values are means ± one standard error.

Date	Sex	Weight (g)	Fat class	Lean dry weight (g)	Lipid (g)	Lipid index
November, 1975	Male	25.6	1.5	6.5	1.3	0.20
December, 1975	Male	28.3 ± 0.6	2.2 ± 0.4	7.0 ± 0.2	2.3 ± 0.1	0.32 ± 0.01
January, 1976	Male	29.3 ± 0.4	3.8 ± 0.2	7.0 ± 0.1	4.3 ± 0.2	0.62 ± 0.03
February, 1976	Male	29.0 ± 0.5	3.6 ± 0.3	6.7 ± 0.1	4.0 ± 0.3	0.59 ± 0.04
March, 1976	Male	27.4 ± 0.6	2.1 ± 0.6	6.9 ± 0.2	1.8 ± 0.1	0.26 ± 0.01
April, 1976	Male	28.0	4.0	6.0	4.5	0.75
November, 1975	Female	30.2	1.0	8.0	1.4	0.18
December, 1975	Female	28.1 ± 0.6	2.2 ± 0.3	7.1 ± 0.2	2.1 ± 0.2	0.29 ± 0.03
January, 1976	Female	32.1 ± 0.8	3.7 ± 0.5	7.6 ± 0.3	4.6 ± 0.4	0.60 ± 0.05
February, 1976	Female	30.3 ± 0.6	3.1 ± 0.3	7.1 ± 0.1	3.8 ± 0.4	0.53 ± 0.06
March, 1976	Female	28.0 ± 0.5	1.5 ± 0.2	7.1 ± 0.2	1.9 ± 0.1	0.26 ± 0.01

Table 5. Results of analysis of variance within House Sparrow measurements. ($P < F$ = probability of obtaining a smaller F value).

Dependent variable	Intersexual variation		Intermonthly variation	
	F	P< F	F	P< F
Lipid	4.95	0.03	0.27	0.90
Lean dry weight	0.23	0.63	0.99	0.42
Lipid index	6.29	0.01	0.67	0.61
Fat class	1.44	0.23	0.06	0.99
Body weight	1.79	0.18	0.39	0.81
Wing length	60.40	0.0001	5.88	0.0003
Culmen length	5.06	0.03	0.77	0.55
Tarsometatarsus length	1.01	0.32	0.73	0.57

utilizing all available independent variables was:

$$\text{Lipid (g)} = 0.967 + 0.129\ (\text{body weight})^{0.72} - 1.206\ \text{fat class} + 0.071\ \text{sex (fat class)} - 0.027\ \text{hours before sunset}$$

As judged by the partial sum of squares, body weight (1.65) and fat class (1.00) are more important than sex (fat class) (0.37) and hours before sunset (0.39) in the equation. The coefficient of determination (R^2) was 0.83.

Some models were generated using only temperature and other environmental variables, however, these proved to be much poorer predictors of lipid levels in sparrows. For instance, the "best" equation using all environmental variables, that is, temporal and weather, is:

$$\text{Lipid (g)} = 2.473 - 0.212\ \text{photoperiod} + 0.044\ \text{hours before sunrise} - 0.44\ \text{dry-bulb temperature (DB)} - 0.612\ \text{dry-bulb temperature (D)} + 0.095\ \text{dry-bulb temperature (DA)} + 0.053\ \text{average dry-bulb temperature (D)} + 0.330\ \text{high dry-bulb temperature} + 0.037\ \text{low dry-bulb temperature} - 0.131\ \text{wet-bulb temperature (DA)} - 0.052\ \text{wind velocity},\ R^2 = 0.40$$

The subscripts D, DB and DA denote the measure is either for the day of collection, day before the collection day or day after the collection day, respectively. All temperatures are in °F.

When only temperature variables were used, efforts to predict lipid levels were even further obscured. The "best" model incorporating only thermal variables was:

$$\text{Lipid (g)} = 1.320 - 0.052\ \text{dry-bulb temperature (D)} + 0.035\ \text{dry-bulb temperature (DA)} + 0.056\ \text{wet-bulb temperature (D)} - 0.034\ \text{wet-bulb temperature (DA)},\ R^2 = 0.25$$

White-throated Sparrows. Analysis of variance (Table 6) indicates significant intersexual variation in lean dry weight (F = 7.81), fat class (F = 4.70), body weight (D = 3.95), wing length (D = 20.28) and tarsometatarsus length (F = 3.91). Significant intermonthly variation was found in lipid levels (F = 24.63), lipid index (F = 29.22), fat class (F = 14.72), body weight (F = 4.10) and (oddly) culmen length (F = 2.51).

The most important single variable in the prediction of lipid reserve of White-throated Sparrows are, as in the House Sparrow, fat class and body weight (Table 7). The "best" model incorporating all available independent variables was:

Lipid (g) = 0.41 month + 1.21 hour + 0.28 body weight - 0.07 wing length + 0.49 fat class - 1.24 hours after sunrise - 9.843

where month is November = 1, December = 2, ..., and hour is given in normal notation except that fractions are given as decimals (e.g. 14:30 = 14.5). The coefficient of determination (R^2) is 0.82.

The "best" model using only environmental variables is:

Lipid (g) = 16.653 - 0.178 photoperiod + 0.040 hours after sunrise + 0.008 relative humidity + 0.009 dry-bulb temperature (DA) - 0.007 wet-bulb low extreme temperature - 0.472 barometric pressure, R^2 = 0.32.

The "best" model using only temperature is:

Lipid (g) = 9.472 + 0.116 dry-bulb (D) - 0.111 dry-bulb (DB) -.123 high extreme, R^2 = 0.37.

It should be noted, however, that the first variable to enter the equation (best one-variable model) was the long-term average dry-bulb temperature for the day of capture. In general, most temperature variables demonstrated significant correlation coefficients with lipid

Table 6. Results of analysis of variance within White-throated Sparrow measurements. ($P < F$ = probability of obtaining a smaller F value).

Dependent variable	Intersexual variation		Intermonthly variation	
	F	P < F	F	P < F
Lipid	1.37	0.25	24.63	0.0001
Lean dry weight	7.81	0.006	1.00	0.42
Lipid index	3.38	0.07	29.22	0.0001
Fat class	4.70	0.03	14.72	0.0001
Body weight	3.95	0.05	4.10	0.002
Wing length	20.28	0.0001	0.86	0.51
Culmen length	1.41	0.24	2.51	0.04
Tarsometatarsus length	3.91	0.05	0.53	0.75

content (Table 7), and average long-term temperatures had slightly greater correlation coefficients than single day measures.

Table 7. Correlation coefficients (r) for equations predicting lipid content of White-throated Sparrows and House Sparrows from single independent variables.

	House Sparrows	White-throated Sparrows
Body weight	0.60	0.69
Fat class	0.80	0.81
Sex	0.20	n.s.
Photoperiod	n.s.	-0.28
Hours after sunrise	0.48	n.s.
Hours before sunset	-0.50	n.s.
Temperatures		
Dry-bulb (DB)	n.s.	n.s.
Dry-bulb (D)	-0.19	-0.39
Dry-bulb (DA)	n.s.	-0.43
Average dry-bulb (DB)	n.s.	-0.53
Average dry-bulb (D)	n.s.	-0.53
Average dry-bulb (DA)	n.s.	-0.52
High extreme	-0.21	-0.47
Low extreme	n.s.	-0.26
Barometric pressure	-0.20	-0.24
Percent sunlight	-0.24	-0.25

Table 8. Correlation coefficients (r) for equations predicting lipid content of White-throated Sparrows from temperature measurements.

Measurement	r
Day of capture (1975-76)	-0.39
Average for day of capture	
2 year	-0.33
3 year	-0.23
4 year	-0.26
5 year	-0.32
30 year	-0.53
Day of capture (1974-75)	-0.11*

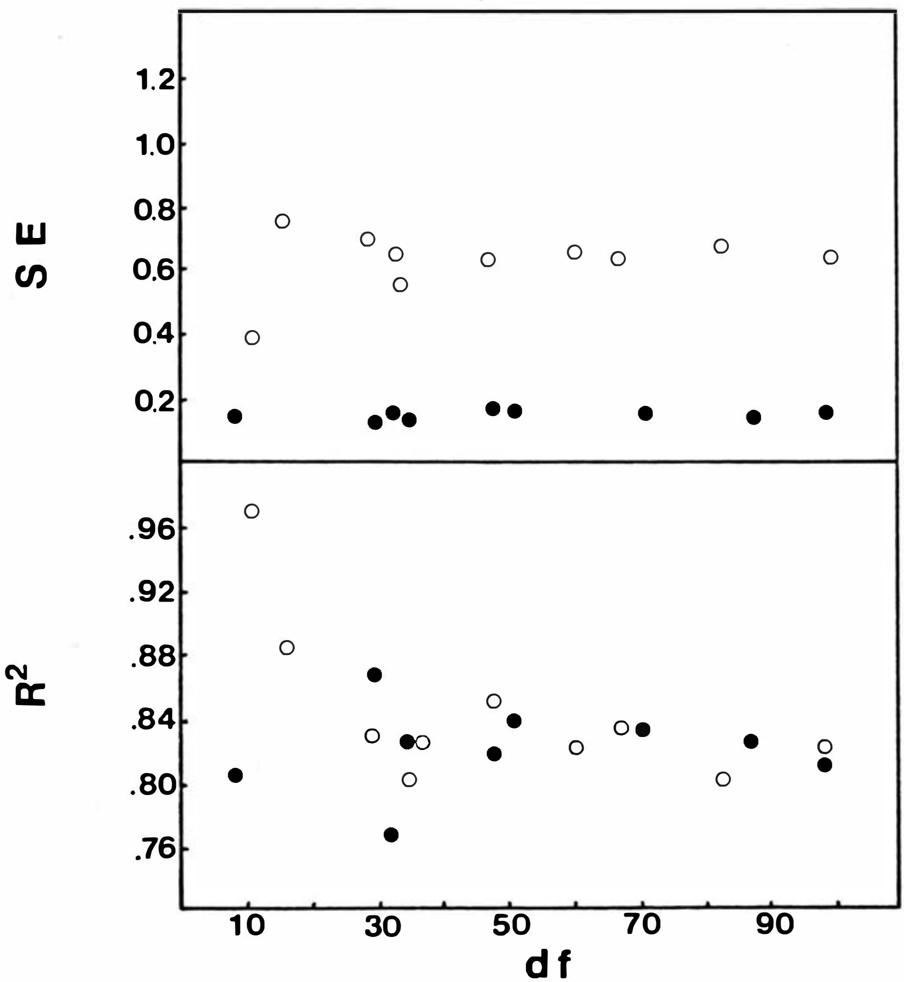
*not statistically significant

DISCUSSION

Quantitative analyses of complex biological phenomena have been greatly advanced by modern multivariate statistical techniques implemented by computers. A major statistical technique which has found much use in recent ecological research is multiple regression analysis. Multiple regression analysis is a statistical technique for partitioning the variation around a dependent variable among all recognized independent variables in the model. Multiple regression is used in situations in which the investigator wishes to identify those variables which are most important to the process under investigation or to produce an equation which accurately predicts values of some dependent variable. In the first situation, variables that have statistical importance when analyzed individually may be obscured by other factors in complex analyses if the method of computation is not chosen carefully. Multivariate models have some inherent weaknesses: (1) Multiple regression equations and associated statistics must be viewed as indicative of the relative statistical importance of independent variables, not their absolute biological importance. (2) One cannot be sure that all significant independent variables have been included. If such variables are added to a later model, one may find the predictive precision is increased and independent variables previously thought to be important are now less important or have become insignificant. (3) The technique used to discover appropriate multivariate equations may influence the exact equations obtained. In searching for an appropriate predictive equation, regression on a subset of variables may be preferable to an equation which contains all of the variables, but is unstable. There are several available methods available for the selection of "best" regression equations. "Best" equations are those that produce maximum coefficients of determination (R^2 values). Coefficients of determination indicate the decimal fraction of total variation explained by the model in use. Most criteria for the selection of "best" equations are functions of the residual sum of squares for subsets having the same number of independent variables (Hocking, 1972). The commonest procedure involves computation of all possible regression equations and the selection of those having the minimum residual sum of squares among all subsets of the same size. For _n_ variables, the number of possible regression equations is $2^n - 1$ and the relative number of operations required to handle each subset is proportional to n^3 (Furnival and Wilson, 1974). In a common alternative procedure, one employs some selection criterion for adding or deleting variables from an analysis. Such methods identify variables for addition or deletion based on the amount of change in the coefficient of determination (R^2). These methods include forward selection ("step=up"), backward elimination ("step-down"), stepwise selection (a combination of the first two), maximum R^2 improvement, minimum R^2 improvement and branch and bound techniques (Furnival and Wilson, 1974). The various merits of these techniques have been widely examined (e.g. Mantel, 1970: Zar, 1974), but an appropriate choice based on similar studies (e.g. Blem, 1976b, 1980) is the maximum R^2 improvement model developed by James H. Goodnight (SAS Institute, 1979). This technique finds the "best" one-variable model first. This is the one-variable equation which produces the maximum R^2. Once that model is found, the variable which would produce the next greatest increase in R^2 is chosen and added to the model. Each of the remaining variables is compared to those already in the model to determine if replacing the included variable by one not already in the model would result in a larger R^2. After all possible comparisons have been made, if a switch of variables has been indicated, it is made. The process continues until it is determined that no exchange of variables could increase R^2, and the resulting model is deemed the "best". The technique selects third, fourth and further variables for inclusion in the same manner.

The "best" overall equations in this study, that is, those containing all statistically significant variables, are relatively accurate. Both coefficients of determination (0.83 for "best" House Sparrow equations, 0.82 for White-throated Sparrows) and standard errors of estimates (House Sparrow, 0.15; White-throated Sparrow, 0.64) indicate relatively precise productions. Analysis of 21 House Sparrows collected in the winter of 1976-1977 (see above) confirm this. The lipid content of these birds was estimated using the "best" overall equation for House Sparrows. Actual lipid content was then measured by extraction. Estimates differ from "real" values by a mean absolute difference of 0.16 g. The average difference (sign included) is -0.004 g ± 0.04 (SE; range: -0.44 to 0.41 g). Fifteen of 21 estimates are different from "real" values by less than 0.16 g. A Monte Carlo analysis of various subsets of the data (Zar, 1974) indicates that the number of birds required for the production of maximum precision appears to be about 30 (Figure 1), although fewer birds might provide relatively accurate predictions, if judiciously chosen and carefully handled. Coefficients of determination appear to vary widely at smaller sample sizes (e.g. 10-25 birds), but the standard error of estimate seems to stabilize rapidly and changes little with sample sizes greater than N = 30. It is important to note the difference in lipid

Figure 1. Coefficients of determination (R^2) and standard errors of estimates (SE) of models of varying degrees of freedom (df). The samples for analysis were chosen randomly. Hollow circles represent White-throated Sparrows, solid circles represent House Sparrows.


S E
1.2
1.0
0.8
0.6
0.4
0.2
R^2
.96
.92
.88
.84
.80
.76
10
30
50
70
90
d f

reserves of the two species in this study. The House Sparrow has a relatively constant, low, fat depot while the lipid reserve of White-throated Sparrows is large and varies greatly over winter. Therefore, the obvious difference in standard errors of the estimate for the two species is a function both of real, seasonal variation and the magnitude of the reserve.

Table 7 demonstrates that morphometric variables are more important statistically to the prediction of lipid reserve in House Sparrows than environmental variables. Additionally, environmental variables are reduced or eliminated from multivariate models where morphometric variables were included. This should not be interpreted to indicate that the environment is unimportant in determining the lipid content of House Sparrows, but rather demonstrates the overwhelming significance of fat class, body weight and perhpas sex in the prediction of lipid reserve. Blem (1973) has previously demonstrated that variation in lipid content of House Sparrows is related to sex and body weight. The relatively smaller importance of environmental variables was also indicated by the lower R^2 values in models that excluded morphometric variables. The "best" environmental model for House Sparrows has 10 variables that are statistically significant; however, none are distinctly more important than the others (see Table 7, appendix), although temperature variables are prominant.

Morphometric variables are also important to prediction of reserves of White-throated Sparrows (Table 7). However, more environmental variables (particularly temperatures) are significantly correlated with lipid content than were found in analysis of House Sparrow data. Also, the "best" overall model includes two temporal and one environmental variable. When one considers the highly significant intermonthly variation and compares the wide range of lipid reserve of White-throated Sparrows with the rather consistent reserve of House Sparrows, it is logical to conclude that White-throated Sparrows are more environmentally sensitive than House Sparrows.

There is much literature available on the relationships of ambient temperature to body temperature and metabolism in small birds but very little information on other environmental variables. Among those phenomena related to temperature are fluctuating levels of visible fat deposits, changes in extractable lipids and changes in body weight. For example, King and Farner (1966) found a positive correlation between lipid reserves and air temperature in White-crowned Sparrows (Zonotrichia leucophrys). Blem (1973) found that lipid levels in House Sparrows collected at night during mid-winter increased with the latitude of the site of capture and these reserves were correlated with the average temperature of the locality of the collection. Barnett (1970) noted that lipid reserves in House Sparrows increase only gradually from summer to winter; however, monthly data from extremes in range were unavailable in this study. Blem (1973) indicates that the difference between summer and winter reserves is probably much larger at more northerly latitudes. However, many birds have adapted behavioral strategies that allow them to cope with temperature extremes that tend to lessen their physiological response (King and Farner, 1966; King, 1972; Vincent and Bedard, 1976; Blem, 1976a). King and Farner (1966) show that some small passerines have very little winter fattening.

Another point to consider that has not been studied is the role of temperature as a proximate or ultimate factor. Evans (1966) found that lipid levels in Yellow Buntings (Emberiza citrinella) were more closely associated with long term temperature averages than collection day figures. There is little support for this as indicated by the results from House Sparrows in the present study and from the work of Vincent and Bedard, 1976. However, lipid levels in White-throated Sparrows are significantly correlated with both long-term average temperatures and temperatures at the time of capture (Tables 7 and 8). Table 8 shows the relationship between lipid levels and temperatures for the capture date. All mean temperatures include the temperature of the day of capture plus 1, 2, 3, 4 or 34 previous years. All average temperatures are significantly correlated with lipid content, but the 35 year average is most highly correlated. This indicates that reserves in White-throated Sparrows are somehow adjusted to long-term averages rather than to the temperatures of the past few years. This would have the advantage of avoiding wide fluctuations of reserve from year to year, but it is not clear how 35 year averages would be most influential on a species having a life span of few years at best or how natural selection might bring about such adaptation.

The results of the analyses of House Sparrows indicate that the long-term average temperature is a significant variable but of a minor importance when compared to all other environmental variables; it was only one of seven temperature variables retained in the program. Also, the correlations between the various temperature measurements tend to minimize the importance of any single temperature variable. The correlation coefficients of any single temperature variable were lower than several other environmental and morphometric variables. When only temperature measurements were considered, long-term averages became non-significant. The low relative importance of temperature variables may be due to several factors. The history of the House Sparrow's close association with man has provided an almost endless food supply even in times of severe temperature stress. Beer (1961) observed that House Sparrows made behavorial adjustments during periods of temperature extremes which would also tend to reduce physiological responses to variation in temperature. The importance of long term average temperatures may also be lessened somewhat by the geographical area where the birds in this study were collected. The location of Richmond tends to be about mid-range in the region usually inhabited by House Sparrows in North America.

The above comparison reveals a fundamental difference between the two species examined. The White-throated Sparrow is oriented strongly toward the environment since its lipid reserves are significantly correlated with many environmental variables and lipid depots vary widely over winter. The White-throated Sparrow forages for the most part on natural food sources which are generally fairly dispersed and not "predictable", therefore reserves to fuel the search for food are needed. The House Sparrow is not so environmentally oriented. Its microclimate is man-modified and its food patches at bird feeders, feed lots and the like are more highly clumped, predictable energy sources. As a result, House Sparrows have lower lipid reserves which are not highly correlated with most environmental variables. It is obvious that a House Sparrow under starvation conditions has less time to locate the next food source than a White-throated Sparrow, but because of the availability of food supplies, requires less time to find it.

No studies have previously analyzed the relationship of a large set of environmental variables to lipid levels of vertebrates (but see Vincent and Bedard, 1976). Although this approach in the present case has only partly clarified the role of such variables in the magnitude of lipid reserves, it has begun to help us understand the impact of many variables that influence lipid levels. Based on the relative accuracy of models, the technique promised to be a usable method for the prediction of lipid levels of live birds which would prove useful to ornithologists conducting field studies. Future investigation might use this technique to examine the effects of severe weather in selecting individuals possessing different degrees of fatness.

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APPENDICES

APPENDIX I

Table 9. Correlation coefficients (r) between independent morphological variables for the House Sparrow.[1]

	LDW	FAT	FI	WL	CL	TL	FCL	GW
BW	0.34*	0.56*	0.36*	0.17	0.12	0.45*	0.35*	0.99*
LDW		0.26*	-0.14	-0.02	-0.11	0.11*	0.18	0.34*
FAT			0.91*	-0.07	0.02	0.24*	0.81*	0.56*
FI				-0.10	0.05	0.12	0.76*	0.36*
WL					0.15	0.26*	-0.06	0.17
CL						0.35*	0.01	0.12
TL							0.10	0.45*
FCL								0.35*

[1]In order, the variables are body weight (fresh weight), lean dry weight, lipid, lipid index, wing length (chord), culmen length, tarsometatarsus length, fat class and good weight ($BW^{0.72}$).

*$P<.05$

APPENDIX II

Table 10. Correlation coefficients (r) between independent climatic variables for the House Sparrow.[1]

	PP	HAS	HBS	DP	DAY	DA	ADP	ADY	ADA	HI	LO	BP	SUN
FAT	0.08	0.47*	-0.50*	-0.07	-0.19	0.08	0.10	0.12	0.03	-0.21*	-0.15	-0.20*	-0.24*
PP		0.50*	-0.29*	0.37*	0.42	0.62*	0.39*	0.48*	0.54*	0.33*	0.51*	-0.37*	-0.19
HAS			-0.97*	0.25*	0.04	0.37*	0.44*	0.47*	0.47*	-0.03	0.12	-0.27*	-0.28*
HBS				-0.17	0.06	-0.24*	-0.38	-0.38*	-0.37*	0.12	0.00	0.21*	0.27*
DP					0.82*	0.49*	0.70*	0.67*	0.69*	0.79	0.82*	0.04	0.08
DAY						0.60*	0.46*	0.44*	0.50*	0.98*	0.97*	0.02	0.09
DA							0.58*	0.62*	0.65*	0.61*	0.55*	-0.02	0.21*
ADP								0.99*	0.98*	0.42*	0.48*	0.18	0.11
ADY									0.99*	0.39*	0.47*	0.11	0.06
ADA										0.44*	0.54*	0.10	0.06
HI											0.92*	0.07	0.22*
LO												-0.03	-0.07
BP													0.04*

[1]In order, the variables are lipid, photoperiod, hours after sunrise, hours before sunset, temperature day prior to collection, temperature collection day, temperature day after collection, long-term average temperature day prior, long-term average temperature collection day, long-term average temperature day after, high extreme, barometric pressure, percent sunlight.

*P<.05

APPENDIX III

Table 11. Correlation coefficients (r) between independent morphological variables for the White-throated Sparrow[1].

	BW	LDW	FAT	FI	WL	CL	TL	FCL
SEX	0.20*	0.27*	-0.12	-0.18	0.42*	0.12	0.20*	-0.21*
BW		0.58*	0.69*	0.57*	0.45*	0.27*	0.20*	0.53*
LDW			0.21*	0.02	0.42*	0.16	0.26*	0.17
FAT				0.98*	0.03	0.08	-0.05	0.81*
FI					-0.06	0.04	-0.09	0.79*
WL						0.14	0.25*	-0.01
CL							0.14	0.04
TL								-0.18

[1]In order, the variables are sex, body weight, lean dry weight, lipid, lipid index, wing length, culmen length, tarsometatarsus length, fat class.

*$P<.05$

APPENDIX IV

Table 12. Correlation coefficients (r) between independent climatic variables for the White-throated Sparrow[1].

	PP	HAS	HBS	DP	DAY	DA	ADP	ADY	ADA	HI	LO	BP	SUN
FAT	-0.28*	0.01	-0.09	-0.18	-0.39*	-0.43*	-0.53*	-0.53*	-0.52*	-0.47*	-0.26*	-0.24*	-0.25*
PP		0.14	0.16	0.37*	0.67*	0.81*	0.83*	0.85*	0.86*	0.64*	0.64*	0.20*	0.29*
HAS			-0.96*	0.03	0.02	0.02	0.24*	0.24*	0.25*	0.03	0.02	0.23	-0.41*
HBS				0.09	0.18	0.23*	0.01	0.01	0.01	0.16	0.17	-0.16	0.50*
DP					0.74*	0.55*	0.32*	0.32*	0.32*	0.70*	0.74*	-0.27*	0.37*
DAY						0.87*	0.62*	0.65*	0.64*	0.97*	0.95*	-0.09	0.44*
DA							0.73*	0.76*	0.75*	0.88*	0.77*	0.17	0.45*
ADP								0.99*	0.99*	0.64*	0.52*	0.30*	0.19
ADY									0.99*	0.68*	0.56*	0.30*	0.21*
ADA										0.66*	0.54*	0.31*	0.20*
HI											0.85*	0.05	0.52
LO												-0.24*	0.30*
BP													0.27*

[1]In order, the variables are lipid, photoperiod, hours after sunrise, hours before sunset, temperature day prior to collection, temperature collection day, temperature day after collection, long-term average temperature day prior, long-term average temperature collection day, long-term average temperature day after, high extreme, low extreme, barometric pressure and percent sunlight.

*P<.05

VITA

[redacted]