AN ABSTRACT OF THE THESIS OF

DAVID R. PARSONS for the degree MASTER OF SCIENCE
(Name) (Degree)

in FISHERIES AND WILDLIFE presented on March 3, 1975
(Major Department) (Date)

Title: TIME AND ENERGY BUDGETS OF A POPULATION OF DIPPERS (CINCLUS MEXICANUS) DURING WINTER IN THE CASCADE RANGE OF OREGON

Abstract approved: Redacted for privacy
Robert L. Jarvis

A time and energy budget was constructed for a population of dippers (Cinclus mexicanus) in the Cascade Range of Oregon during winter. A total of 12,202 point observations of activity were made from nine observation blinds from 19 November 1973 to 10 February 1974. Approximately 50 percent of all observations were of foraging activity and no significant differences were observed between morning and afternoon activity patterns. Multiple linear regression analysis indicated significant negative correlations between time spent foraging and mean temperature during the active day ($P < 0.01$), mean temperature of the previous night ($P < 0.05$), and mean temperature of the 24-hour period ($P < 0.05$). Exploratory behavior was negatively correlated to mean temperature during the active day ($P < 0.01$); however, in the regression equation, this relationship was masked by the

strong negative correlation between exploratory behavior and foraging. Passive behavior was inversely related to foraging and directly related to the length of the photoperiod (P < 0.01). Estimates of rates of energy consumption of 3.4, 3.0, and 1.2 times the resting metabolic rate were determined for foraging, exploratory behavior, and passive behavior respectively. Nighttime metabolic activity was assumed to be equivalent to the standard metabolic rate. Daily energy requirements for foraging, exploratory behavior, passive behavior, and nighttime activity were estimated to be 15.2, 7.7, 2.1, and 8.5 kcal/ bird day, respectively, for the average day during the study. The caloric equivalent of food consumed was estimated to be 47.9 kcal/ bird day. The population of dippers on the 5.5 km of stream investigated ingested an estimated 51,207 kcal from 15 November to 15 February.

Time and Energy Budgets of a Population of Dippers (*Cinclus mexicanus*) during Winter in the Cascade Range of Oregon

by

David R. Parsons

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed March 1975

Commencement June 1975

APPROVED:

Redacted for privacy

Assistant Professor of Wildlife Ecology
in charge of major

Redacted for privacy

Head of Department of Fisheries and Wildlife

Redacted for privacy

Dean of Graduate School

Date thesis is presented March 3, 1975

Typed by Mary Jo Stratton for David R. Parsons

ACKNOWLEDGMENTS

I would like to express my thanks to Dr. R. L. Jarvis for his professional guidance, assistance, and continued encouragement during this study. I would also like to express my appreciation to Dr. C. E. Warren, former Acting Department Head, and the staff of the Department of Fisheries and Wildlife for their philosophical and academic guidance. Statistical advice provided by Dr. G. D. Faulkenberry was invaluable. Capture and marking operations could not have been successful without the assistance of fellow graduate and undergraduate students. I am grateful to my graduate committee (Dr. R. L. Jarvis, Dr. G. D. Faulkenberry, and Dr. E. C. Meslow) for their review of the thesis.

The study was supported in part by the Agricultural Experiment Station. Field accommodations were provided by the Coniferous Forest Biome of the U. S. International Biological Program.

I would especially like to thank my wife for her continued support and tolerance throughout the study.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

TIME AND ENERGY BUDGETS OF A POPULATION OF DIPPERS (*CINCLUS MEXICANUS*) DURING WINTER IN THE CASCADE RANGE OF OREGON

INTRODUCTION

The dipper is a non-migratory, aquatic, passerine bird that inhabits western mountain streams from Alaska to Central America (Bent 1948). Its diet consists mainly of aquatic insect larvae of the orders Ephmeroptera, Plecoptera, Trichoptera, and Diptera (Mitchell 1968, Thut 1970). Other food items in the diet include small fish, salmon eggs, snails, and adult insects (Burcham 1904, Michael 1922, Ehinger 1930, Herman 1944, Bakus 1959a, Mitchell 1968, Thut 1970, Sullivan 1973).

Dippers occupy and defend linear territories which include the stream, its banks, and usually a nest site throughout the year. However, certain environmental extremes such as freezing or high water may cause movements out of established territories. Pairing takes place in mid- to late-winter and nesting occurs from March to June (Sullivan 1973).

Although food habits of dippers have been investigated, little is known of the energy requirements of a free-living population of dippers. This study was undertaken to determine energy requirements of a population of dippers during winter. Reasons for selecting winter as the study period were: (1) presumably, the relative significance of dippers as consumers in the stream ecosystem should be greater in winter than any other season since dippers may compete (directly or indirectly) for food with fish and amphibians which are poikilothermic; (2) population structure was relatively stable and individual energy requirements were not complicated by reproductive functions, molting, or growth; and (3) winter was assumed to be the most energetically demanding time of year for dippers.

Energy flow through a population is composed of energy of production and energy of respiration (Odum et al. 1962). Energy of production constitutes only a minor portion of total energy flow for homeothermic organisms (Krebs 1972:477) and was assumed to be equal to the caloric equivalent of fat for any net change in weight during the study. Energy of respiration was estimated using the time and energy budget approach (Pearson 1954, Orians 1961, Schartz and Zimmerman 1971, Stiles 1971, Wolf and Hainsworth 1971, Utter and LeFebvre 1973). The time and energy budget approach consists of four basic steps: (1) classification of types of activity, (2) quantification of daily activity patterns (the time budget), (3) estimations of rate of energy consumption for each type of activity, and (4) conversion of time budget to energy budget.

Study Area

The study was conducted on the lower 5.5 km of Lookout Creek on the west slope of the Cascade Range of Oregon. Lookout Creek is located on the H. J. Andrews Experimental Forest (Blue River Ranger District, Willamette National Forest) near Blue River, Oregon, and is a minor stream in the McKenzie River watershed.

The creek was characterized by a streambed of large boulders and rubble with an average gradient of approximately 22 m/km. The width of Lookout Creek in the study area was 10-20 m; depth in riffles was 0.25-1.0 m and depth in pools was 1-3 m. Stream flow was lowest in summer and highest, but highly variable, during winter.

Elevation of the study area was 400-500 m. Precipitation averages 225 cm per year most of which falls as rain from November to March. Snow storms do occur in the vicinity of the study area but a permanent winter snow-pack usually does not develop. Lookout Creek drainage was characterized by a vegetative cover of coniferous forest in which only moderate clearcutting had occurred.

METHODS

Daytime activities of dippers were classified into seven categories. Foraging by diving included swimming and floating on the surface, diving, underwater locomotion, and capture and handling of prey. Handling of prey usually occurred out of the water and included beating of larger prey (especially fish) against a rock, removal of protective coverings, washing, and ingestion of prey.

Dippers also foraged by walking or standing in or near the water and repeatedly submerging their heads to search for and seize prey. This activity, which I classified as foraging by wading, occasionally included lifting or turning of rocks and other objects on the bottom. Capture and handling of prey and drinking were also included.

The category of rock hopping included hopping, walking, running, and the familiar dipping motions. Rock hopping occurred primarily between aquatic foraging attempts but was also associated with terrestrial foraging, territorial defense, pair formation, and defecation.

Flying consisted of all flying.

Dippers were considered to be resting when movement was restricted mainly to the head. Resting was generally a prolonged activity. Dippers usually sang from a resting posture; and since vocalizations were often difficult to detect above the noise of the stream, singing was included in the resting category.

Arrangement and maintenance of feathers, maintenance of other body surfaces, and bathing were classified as preening.

Displaying included posturing associated with territorial defense and pair bond formation.

Nighttime activity was defined as the period of time during which dippers were on the roost.

The active day (period of time dippers were off the roost each day) was determined from the times of the first and last observed activity and a limited number of observations of departure from and arrival at a roost. The active day was divided into two equal activity periods (morning and afternoon) for data analysis.

Data for construction of a time budget were collected by observing dippers on 33 days from 3 November 1973 to 10 February 1974. Activity patterns were quantified by recording point observations of activity every 20 seconds during 15-minute sampling periods. Timing of the sample points was accomplished by recording mechanical clicks on a cassette tape at 20-second intervals and continuously playing the tape during 15-minute sampling periods. This procedure allowed the observer to continuously observe a dipper and record activity each time a click was heard. An earphone attachment was used so the tape player could be operated at a low volume. At the end of each day observations were summarized; each sampling period could contain a maximum of 45 observations.

Dippers were observed with tripod-mounted 7 x 35 binoculars from nine observation blinds constructed along Lookout Creek on sites that afforded good visibility of the stream.

Twenty-eight dippers were captured with mist nets and marked for identification with colored leg bands. Weights were obtained with an Ohaus model 8011 spring scale.

Censuses were taken by walking in or along the stream for the entire length of the study area. Birds were counted each time they passed the observer and the number of birds passing the observer from behind was subtracted from the total. Bakus (1959_b_) noted that dippers sometimes remained motionless along the bank until he had passed and then flew in a direction opposite to his direction of travel. This type of flushing was not observed during my study; consequently, census counts were considered to be total counts.

Weather data for the immediate vicinity were continuously recorded by the U.S. Forest Service; continuous stream flow data were provided by the U.S. Geological Survey.

Two assumptions were made in using the point sample method: (1) all types of behavior were equally likely to be observed when they occurred and (2) the behavior of birds when out of view was similar to behavior exhibited when being observed. These assumptions were not needed by some investigators when knowledge of the behavior of the species being studied allowed the observers to make assumptions about the type of activity in which the organism was most likely to be engaged when out of view (Verner 1965, Schartz and Zimmerman 1971, Wolf and Hainsworth 1971, Utter and LeFebvre 1973). Weins et al. (1970) discussed the potential of the point sample technique for quantifying activity patterns.

Due to initial inconsistencies in recording activities and occasional disproportionate or insufficient sample sizes, criteria were established for the rejection of certain data from the total sample. Observations made on the first 7 days of the study were eliminated because of recording problems. Data from morning or afternoon activity periods with fewer than 100 observations of activity were considered insufficient to be representative of the activity pattern of that period and were rejected. Data from activity periods in which all observations were made within a 90-minute period were also rejected. The above criteria resulted in the rejection of data collected on 12 full days and 7 half days. However, because of the relatively small sample sizes associated with most rejected data, only 19 percent of the total sample was eliminated. Data used in the analysis were collected between 19 November 1973 and 10 February 1974.

RESULTS

Body Weight

Pre-winter weights of 16 dippers captured on 6 and 7 October 1973 ranged from 47 to 67 g with a mean weight of 54.5 g. Post-winter weight of one recaptured dipper obtained on 16 February 1974 exceeded its pre-winter weight by 1 g; this difference was not considered significant. Since dippers are non-migratory, one would not expect to observe significant weight changes during winter. Consequently, all energy flow through the population in winter was attributed to the process of respiration.

Population Estimates

Estimates of population levels on the 5.5-kilometer study area ranged from a high of 24 dippers (14 October 1973) to a low of only six birds on 24 November 1973 (Table 1). Numbers subsequently increased to 19 dippers at the end of the study (11 February 1974). Pair bond formation was nearly completed by 11 February 1974.

These data suggest an initial emigration from the study area in late fall followed by a gradual return prior to the breeding season. Movements of adult dippers on the Lookout Creek study area are probably a response to reduced food availability or foraging efficiency or both because of increased stream flow in late fall and winter.

Table 1. Numbers, identities, and population densities of dippers seen during five censuses on Lookout Creek in western Oregon.

Date	Identity			Total	Population Density (birds/km)
	Marked	Unmarked	Unidentified		
14 Oct 1973	11	8	5	24	4.4
24 Nov 1973	2	0	4	6	1.1
4 Jan 1974	4	2	3	9	1.6
29 Jan 1974	7	4	1	12	2.2
11 Feb 1974	8	4	7	19	3.5

Winter population densities were computed by dividing the number of birds present by the length of the study area. Estimates of population density ranged from 1.1 to 4.4 birds/km (Table 1). The 24 dippers seen in October probably included juveniles; whereas, the count of 19 dippers in February may have more closely approximated breeding population levels.

Time Budget During Winter

A total of 12,202 observations, which represents approximately 67.8 hours of observed activity, was analyzed. The data included observations of activity of six marked and an undetermined number of unmarked or unidentified dippers. However, observations of activity of two marked dippers accounted for 31 and 34 percent of the total sample. These two birds maintained territories near the lower end of the study area; this area was easily observed and always accessible during the study.

Dippers were active from approximately 20 minutes before official sunrise to approximately 20 minutes after official sunset.

Average activity patterns for morning and afternoon activity periods during winter were comparable (Table 2). The combination of foraging by wading and foraging by diving accounted for 52.2 and 48.5 percent of all morning and afternoon observations, respectively. Rock hopping accounted for an average of 27.1 percent of all recorded activity; other activities accounted for lesser proportions of the total.

Table 2. Average morning, afternoon, and daily time budgets for dippers observed between 19 November 1973 and 10 February 1974 on Lookout Creek in western Oregon.

Activity	Percent time spent		
	AM	PM	Daily
Foraging by diving	31.4	32.3	31.8
Foraging by wading	20.8	16.2	18.5
Rock hopping	26.6	27.6	27.1
Flying	2.3	2.1	2.2
Resting	13.7	13.7	13.7
Preening	4.5	7.7	6.1
Displaying	0.7	0.5	0.6
Total	100.0	100.1	100.0

To simplify additional analysis, the seven previously defined activity categories were grouped into three general categories. The two types of foraging were combined and called foraging. Rock hopping and flying comprised the new category, exploratory behavior, and the remaining activities (resting, preening, and displaying) were collectively termed passive behavior. As before, the active day was divided into two equal activity periods. Foraging, exploratory behavior, and passive behavior accounted for 50.3, 29.3, and 20.4 percent of all observations, respectively.

Assuming that the distribution of observations for each activity period was representative of the activity pattern for that period, the data were converted from percent of total observations to hours spent in each activity. This conversion adjusted the data for the length of the active day, which varied from 9.43 to 10.85 hours during the study.

Data from 13 days on which adequate samples were obtained during morning and afternoon activity periods indicated no significant difference between time spent in each general type of activity during morning and afternoon ($P > 0.05$ for each type of activity). For the remaining analysis, observations made during a morning or afternoon activity period (34 samples) were considered to be representative of the activity pattern of the entire active day.

Activity in Relation to Environmental Factors

I used multiple linear regression analysis (Draper and Smith

1966) to determine relationships between time spent in each of the three types of activities and the following environmental factors: mean temperature during the previous night (an average of temperatures recorded at 2-hour intervals from 1800 to 0600); mean temperature during the active day (an average of temperatures recorded at 2-hour intervals from 0800 to 1600); mean temperature during the 24-hour period (an average of temperatures recorded at 2-hour intervals during the two previously defined periods); water level at noon; and length of the active day (20 minutes before sunrise to 20 minutes after sunset)(Table 3).

Foraging. There were significant negative correlations between time spent foraging and mean temperature during the active day ($P < 0.01$), mean temperature of the previous night ($P < 0.05$), and mean temperature of the 24-hour period ($P < 0.05$). All three temperature measurements were included in the linear prediction model (Table 3).

Inverse relationships between time spent foraging or food consumed and ambient temperature have been reported by several investigators (Kendeigh 1949, Seibert 1949, Cox 1961, Verbeek 1964, 1972, Zimmerman 1965, Kontogiannis 1968). Verner (1965) observed that early morning singing patterns of long-billed marsh wrens (*Telmatodytes palustris*) were influenced by the temperature of the previous night, with warmer nights being followed by longer continuous

Table 3. Multiple linear regression analysis of activity data versus various environmental factors for dippers on Lookout Creek in western Oregon.

Activity	Model (hours/day)	F	df	R^2
Foraging	$5.594 - 2.545X_1 - 3.028X_2 + 5.435X_3$	8.48	3, 30	0.46
Exploratory	$5.659 - 0.548X_4$	31.98	1, 32	0.50
Passive	$-4.370 - 0.453X_4 + 0.870X_5$	23.59	2, 31	0.60

X_1 = mean temperature in C during the active day

X_2 = mean temperature in C during the previous night

X_3 = mean temperature in C during the 24-hour period comprised of the previous night and the active day

X_4 = observed time spent foraging in hours

X_5 = length of active day in hours

periods of singing at dawn. This would suggest a reduction in time spent in other activities such as foraging. Kontogiannis (1968) found that white-throated sparrows (Zonotrichia albicollis) subjected to increased nighttime metabolic levels induced by forced activity consumed more food during daylight hours than birds in control groups. It seems reasonable to assume that birds subjected to increased nighttime metabolic demands induced by low temperatures would also increase food consumption in order to maintain constant body weight. Since all mean temperatures during my study were below the lower critical temperature for the dipper (Murrish 1970), negative correlations between mean temperatures and time spent foraging were not unexpected. Kendeigh (1969) suggested that increased food consumption would occur on longer days, but no such relationship was detected in my analysis.

Theoretically, high water levels should reduce food availability and foraging efficiency of dippers (because of increased depth, velocity, and turbidity of the water) forcing an increase in foraging activity. However, no significant relationships between water levels and activity patterns were detected. Dippers were increasingly difficult to observe as water levels increased, and consequently, data for periods of high water levels are lacking. Thus, the failure to detect a relationship between water level and foraging activity may have resulted from a lack of data during periods of extremely high water levels.

Since time available for activity on any given day was predetermined by the photoperiod, it was not surprising that significant negative correlations ($P < 0.01$) were found between time spent foraging and time spent in the other two categories of activity. However, the lack of a significant correlation between exploratory and passive behavior suggested that foraging took precedence over other activities.

Exploratory Behavior. The analysis revealed a significant positive correlation between time spent in exploratory behavior and mean temperature during the active day ($P < 0.01$); however, this relationship was masked by the stronger negative correlation between exploratory behavior and foraging. Only time spent foraging had a significant regression coefficient ($P < 0.01$) in the linear regression model for exploratory behavior. When energy demands were low and time spent foraging reduced, more time would be available for exploratory behavior.

Passive Behavior. Passive behavior was significantly correlated to time spent foraging and length of the active period ($P < 0.01$). These correlations were negative and positive, respectively. An examination of the linear regression model (Table 3) revealed that if time spent foraging was held constant, a 1-hour increase in daylength would result in an increase in time spent in passive behavior of approximately 52 minutes. Apparently, as days became longer, more time was available for activities other than those related to foraging.

DISCUSSION

Energy Cost of Activities

It is customary to express the increased metabolic demands of various activities as some factor increase of either the standard or resting metabolic rate (Orians 1961, Schartz and Zimmerman 1971, Utter and LeFebvre 1973). In this paper the resting metabolic rate is used as the base; and, for conversion purposes, it is assumed that the ratio of resting metabolism to standard metabolism is 1.5 (Brody 1945).

A conversion factor was determined for each general category of activity by estimating energy demands of specific types of activity within each general category and computing a weighted average. Estimates of energy costs of activity were either taken directly from the literature or extrapolated from values in the literature. Relative frequencies for all types of activity are listed in Table 2.

Foraging required an estimated 3.4 times more energy than resting based upon conversion factors of 4.0 and 2.5 for foraging by diving and foraging by wading, respectively. My estimate of 3.4 falls within the range of 3 to 8 suggested by Brody (1945) for sustained heavy work.

A factor of 3 times the resting rate was used for exploratory behavior which consisted of rock hopping and flying (92 and 8 percent, respectively). Rock hopping was considered to be more demanding than walking. Brody (1945) concluded that walking required about twice as much energy as standing for horses and Deighton and Hutchinson (1940) found that standing metabolism was 40 to 45 percent above sitting metabolism for light Sussex cockerels. Accordingly, the ratio of energy required for rock hopping to that required for resting was estimated to be 2.5 for dippers. Results of studies designed to determine energy requirements of flapping flight for birds vary (Pearson 1950, 1964, Farner 1970, Utter and LeFebvre 1970). I used a factor of 8 times the resting metabolic rate, which falls within the range of results of the above mentioned studies and also coincides with Brody's (1945) estimate of maximum energy requirements for sustained hard work. LeFebvre (1964) argues that Brody's (1945) ratios of metabolic requirements of sustained hard work to resting requirements for domestic mammals are generally applicable to birds as well.

Using factors of 2 (Orians 1961:304), 1.5, and 1 times the resting level for displaying, preening, and resting respectively, a factor of 1.2 times the resting metabolic rate was computed for passive behavior.

Both standard and resting metabolic rates have been used by other investigators as estimates of nighttime metabolic activity of birds (Schartz and Zimmerman 1971, Utter and LeFebvre 1973). The dipper is obviously not in a resting, post-absorptive condition for the entire time it is on the roost, which suggests that an estimate somewhat higher than the standard metabolic rate would be appropriate. However, since nocturnal reduction of the standard metabolic rate is a common phenomenon in many passerine birds (King and Farner 1961, Sturkie 1965), the standard metabolic rate as determined by Murrish (1970) probably provides the best estimate of nighttime metabolic activity.

Prediction of Behavior Patterns

To demonstrate the predictive capability of the regression equations for time spent in each activity (Table 3), each equation was solved by replacing variables with appropriate values for 4 days for which activity data were available for comparison (Table 4). Three of the days selected represented extremes of environmental factors that were found to influence behavior and the fourth possessed intermediate levels. Differences between predicted and observed values ranged from 0.03 to 0.56 hours, demonstrating a general agreement between predicted and observed activity patterns.

Table 4. Observed versus predicted time expended in activities on 4 selected days during winter for dippers on Lookout Creek in western Oregon.

Date	Time Spent (hours)					
	Foraging		Exploratory		Passive	
	Observed	Predicted ±95% C.I.	Observed	Predicted ±95% C.I.	Observed	Predicted ±95% C.I.
21 Dec 73[a]	4.34	4.47 ± 1.57	3.31	3.28 ± 1.11	1.75	1.88 ± 1.19
2 Jan 74	6.28	6.50 ± 1.70	2.14	2.22 ± 1.13	1.14	1.07 ± 1.19
28 Jan 74	4.30	4.86 ± 1.54	3.68	3.30 ± 1.11	2.25	2.59 ± 1.17
10 Feb 74	3.96	4.05 ± 1.64	3.20	3.49 ± 1.13	3.64	3.27 ± 1.22

[a]21 Dec 73 had the shortest photoperiod and the highest mean temperature of all days on which data were collected; 2 Jan 74 was the coldest day; 28 Jan 74 had an intermediate temperature and photoperiod; 10 Feb 74 had the longest photoperiod.

However, because of the variability associated with predictions (wide 95 percent confidence intervals), no significant differences in predicted activity patterns could be demonstrated among days having maximum and minimum extremes of temperature and daylength (Fig. 1). Hence, predicting activity patterns and subsequently estimating energy requirements on a day-by-day basis was not justified. The preceding exercise led to a decision to calculate daily energy requirements on the basis of temperature and daylength values averaged over the entire study period.

Daily Energy Budget

Temperature and daylength data were averaged over a period of 93 days from 15 November 1973 to 15 February 1974. The average day during this period had a mean temperature during the active day of 2.2 C, a mean nighttime temperature of 1.2 C, and a mean temperature during the 24-hour period (consisting of the active day plus the previous night) of 1.6 C. The mean length of the active day was 9.91 hours, during which a predicted 5.06, 2.89, and 1.96 hours were spent in foraging, exploratory, and passive behavior respectively (Table 5).

Since average temperatures were below the lower critical temperature of the dipper (11.5 C), the standard metabolic rate was determined by the linear equation

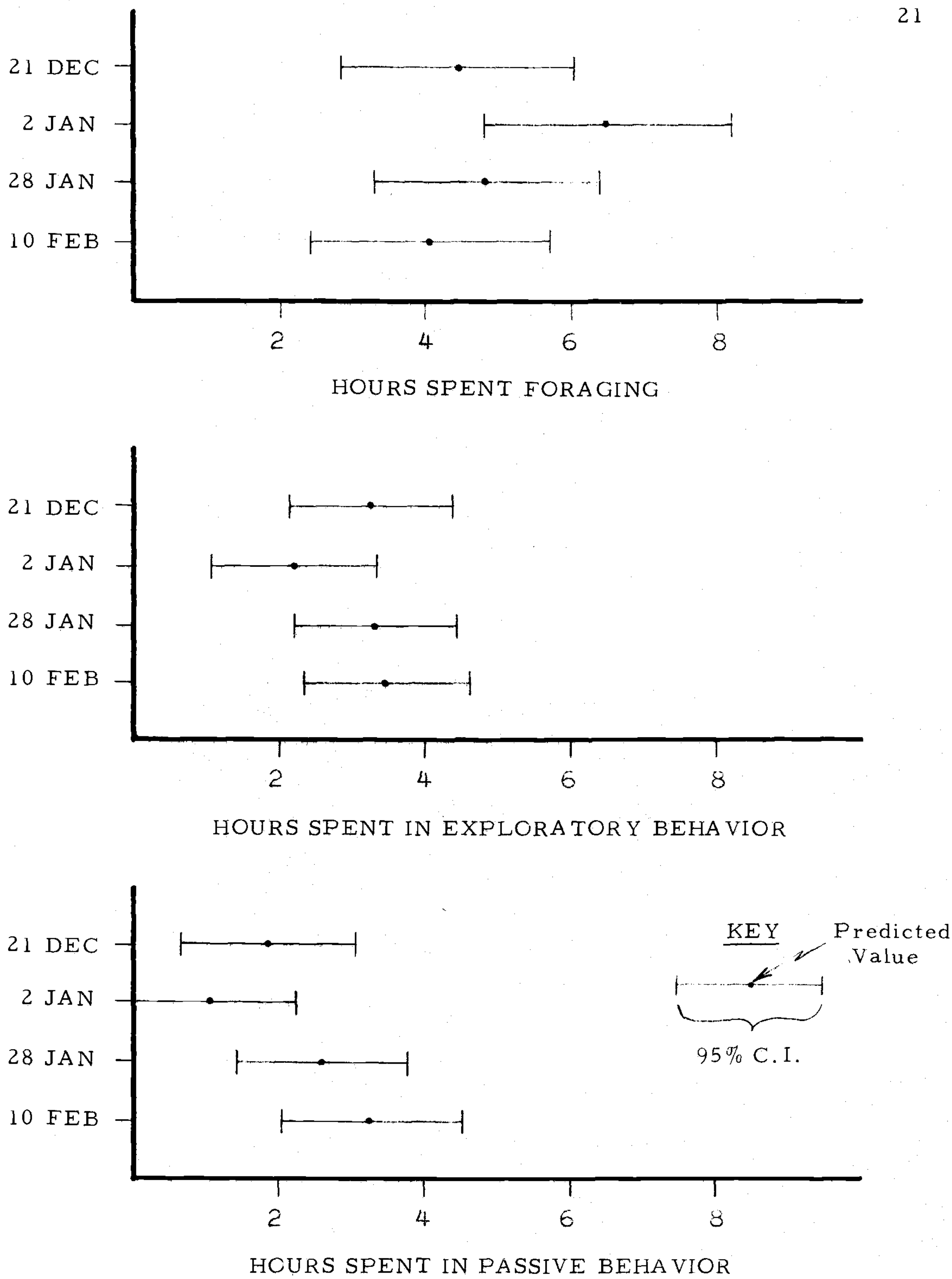

Fig. 1. Predicted time spent in three general types of activity for dippers in western Oregon on 4 days during the winter of 1973-74.

$$\text{ml } O_2/\text{g hour} = 2.40 - 0.065T$$

where T is air temperature in C (Murrish 1970). (1)

Table 5. Predicted daily activity and estimated energy requirements of dippers for the average day from 15 November 1973 to 15 February 1974 on Lookout Creek in western Oregon.

Activity	Predicted Time Spent (hours/day)	Average Energy Required (kcal/bird day)
Foraging	5.06	15.2
Exploratory	2.89	7.7
Passive	1.96	2.1
Subtotal	9.91	25.0
Nighttime	14.09	8.5
Total	24.00	33.5

Using Murrish's (1970) estimate of the respiratory quotient (0.78) and the corresponding conversion factor of 4.80 cal/ml O_2 (Brody 1945, Kleiber 1961), Equation 1 becomes

$$\text{cal/g hour} = 11.5 - 0.312T, \tag{2}$$

which yields an average daytime standard metabolic rate of 10.8 cal/g hour and an average nighttime standard metabolic rate of 11.1 cal/g hour.

Energy required by the various activities can be expressed as

(10.8 cal/g hour)(1.5)(5.06 hour/day)(54.5 g/bird)(3.4)

or 15.2 kcal/bird day for foraging,

(10.8 cal/g hour)(1.5)(2.89 hours/day)(54.5 g/bird)(3.0)

or 7.7 kcal/bird day for exploratory behavior,

(10.8 cal/g hour)(1.5)(1.96 hours/day)(54.5 g/bird)(1.2)

or 2.1 kcal/bird day for passive behavior, and

(11.1 cal/g hour)(14.09 hours/day)(54.5 g/bird)

or 8.5 kcal/bird day for nighttime activity (Table 5). The result was a total average daily energy expenditure of 33.5 kcal/bird day, which represented an energy requirement of approximately 2.3 times the standard metabolic rate.

Assuming an assimilation efficiency of 70 percent which was used by Weins and Innis (1974) in their population bioenergetics model and is comparable to values reported by Kale (1965) for the carnivorous long-billed marsh wren and Zimmerman (1965) for the partially insectivorous dickcissel (Spiza americana), a dipper would have to ingest an average of 47.9 kcal/day in order to maintain an energy balance in winter. This implies a return of 3.2 kcal for every kilocalorie expended in foraging, a value much lower than Schartz and Zimmerman's (1971) estimate of 12.8 kcal for every kilocalorie expended for foraging by male dickcissels during the breeding season. However, these values are not directly comparable since one would expect food to be more abundant during the breeding season than during winter, resulting in a greater caloric return per unit effort in foraging during the breeding season.

Population Energy Requirements

Population trends during the study were estimated by a linear function of time fitted by eye to the plotted census data (Fig. 2). The line was purposefully fitted slightly high because census counts were based only upon birds seen and represented minimum population estimates at best. The area under the line bounded by the points corresponding to 15 November 1973 on the left and 15 February 1974 on the right represents the number of bird days during that period. The total metabolic energy requirement for the population of dippers on the Lookout Creek study area during the previously defined winter period was estimated by the expression

(33.5 kcal/bird day)(1070 bird days),

which reduced to 35,845 kcal. The corresponding gross energy of ingested food (assuming an assimilation efficiency of 70 percent) for the same period was 51,207 kcal.

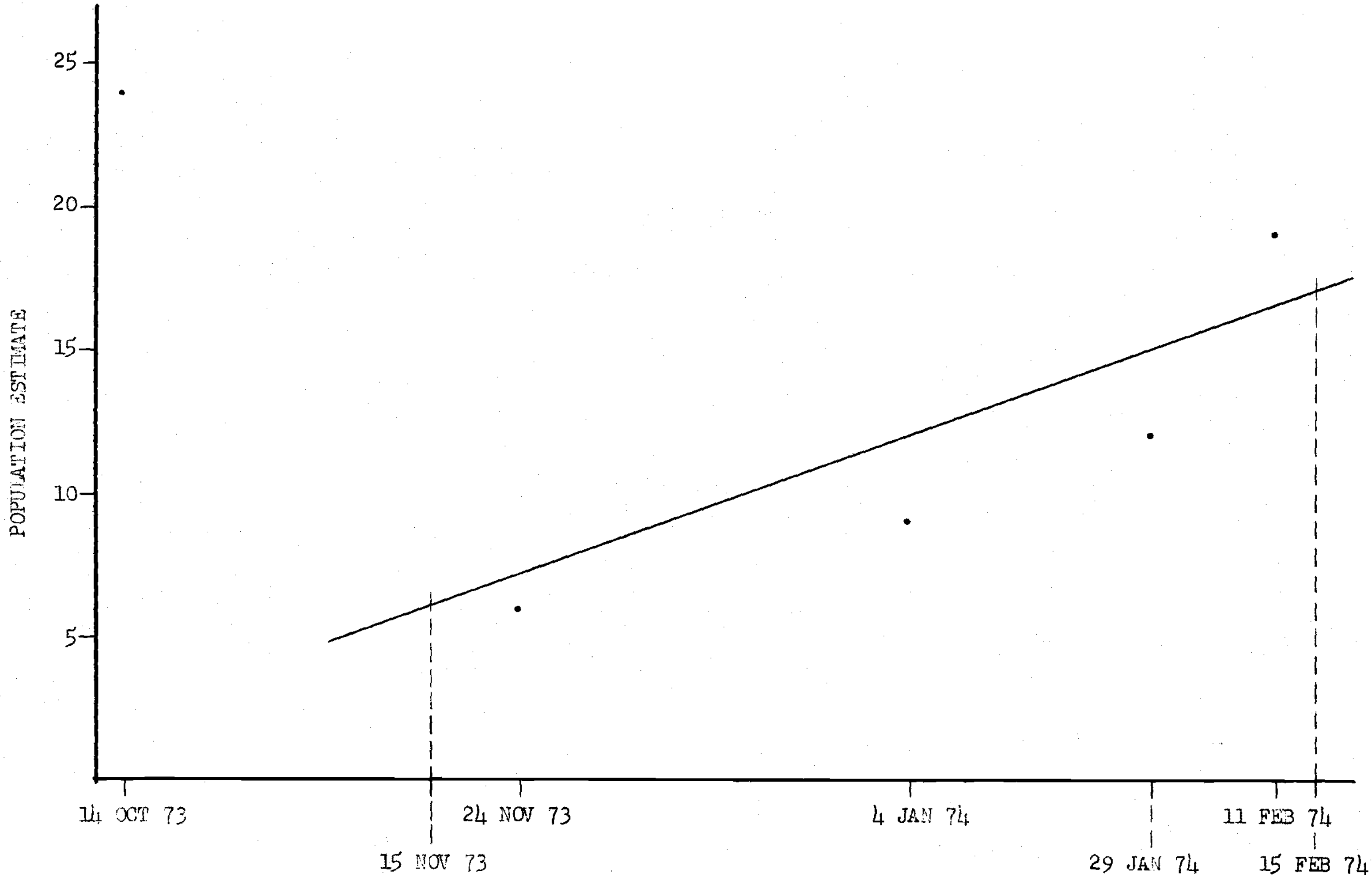

Fig. 2. Trends in dipper numbers on the lower 5.5 km of Lookout Creek in western Oregon during the winter of 1973-74.

LITERATURE CITED

Bakus, G. J. 1959a. Observations on the life history of the dipper in Montana. Auk 76(2):190-207.

________________. 1959b. Territoriality, movements, and population density of the dipper in Montana. Condor 61(6):410-425.

Bent, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U. S. Natl. Mus. Bull. 195. 475pp.

Brody, S. 1945. Bioenergetics and growth. Reinhold Publishing Corp., New York. 1023pp.

Burcham, J. S. 1904. Notes on the habits of the water ouzel (Cinclus mexicanus). Condor 6(1):50.

Cox, G. W. 1961. The relation of energy requirements of the tropical finches to distribution and migration. Ecology 42(2):253-266.

Deighton, T., and J. C. D. Hutchinson. 1940. Studies on the metabolism of the fowls. II. The effect of activity on metabolism. J. Agric. Sci. 30(1):141-157.

Draper, N. R., and H. Smith. 1966. Applied regression analysis. John Wiley and Sons Inc., New York. 407pp.

Ehinger, C. E. 1930. Some studies of the American dipper or water ouzel. Auk 47(4):487-498.

Farner, D. S. 1970. Some glimpses of comparative avian physiology. Fed. Proc. 29(5):1649-1663.

Herman, C. M. 1944. Notes on a water ouzel. Condor 46(6):297.

Kale, H. W., II. 1965. Ecology and bioenergetics of the long-billed marsh wren in Georgia salt marshes. Publ. Nutall Ornithol. Club 5:1-142.

Kendeigh, S. C. 1949. Effect of temperature and season on energy resources of the English sparrow. Auk 66(2):113-127.

Kendeigh, S.C. 1969. Energy responses of birds to their thermal environments. Wilson Bull. 81(4):441-449.

King, J.R., and D.S. Farner. 1961. Energy metabolism, thermoregulation, and body temperature. Pages 215-228 in A.J. Marshall, ed. Biology and comparative physiology of birds. Academic Press, New York. Vol. II.

Kleiber, M. 1961. The fire of life. John Wiley and Sons Inc., New York. 454pp.

Kontogiannis, J.E. 1968. Effect of temperature and exercise on energy intake and body weight of the white-throated sparrow, Zonotrichia albicollis. Physiol. Zool. 41(1): 54-64.

Krebs, C.J. 1972. Ecology: The experimental analysis of distribution and abundance. Harper and Row, Publishers, Inc., New York. 694pp.

LeFebvre, E.A. 1964. The use of D_2O^{18} for measuring energy metabolism in Columbia livia at rest and in flight. Auk 81(3):403-416.

Michael, C.W. 1922. Water ouzel eating a fish. Condor 24(3):98-99.

Mitchell, P. 1968. The food of the dipper (Cinclus mexicanus Swainson) on two western Montana streams. M.A. Thesis. Univ. of Montana. 82pp.

Murrish, D.E. 1970. Responses to temperature in the dipper, Cinclus mexicanus. Comp. Biochem. Physiol. 34(4):859-869.

Odum, E.P., C.E. Connell, and L.B. Davenport. 1962. Population energy flow of three primary consumer components of old-field ecosystems. Ecology 43(1):88-96.

Orians, G.H. 1961. The ecology of blackbird (Agelaius) social systems. Ecol. Monogr. 31(3):285-312.

Pearson, O.P. 1950. The metabolism of hummingbirds. Condor 52(4):145-152.

______________. 1954. The daily energy requirements of a wild Anna hummingbird. Condor 56(6):317-322.

Pearson, O. P. 1964. Metabolism and heat loss during flight in pigeons. Condor 66(3):182-185.

Schartz, R. L., and J. L. Zimmerman. 1971. The time and energy budget of the male dickcissel (Spiza americana). Condor 73(1):65-76.

Seibert, H. C. 1949. Differences between migrant and non-migrant birds in food and water intake at various temperatures and photoperiods. Auk 66(2):128-153.

Stiles, F. G. 1971. Time, energy, and territoriality of the Anna hummingbird (Calypte anna). Science 173(3999):818-821.

Sturkie, P. D. 1965. Avian physiology. 2nd ed. Cornell University Press, Ithaca, New York. 766pp.

Sullivan, J. O. 1973. Ecology and behavior of the dipper, adaptations of a passerine to an aquatic environment. Ph. D. Thesis. Univ. of Montana. 212pp.

Thut, R. N. 1970. Feeding habits of the dipper in southwestern Washington. Condor 72(2):234-235.

Utter, J. M., and E. A. LeFebvre. 1970. Energy expenditure for free flight by the purple martin (Progne subis). Comp. Biochem. Physiol. 35(3):713-719.

__________, and __________. 1973. Daily energy expenditure of purple martins (Progne subis) during the breeding season: estimates using D_2O^{18} and time budget methods. Ecology 54(3):597-604.

Verbeek, N. A. M. 1964. A time and energy budget study of the brewer blackbird. Condor 66(1):70-74.

_______________. 1972. Daily and annual time budget of the yellow-billed magpie. Auk 89(3):567-582.

Verner, J. 1965. Time budget of the male long-billed marsh wren during the breeding season. Condor 67(2):125-139.

Weins, J. A., and G. S. Innis. 1974. Estimation of energy flow in bird communities: a population bioenergetics model. Ecology 55(4):730-746.

Weins, J. A., S. G. Martin, W. R. Holthaus, and F. A. Iwen. 1970. Metronome timing in behavioral ecology studies. Ecology 51(2):350-352.

Wolf, L. L., and F. R. Hainsworth. 1971. Time and energy budgets of territorial hummingbirds. Ecology 52(6):980-988.

Zimmerman, J. L. 1965. Bioenergetics of the dickcissel, Spiza americana. Physiol. Zool. 38(4):370-389.