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FEEDING ECOLOGY AND NESTING BEHAVIOR OF GRASSLAND BIRDS AT THE PAWNEE SITE, 1971

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TABLE OF CONTENTS

ABSTRACT

Part I

Dietary studies were continued on insectivorous and granivorous birds of the shortgrass prairie as found at the Pawnee Site. In 1971, 281 stomach samples were obtained for 23 species of grassland birds. Laboratory analyses for identification and measurement of foods were carried out on 223 stomach content samples. Technical reports were prepared on the diets of three birds: the Mountain Plover, the Killdeer, and the Mourning Dove. All birds so far examined feeding at the Pawnee Site are utilizing approximately 125 genera of seeds for food. These organisms comprise the principal pathways for materials and energy in that part of the food net with which birds are concerned.

Part II

Field studies of the interrelationships of four species of grassland passerines, Lark Buntings (*Calamospiza melanocorys*), McCown's Longspurs (*Rhynchophanes mccownii*), Chestnut-collared Longspurs (*Calcarius ornatus*), and Horned Larks (*Eremophila alpestris*), were made at the Pawnee Site during the spring and summer of 1971. Investigations were initiated with two questions in mind: (i) Are there temporal segregations of ecological demands of these species on the ecosystem, and (ii) Is there a spatial distribution and vegetational preference shown by these species?

Food capture tactics and formation of species ethograms were studied by taking behavioral schedules of randomly selected birds for 20-minute periods. Discrete behaviors are analyzed for relative frequency of performance and correlated to known stages of the nesting cycle. Spatial

distribution is observed by censusing random areas of the Central Plains Experimental Range and recording the vegetational type referenced by each bird sighting.

Computer analysis of behavioral and vegetational observations is incomplete; however, preliminary examination of the data indicates competition is reduced by temporal differences in initiation of nesting, by nesting in discrete habitats, and by employing different prey capture tactics.

PART I: FEEDING ECOLOGY OF GRASSLAND BIRDS

INTRODUCTION

Studies in feeding ecology were conducted to expose feeding pathways with which birds at the Pawnee Site are involved. Consideration was limited to insectivorous and granivorous species of birds. Information on both animal and plant types of foods was sought to obtain as complete an enumeration of taxa eaten, dimensions and biomass content of foods, and quantities eaten by the grassland birds, individually and as a whole. Feeding activities were also observed directly in the field to determine where the birds obtain food and how much feeding is done in each type of environment.

PERSONNEL AND LOCATION

Persons outside of the project who cooperated in various ways were Drs. Charles W. O'Brien, Ross Bell, Charles A. Triplehorn, Theodore O. Thatcher, and Robert J. Lavigne, and Theresa M. Foppe.

The entire field study was situated at the Pawnee National Grassland, Weld County, Colorado. Observations of feeding behavior and non-destructive sampling of nestling foods were done on the Intensive or Pawnee Site at the Central Plains Experimental Range. Collecting of adult birds for stomach content samples was done in an area immediately east of the Intensive Site but not more than 20 miles east of it. Statuses of stomach samples are given in Table 1.

Laboratory analyses were carried out primarily at the principal investigator's laboratory at Colorado State University and secondarily at Dr. R. M. Hansen's foods analysis laboratory at Colorado State University.

Table 1. Statuses of stomach samples taken in 1971.

Species	Number of Samples of Food Contents	Number of Stomach Samples[a/]	Number of Stomach Samples Processed
Lark Bunting	1	53	47
Horned Lark	6	75	97
McCown's Longspur	20		24
Western Meadowlark	12	21	
Mourning Dove	13		33
Vesper Sparrow	1	3	
Lark Sparrow	1		
Chipping Sparrow	1		
Brewer's Sparrow	20		
Sage Thrasher	1		
Chestnut-collared Longspur	4		
Eastern Kingbird	9		
Killdeer	1		4
Loggerhead Shrike	6		
Common Nighthawk	2		2
Mountain Plover	10		15
Grasshopper Sparrow	6		
House Sparrow		4	
Starling		3	
Rufous-sided Towhee		1	
Black-billed Magpie		4	
Ring-necked Pheasant		1	
Brown-headed Cowbird			1

[a/] Received from Dr. Ryder.

METHODS

Dietary components were determined by stomach analyses. Birds were collected from the shortgrass prairie at regular intervals throughout the period of their occupancy of the Pawnee Site. All contents of the stomachs were identified and measured in the laboratory. Reference collections of arthropods and seeds were assembled to facilitate identification, and the help of specialists was obtained for certain groups of insects. Details of the laboratory procedures were written up and submitted to the Natural Resource Ecology Laboratory under the title "Methods for Dietary Analysis of Small Vertebrates," a copy of which is included as Appendix I.

Data have been submitted to the Central Processing Laboratory for storage and processing. Much of the data has been analyzed by desk calculator. All samples have received initial steps in processing, which include placing samples in a vial with preservative, labelling samples, and preparation of a data card. Data on the birds have been taken in each case and sent to the data bank on the standard IBP forms. Species which have been significantly processed to date are Lark Bunting, Horned Lark, McCown's Longspur, Chestnut-collared Longspur, Mountain Plover, Killdeer, Mourning Dove, and Common Nighthawk.

RESULTS

The following is a summary of reports written by Baldwin (1971*a*,*b*; 1970*a*,*b*,*c*); Baldwin, Crieghton, and Kisiel (1971); Baldwin et al. (1969); and Creighton (1971*a*,*b*). The summary also includes a special report written by Baldwin at the request of Dr. N. R. French for the use of Dr. J. A. Wiens at the AIBS meeting. The report consisted of several tables on Horned Lark and Lark Bunting diets at Pawnee.

The diet of the Mountain Plover (*Eupoda montana*) in Weld County, Colorado, was studied for the spring and summer periods between May 4 and August 11. Thirteen birds (eight adults and five juveniles) were available for analysis of the stomach contents. Identifications of 90 food taxa and estimates of dry weight parameters for each type of food showed the diet to consist of 99.7% arthropods and 0.3% seeds. The most important food types were ground-dwelling beetles (60.0%), grasshoppers and crickets (24.5%), and ants (6.6%). The most important genus eaten was *Eleodes* (a darkling beetle), comprising 22% of the diet. Comparisons of diets of juvenile and adult Mountain Plovers revealed that juveniles ate smaller insects such as ants, bees, wasps and parasites, leaf and flower beetles, and leafhoppers in slightly greater proportions than did adults. Adults, however, ate larger insects such as caterpillars, billbugs, and darkling beetles in somewhat greater proportions than did juveniles. The mean length of food items eaten by all adults and by juveniles was 10.0 mm and 8.5 mm, respectively. Overlap in size, i.e., length, of food items eaten by the two age groups was 60.3%.

The diet of the Mourning Dove (*Zenaidura macroura*) was studied in the spring and summer months of 1970 and 1971. Thirty-one birds (28 adults and 3 juveniles) were collected for analysis of the stomach contents. Identification of 45 food taxa and estimates of dry weight parameters showed the diet to consist of over 99.9% seeds and less than 0.1% arthropods and molluscs. The most important food types were beeplant (*Cleome serrulata*) (28.1%), grasses (24.3%), and composites (19.6%). Almost 76% of the Mourning Dove diet was composed of seeds from plants characteristic of disturbed habitats, i.e., roadsides, cultivated fields, and abandoned fields. Comparisons of adult and juvenile diets during midsummer revealed that juveniles ate mainly composites and grasses (96%), while adults consumed seeds of beeplant and spiderwort (*Tradescantia occidentalis*) (68%). Selection of seed size (length) by the two age classes also varied, with juveniles taking about 80% of their seeds in the 4.1 to 4.5-mm size class. Some 84% of the adult diet was composed of seeds less than 3.5 mm in length. This difference in seed size for juveniles and adults apparently resulted from the heavy use by juveniles and the light use by adults of a single seed type, sunflower (*Helianthus annuus*), which was approximately 4.2 mm in length. Although sunflower seeds were equally available to both age classes, they were not the preferred food of adults.

The diet of the Killdeer (*Charadrius vociferus*) in the shortgrass prairie of Weld County, Colorado, was studied for the summer period, June 16 to July 23. A similar bird, the Mountain Plover (*Eupoda montana*), also feeds in the same shortgrass prairie during this period so that the two diets were compared to determine the amount of overlap. The food of the Killdeer was 99.7% animal and 0.3% plant on the basis of biomass consumed. Types of food eaten in greatest quantities were ground-dwelling beetles (77.0%), aquatic arthropods (13.6%), and crickets (5.0%). The most important family was the Carabidae (33.0%), and the second was the Tenebrionidae (26.3%). The mean length of food items eaten by the Killdeers was 8.0 mm, and the mean dry weight was 0.01 g.

The diets of Killdeer and Mountain Plover showed much overlap. Each bird obtained 77.3% of its food biomass from taxa eaten also by the other bird. Most of the overlap was from consumption of ground-dwelling beetles by both birds. The use of aquatic beetles by the Killdeer accounted for much of the non-overlapping foods. The similarities in diet resulted mainly from both birds feeding in the dry, upland, shortgrass vegetation; the differences resulted from the Killdeer feeding frequently at water and on damp ground.

PART II: BIRD FEEDING AND NESTING BEHAVIOR

OBJECTIVES

The purpose of this field study is to investigate habitat exploitation patterns of four species of grassland passerines: Lark Bunting (*Calamospiza melanocorys*), McCown's Longspur (*Rhynchophanes mccownii*), Chestnut-collared Longspur (*Calcarius ornatus*), and Horned Lark (*Eremophila alpestris*).

Root (1967) introduced the innovative concept of the *guild*, which he defined as "a group of species that exploit the same class of environmental resources in a similar way." Such a concept is applicable in this current study. Because similar environmental resources are available to all four of the above songbirds, slight behavioral differences in foraging stratagems of each increases efficiency of habitat utilization, reduces interspecific competition, and contributes to ecosystem stability. Quantification of foraging and prey capture techniques is then the first objective of this research.

Interspecific competition is also reduced by temporal and spatial segregation during time of maximum energy demand, i.e., initiation of nesting (Lack, 1954). The second objective is to complete ethograms of these four species and to correlate behavioral patterns with discrete nesting cycle stages. Once this correlation is made, it is possible, by cataloging behaviors of any individual, to approximate what stage of nesting in which that bird is involved, and what degree of environmental pressure is being applied. Comparisons of species' behavioral schedules are then used to indicate degrees of temporal segregation of nesting cycles.

The third objective is concerned with observations of spatial segregation by both gross habitat separation and by niche partition. Gross habitat segregation is reinforced by habitat preference or vegetative association, interspecific dominance relationships, and specific nest-site requirements. Niche partition is accomplished behaviorally by differential exploitation of available uniform habitat, i.e., prey capture in vegetation vs. ground or aerial capture.

PERSONNEL AND LOCATION

Field studies were conducted by myself, although Drs. Paul H. Baldwin, Ronald A. Ryder, and Stephen G. Martin assisted in various aspects of the investigation. Mr. Mark Strong lent valuable assistance in many phases of the work throughout the summer. Identification of nestlings' foods was done by Dr. Baldwin and Mrs. Terry Foppe.

All observations and food samples were collected at the International Biological Program's Pawnee Site, including portions of the Central Plains Experimental Range and the Pawnee National Grassland. Permanent study areas are located in Sections 28W and 23W of Township 10N, Range 66W in Weld County, Colorado. Both plots are lightly-grazed, summer use pastures.

METHODS

To accomplish the initial objectives, recognition of food capture techniques and formation of species' ethograms, behavioral schedules are made for a continuous 20-min period. During this time each activity and activity site is recorded through shorthand or coded notation. Examples of the shorthand notations and their meanings are shown in Appendix II.

To maximize opportunities for survival and reproduction, behaviors must be performed effectively, each behavior requiring an expenditure of time. Time budgets are constructed by recording how much time is spent in each activity (Verner, 1965). Thus, behavioral schedules are used as species' time budgets or catalogs of how and where individuals spend their time. Weins et al. (1969) presented sound arguments for the importance of a standardized interval for frequency analysis of behaviors; therefore, activities are partitioned by a timed sequence base. In this study the 20-min observational periods are divided into 10-sec intervals and relative frequency of specific behaviors are based on this interval. Intervals are obtained from audible pulses emitted by a variable frequency metronome, built from information from Weins et al. (1969).

Observations are made from either permanent towers constructed in Section 23W, or from a portable tower bolted to the bed of a pickup truck. To observe selected birds, a 20X and a 15-60X zoom telescope are used from the towers to give an effective viewing radius of 50 m. The towers are so positioned as to give coverage of the whole 10.4-ha plot. At this phase of investigation when specific behaviors are correlated to stages of known nesting cycles, efforts are made to find all nests within the study areas and to record nesting progression daily. An example of the form used for nesting records is shown in Appendix III. Nests are grouped as to stage, i.e., egg laying, incubation, etc., and a pair of birds involved in a particular stage is randomly selected for observation.

Color marking for individual recognition is essential and is based on the section of capture, i.e., red bands for Section 28W, orange for Section 23W, plus bands representing the nest number of that individual (Creighton, 1971*a*). Birds incubating or brooding are easily captured at nests by using a mist netting technique slightly modified from Martin (1969). A 12-m mist net is placed in a "V" arrangement around nests. Once the adult returns to the nest, the bird is flushed toward the vortex of the net where it becomes entangled or trapped against the net.

Spatial distribution of the four species is observed by censusing random areas on the Central Plains Experimental Range. After selection of a 1/16th sq mile area, it is referenced by numbered flags which are placed in a grid every 100 ft. A compass and tape measure are used to position grids. The censusing technique consists of recording locations of all birds seen during a 30-min interval as a walk is made through the selected plot. The interval is divided into six 5-min tallies during which symbols of each species are positioned on a reference grid and the vegetation type associated with each position is recorded. Vegetational types are identified by the procedure of Kuchler (1955). Flying birds are not tallied unless points of takeoff can be pinpointed.

Foods fed to nestlings are used as an index of differential exploitation of available habitat. Food samples from nestlings are obtained by tying a no. 3 white thread around the bird's throat, preventing it from swallowing any foods fed by the adults. After each visit of an adult to the nest, young are inspected for food. If present, prey is removed by forceps and placed in vials containing 75% alcohol until later laboratory inspection (Creighton, 1971*b*). Foods are characterized as to ecotype, i.e., ground beetle, hopping insect, flying insect, etc., which, when coupled with observed food capture technique, indicates exploitation patterns. Size and weight of prey are estimated from reference samples and serve as an indication of food size selection.

RESULTS

Computer analysis of behavioral and vegetation observations, and identification of nestling foods are incomplete. Over 230 hr of behavior schedules were taken; 30 random areas were censused for bird-vegetation associations, and 97 food samples were removed from nestlings during the summer of 1971. Nesting success, nestling growth rates, and production are discussed in Dr. Ronald Ryder's final report (1972), and data from this research are combined with his results.

Nesting sequences were referenced by date of initiation of egg laying; these dates for Lark Buntings, Horned Larks, McCown's Longspurs, and Chestnut-collared Longspurs are shown in Fig. 1. Temporal segregation of nesting cycles is indicated by variations in dates of maximal initiation. Horned Larks began nesting earliest in the spring with 42% of the total nests found initiated before May 10, 1971. Nesting peaks of McCown's Longspurs and Lark Buntings further indicate temporal segregation, while Chestnut-collared Longspurs maintain reduced levels of reproduction throughout the

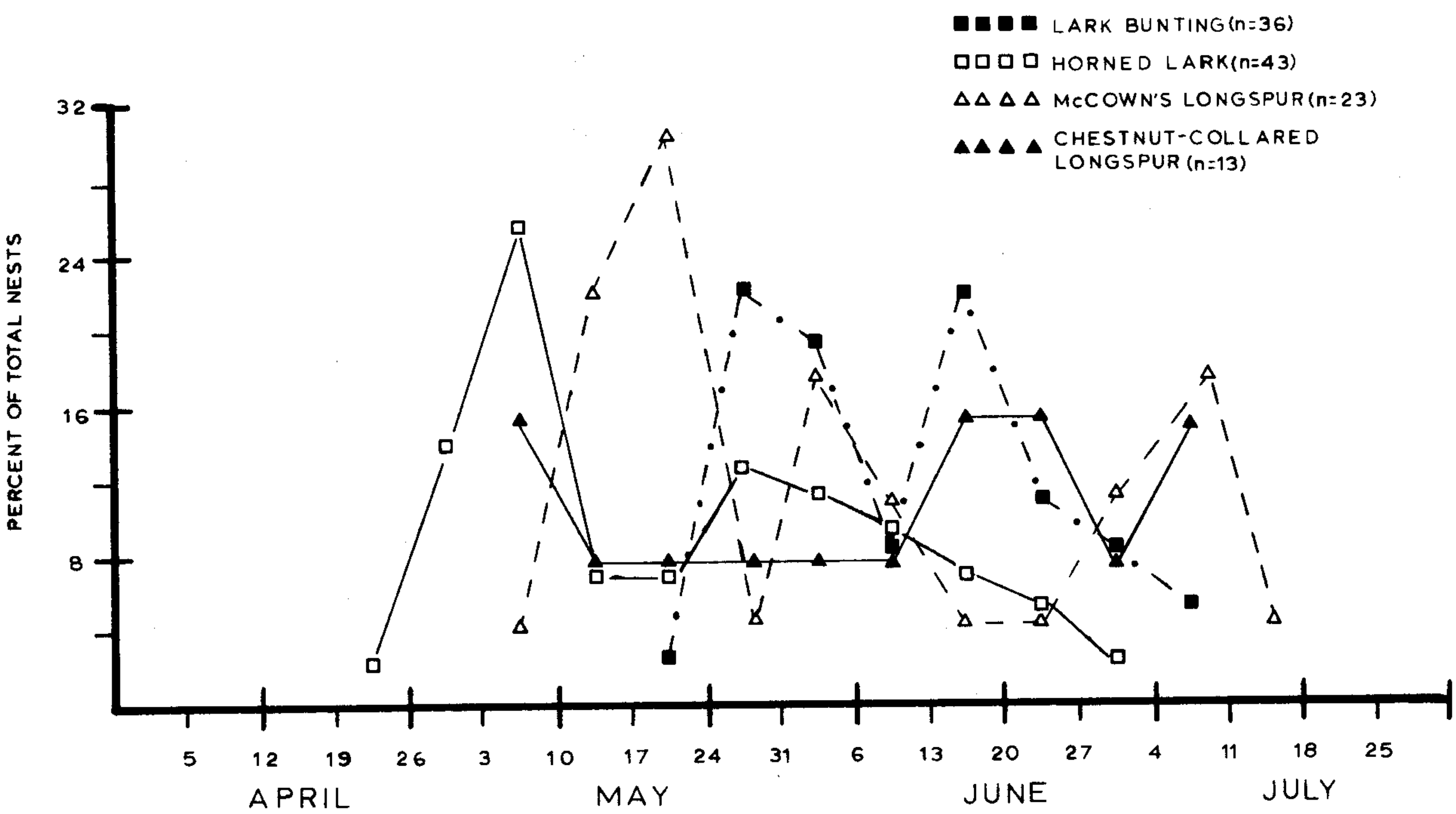

Fig. 1. Initiation of nesting by four species of grassland passerines.

spring and summer months. Secondary nesting peaks are influenced by renesting attempts and do not reflect the same degree of segregation as the primary peaks. Behavioral schedules and ethograms, correlated with discrete nesting cycle stages, greatly increase the sampling size of the reproducing population because estimates for any individual can be made and it is no longer necessary to locate the nest or to know the nesting sequences of a particular pair of birds.

Food capture tactics used by the four species are shown in Table 2 and Fig. 2. Definitions of the tactics (as modified from Root, 1967) are as follows:

Tactic	Position of Prey	Position of Bird
Hawking	In the air	In the air
Gleaning	In vegetation	On or near vegetation
Stalking	On the ground	On the ground

The two longspurs employ similar hunting tactics; however, competition is reduced by temporal and spatial segregation. Preliminary examination of the vegetational association observations indicate that the Chestnut-collared Longspurs are found in taller grass areas, i.e., areas of *Agropyron*, *Aristida*, and *Stipa*; and McCown's Longspurs are found in shorter grass areas, i.e., *Bouteloua*, *Buchloe*, and *Opuntia*. Horned Larks also were more abundant in shorter grass areas, and Lark Buntings, although fairly evenly dispersed over many vegetational types, were more common in taller grass areas. Although Horned Larks and Lark Buntings are the most abundant songbirds

Table 2. Summary of prey capture techniques of four species of grassland passerines.

Species	Frequency of Prey Capture Tactic[a]		
	Hawking	Gleaning	Stalking
Lark Bunting	37.8	3.8	58.4
McCown's Longspur	33.4	14.2	52.4
Chestnut-collared Longspur	21.0	31.0	48.0
Horned Lark	4.8	53.9	41.3

[a] Percent of total prey capture technique for each tactic employed.

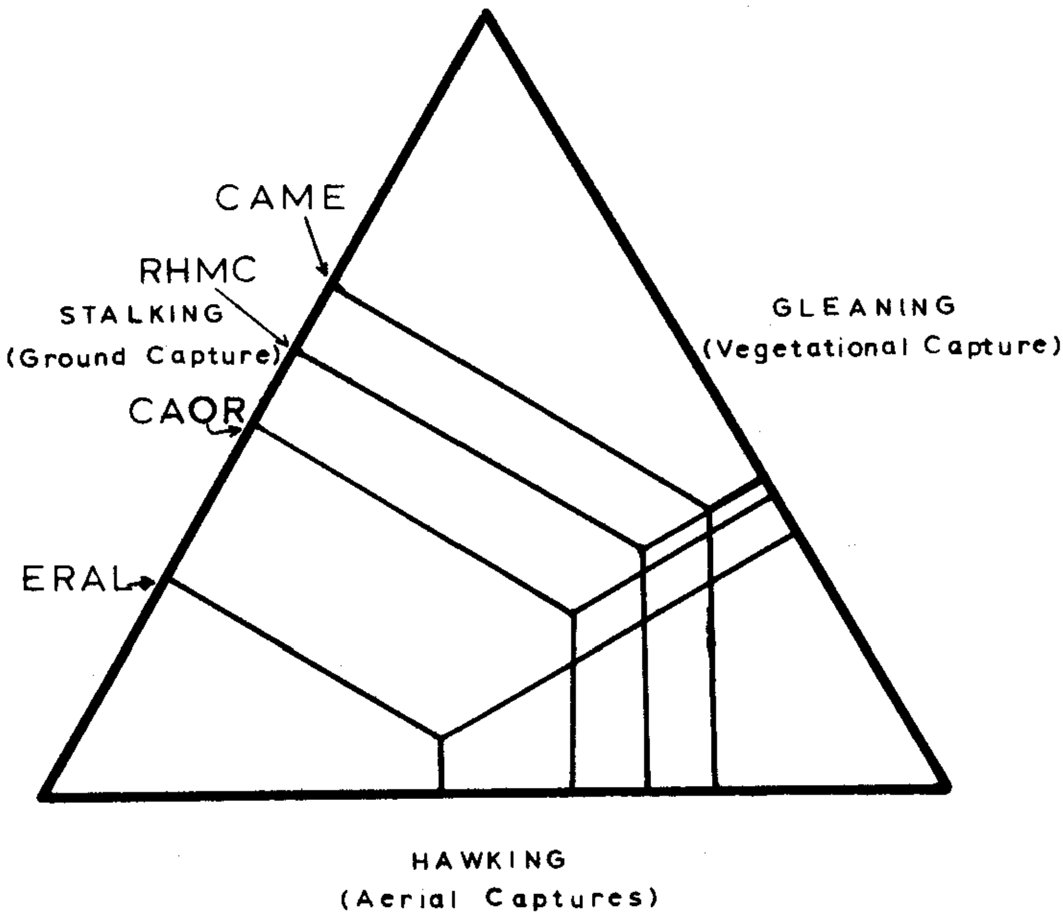

Fig. 2. The foraging techniques of four species of grassland passerines. The length of each line segment represents the percent of total animal prey captured by each tactic. The species involved are Horned Lark (ERAL), Chestnut-collared Longspur (CAOR), McCown's Longspur (RHMC), and Lark Bunting (CAME).

during the breeding season (Giezentanner, 1970), competition is reduced by their employing different prey capture tactics, nesting in discrete habitats, and nesting at different times.

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APPENDIX I

METHODS FOR DIETARY ANALYSIS OF SMALL VERTEBRATES

Objective

The object of this work is to identify insects and seeds eaten by small, terrestrial vertebrates. The general method was worked out for insectivorous and granivorous birds, but it is applicable to other small terrestrial vertebrates with similar diets.

Insect Identification and Quantitation

The procedure is to recover insects or parts of insects from the gut of the animal, then to identify each insect represented by comparing the insect or its parts with an identified reference collection. The reference collection is assembled from insects collected at each site and identified in advance with the aid of entomologists. The reference collection should be started during the first season of field work at each site.

Since the object is to determine energy flow and biomass movement, quantitative information is needed. The length of each insect eaten is estimated on the basis of direct measurement with micrometer or ruler, or by inference from size of fragments. Insects in the reference collection provide a basis for comparisons in estimating lengths from fragments. The number of each kind of insect eaten is determined by counting the parts repeated in a stomach sample, such as the number of head capsules, thoraces, elytra, etc., and using whichever part gives the highest count. Adult and immature stages of insects are identified and each handled on the same basis. The length of insect, as recorded at the time of examining the stomach sample, serves as the index to the dry weight of the insect eaten. A chart or graph for calibration of length with dry weight for each type of insect (i.e., family usually) is made up by collecting specimens of different sizes, oven-drying them, and weighing them. Life history stages of different forms are similarly calibrated. Note that it is *not* necessary to measure the volume or weight of insect remains present in the gut.

Seed Identification and Quantitation

The seeds, seed coats, or kernels are recovered from the general mass of food remains previously removed from the gut under a dissecting microscope. Identifications are then made by comparing them with a reference collection of seeds from locally occurring seed plants. In addition, quantitative data are desired, as with insects. Measurements of seed size are made to obtain mean length of each seed type as it occurs in the sample being examined. The length serves as the index to dry weight for seeds of each species and size. Calibration of length with dry weight is done with information assembled separately on seed weights from the literature or by collecting fresh seeds, oven-drying them, and weighing them. Some discretion is necessary due to variations in feeding mechanisms employed by birds, resulting in the presence or absence of seed coatings. The numbers of seeds eaten are determined by counting the seeds or parts of seeds.

Operational Steps

Collect the bird at the time it is feeding. Attach a tie-on label to the leg with the collector's number, name of bird, and date. Make a catalog entry for the locality, time of day, habitat, etc. Lay the bird on a piece of Saran Wrap (standard size square) and flow 70% ethanol deep into the esophagus with a medicine dropper (calibrated). Record the amount of alcohol accepted. Wrap the bird tightly in Saran Wrap, retaining any alcohol spilled from the bird. Place the bird in a car cooler until return to the laboratory. At the laboratory, weigh the package without unwrapping it, subtract the weight of the label, alcohol, and Saran Wrap, and record the weight of the bird. Place the bird package in the freezer.

Remove the bird from the freezer and thaw. Record the data from the bird specimen. Skin the bird, open the abdominal cavity, and remove the stomach (proeventriculus and gizzard). Examine the esophagus and pharynx for possible food items; if any are found, place them in a 4-dram, homeopathic vial in 70% alcohol with a size 0 rubber stopper. Cut open the stomach and add the contents to the vial. Slip in a label on which is recorded the collector's number, the species of bird, and the date collected. Record the sex, gonad condition and size, and the amount of fat deposit in birds on an IBP Grassland Biome Field Data Sheet (NREL-23)--Avian Collection, Internal.

The identification of foods is carried out as follows:

1. Get the diet specimen and the data card (Appendix Fig. 1).
2. Empty the specimen into a small glass dish. Pour off the murky fluid and replace it with fresh 70% alcohol. Retrieve any food fragments inadvertently poured off with the old fluid.
3. Use a dissecting microscope at 10 or higher power of magnification. Sort the stomach contents enough to allow a visual estimate of percent plant remains and percent animal remains on the basis of bulk.
4. Sort the grit and count the number of pieces greater than 0.5 mm.
5. Sort all of the plant items.

Species:________________________ Sex:____ Age:______ Serial number:__________

State:__________ County:__________ Month:______ Day:_____ Year:_____ Hr:________

T.____N., R.___ W., Section________ Collector:____________ Coll. no.____________

Crop:________ Stomach:__________ Diagnosis by:____________ Date:__________

% Plant:_____; % Animal_______; Total number of animal items:_____ Grit______

ANIMAL: Order | Family | Identification | Condition | No. | Stage | Size (mm)

UNISORT ANALYSIS CARD FORM YD BURROUGHS CORPORATION - TODD DIV. - L HADLEY PRINTED IN U.S.A.

PLANTS: % Name Length (mm) Description Number of seeds

Total number of seeds:

Appendix Fig. 1. Data card.

6. For each seed type, record the identification, the number present, and the size. If identification is not apparent, record the color, dimensions, surface characters, and make a sketch. Estimate and record the percent of plant matter each type represents. Seeds needing further work should be placed in mini-vials with the sample number on the cork.
7. Record the identity of plant fibers and leafy tissues and indicate the percent of plant matter in the sample they represent. For non-identified plant fibers and leafy material, record the characteristics and place a generous sample in a mini-vial for future identification at the IBP central laboratory. Record the sample number on the cork.
8. Sort all animal items. Several dishes may be used.
9. Identify the animals order by order to the lowest feasible taxonomic category. Record the identification and also the parts present, color, developmental stage of each specimen, and length. If a wide range in size is found, record the numbers of each size. Sketch the enigmatic specimens for future reference.
10. Store the specimens in a main vial, separate the vials or mini-vials, all of which are labeled. The need for maintaining segregation will vary according to the complexity of the dietary sample and the completeness of the immediate identifications. If all of the data are obtained, lump them; if further work is needed, use several vials. Unusual specimens may be added to the reference collection when they are identified.
11. Count and record the total number of animal prey items.
12. Count and record the total number of seeds.

The above procedure deals with three sorts of foods: animal items, seeds, and plant fibers or soft tissues of non-fruit origin. For animal items and for seeds, the above analysis should give the identification, number of items, and biomass (dry weight) eaten of each item. For plant fibers and soft parts of non-fruit origin, outside help may be needed on identification. Samples of the fibers and tissues are sent to the central foods identification laboratory for cellular analysis. However, the amounts of these substances present in the dietary sample can be roughly estimated from the original dietary analysis outlined above. This is the reason for recording visually estimated percentages of all food items. For example, after data on the seeds are all in, it might turn out that seeds totalled 90% of the plant matter in the sample and 180 mg dry weight. Then, if plant fibers had been recorded as 10% of the plant matter present, it could be inferred that they represented about 20 mg of dry weight. Sometimes the plant fibers are from seed coats and should be included with the seed rather than separately estimated (often true with wheat and sunflower). This procedure may be helpful for quantitating fibers found in insectivorous and granivorous birds, where fibers are almost invariably a minor component of the diet. For small vertebrates that eat a great deal of plant fiber and leafy material, this method is not recommended.

Amounts of Food Eaten per Unit Time

The amount of food eaten per unit of time, such as one day, must be calculated indirectly. Data produced by the foregoing procedures permit ready calculation of the proportion of each food type eaten; for example, the weevil might comprise 20% of the diet and buffalo grass seed 15% in the month of May for a grassland bird.

Let us say we wish to calculate the mean daily consumption of each of these foods by a Lark Bunting in May. Studies in bioenergetics tell us that the daily gross intake of food for a small bird living in a cage can be calculated. The amount below explains and illustrates the computation. S. C. Kendeigh (1963) has worked out equations which can provide an estimate of the energy required to sustain a small bird for a day in caged existence (existence energy). Important variables are weight of the bird and the temperature of the environment.

> Existence energy is the food metabolized by a bird maintaining constant weight in a small cage at a constant temperature and photoperiod. The regression line for eight species, varying from 10 to 4000 grams, at 9-12-hour photoperiod and 30°C is represented by the equation: $M = 1.5860\ W^{0.601}$ and at 0°C: $3.8578\ W^{0.550}$, where M is Kcal/bird/day and W is weight in grams. Regression lines for a 15-hour photoperiod are not significantly different. The lower weight exponent at 0°C than at 30°C, lower than that given for standard metabolism ($m = 0.8446 + W^{0.659}$) by King and Farner (Marshall's "Biology and comparative physiology of birds": II:215-288, 1961), also indicates that small birds expend proportionally more energy for existence than do large birds. The difference of values for the Y intercept, from 0.845 for standard metabolism to 1.5860 at 30°C to 3.8578 at 0°C, reflect the influence of feeding and activity compared with fasting and rest and of low temperature stress. These equations are considered only preliminary formulations. Because of the small number of species included only the equations for standard metabolism and existence metabolism at 0°C are statistically significant."

After publishing the above in 1963, Kendeigh sent me (in lit.) the following revised equations, which I received January 12, 1966:

Existence energy at 30°C: $M = 1.368\ W^{0.674}$

$$(\log M = 0.136 + 0.562 \log W)$$

Existence energy at 0°C: $M = 3.974\ W^{0.562}$

$$(\log M = 0.599 + 0.562 \log W)$$

M = kcal/bird-day

W = weight in grams

In order to determine the amount of food needed per day by a small bird living in the wild, the value for existence energy must be raised by two factors. One factor is for efficiency of digestion, and the other is for additional energy used in activity. Kendeigh is currently employing a digestive efficiency factor of 80%, in work reported at the September 1971 IBP meeting in Holland. Schartz and Zimmerman (1971) found that Dickcissels in the wild needed 1.4 times existence energy. In the following calculation, therefore, I have used the value of 80% for efficiency of digestion and 1.4 as the factor for normal activity in the wild, since the latter is the best estimate now available for a small, grassland bird.

A sample calculation will now be made, using the two equations, for 0°C and 30°C. Take a bird having a body weight of 38.7 g (Lark Bunting male). First, the calculations for 30°C:

1. Take the log of both sides of the equation: $M = 1.368\ W^{0.674}$.

   $\log M = \log 1.368 + 0.674 \log W$

2. Substitute 38.7 g for W.

   $\log M = 0.136 + (0.674)(1.588) = 1.206$

3. Find the antilog of log M.

   antilog 1.206 = 16.1

   Hence, M = 16.1 kcal/bird-day.

4. Calculate existence energy as kcal/kg-day:

$$\frac{16.1 \text{ kcal/bird-day}}{38.7 \text{ g}} = \frac{x \text{ kcal/kg-day}}{1000 \text{ g}}$$

Also, insert the efficiency factor (for 80%):

$$\frac{16.1 \times 1000 \times 1.25}{38.7} = 520 \text{ kcal/kg-day}$$

= gross energy intake at 30°C

Second, for 0°C, same steps:

$$M = 1.368\ W^{0.674}$$

$$\log M = 0.599 + (0.562)(1.588) = 1.491$$

$$\text{antilog } 1.491 = 31.0$$

$$M = 31.0 \text{ kcal/bird-day}$$

$$\frac{31.0 \times 1000 \times 1.25}{38.7} = 1001 \text{ kcal/kg-day}$$

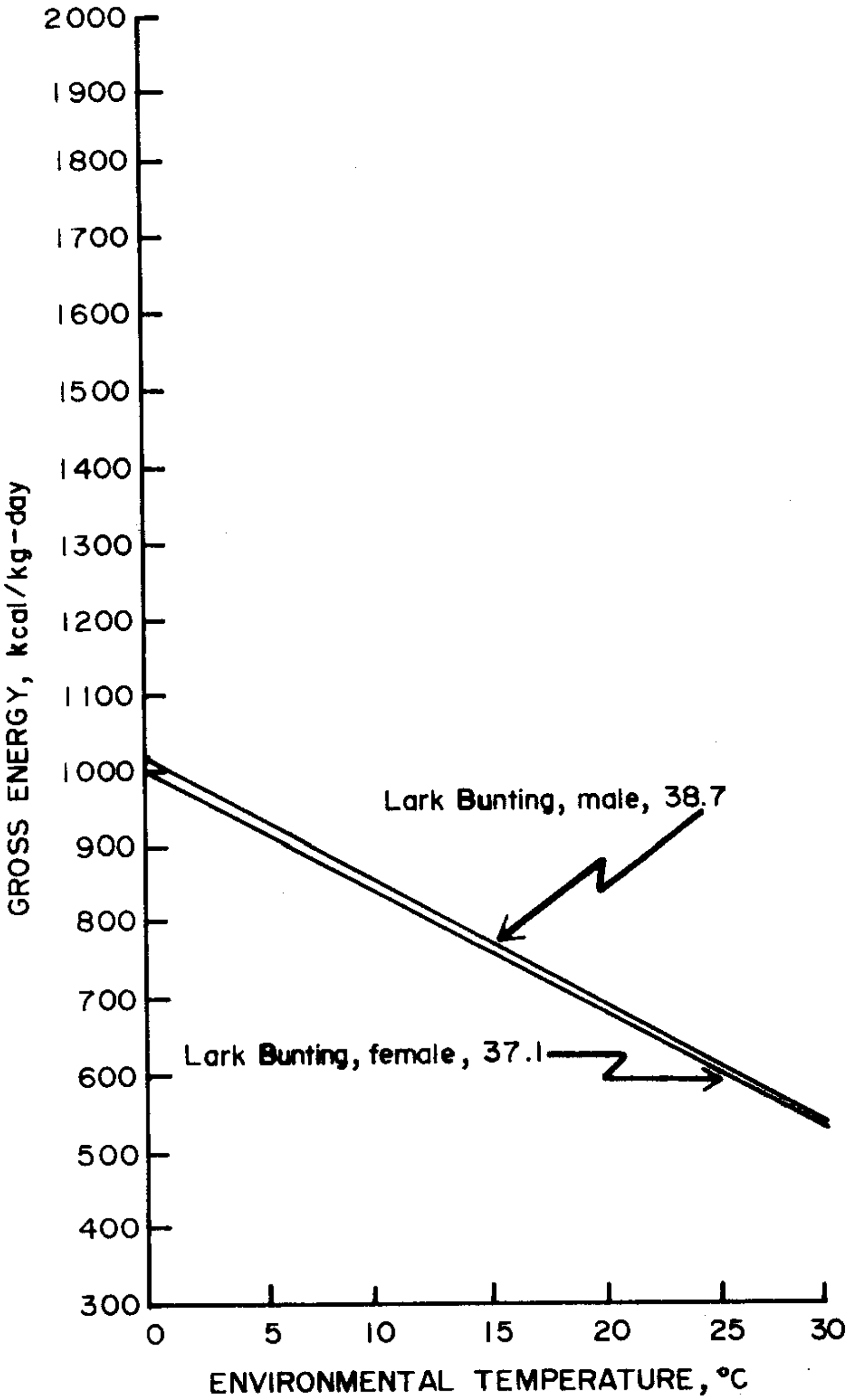
= gross energy intake at 0°C

A line is plotted (Appendix Fig. 2). Lines for birds of other sizes can be added to the graph.

Third, calculate the mean daily energy intake for male Lark Buntings in May. In May at the Pawnee Site, the mean monthly temperature is 12.7°C. Reading from the graph, gross energy at this temperature is 810 kcal/kg-day. Derive gross energy intake needed per bird-day in the wild in May:

$$\frac{810 \times 38.7 \times 1.4}{1000} = 43.9 \text{ kcal/bird-day}$$

Since we know the proportions of the different foods eaten and the caloric equivalents for those foods, we can calculate the mean amounts of all foods eaten per day. Caloric equivalents are obtained from the literature or from the IBP central laboratory.



Appendix Fig. 2. Lines for gross energy requirements at constant temperatures for small birds based on Kendeigh's equations for existence energy in relation to size of bird and an assumed digestive efficiency of 80%.

APPENDIX II

SYMBOLS AND MEANINGS USED IN BEHAVIORAL SCHEDULES

Symbols	Meanings
/	Metronome pulse
//	Behavior continues into next interval
-(10)-	Behavior continues through 10 intervals
F	Flight
sF	Short flight
CF	Circular flight
MF	Moth flight, slow wing beat
MF_n	Moth flight, joined by (n) other males
FS	Flight song
S	Song
S_a	Abbreviated song
...n	Number of notes in song
c	Call
cc	Chitter call
P	Preen
str	Stretch
scr	Scratch
sk	Shake
ff	Feather fluff
wf	Wing flick
ws	Wing spread
wd	Wing droop
cr	Crouch
C	Copulation
Ca	Attempted copulation
PCD	Post-copulatory display
FO	Face off
EFO	End of face off
w	Walk
rw	Rapid walk
h	Hop
pw	Parallel walk
j	Join
ch	Chase
sup	Supplant intruder
I	Incubation
stl	Stationary look
LPC	Ground prey capture
APC	Aerial prey capture
VPC	Vegetational prey capture
ef	Eat vegetation
BW	Bill wipe
BT	Bill tilt
shr	Shrub
gd	Ground
fp	Fence pole
fn	Fence
st	Stake
rd	Road
N	Nest site

APPENDIX III

FIELD DATA

Avian Nesting

Avian nesting data collected in 1971 at the Pawnee Site is Grassland Biome data set A2U209B. Data were reported on form NREL-26. A sample data form and an example of the data are attached.

IBP

GRASSLAND BIOME

U.S. INTERNATIONAL BIOLOGICAL PROGRAM

FIELD DATA SHEET--AVIAN NESTING A2U209

Data Type	Site	Gen/Spp	Nest No.	TWP	Range	Sec	Ht (cm)	Habitat	Code
1-2	3-4	5-8	9-12	13-15	16-18	19-20	21-24	25-69	70

Data Type	Site	Initials	Date			Time	Eggs	Young	Age	Adult	Number	Weight	Length	Primary	Number	Weight	Length	Primary	Number	Weight	Length	Primary	Number	Weight	Length	Primary	Code
			Day	Month	Year																						
1-2	3-4	5-7	8-9	10-11	12-13	14-17	18-19	20-21	22-23	24-25	26	27-30	31-33	34-36	37	38-41	42-44	45-47	43	49-52	53-55	56-58	59	60-63	64-66	67-69	70
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Site
01 ALE
02 Bison
03 Bridger
04 Cottonwood
05 Dickinson
06 Hays
07 Hopland
08 Jornada
09 Osage
10 Pantex
11 Pawnee

Number
E Egg
1,2,...,N
Bird No.

Code
C Comment follows
S Nest summary card follows

Adult
01 Building
02 Incubating
03 Brooding
04 Near nest, alarmed
05 Not seen
06 Other

Outcome
01 Fledged, young seen leaving nest
02 Fledged, adults excited near
03 Fledged, adults with young near
04 Fledged, nest empty, in tact
05 Failure, nest deserted
06 Failure, weather
07 Failure, predator
08 Failure, other
09 Unknown

Data Type	Site	Initials	Date			Time	Outcome	Eggs Laid	Incubation Period	Eggs Hatched	Fledging Period	Young Fledged	Comments	Code
			Day	Month	Year									
1-2	3-4	5-7	8-9	10-11	12-13	14-17	18-19	20-21	22-23	24-25	26-27	28-25	30-69	70
26														

+++ EXAMPLE OF DATA +++

```
         1         2         3         4         5         6         7         8
12345678901234567890123456789012345678901234567890123456789012345678901234567890

2611FRAL1-0110N66W23   0GRASSLAND-RED THREE-AWN
2611MAS210471141503    02
2611MAS290471095003    05
2611MAS030571130000    05                                                  S
2611MAS03057113000703  00   00EGGS SHELLS IN NEST
2611FRAL1-0610N65W26   0GRASSLAND-BLUE GRAMA
2611MAS040571144503    02
2611MAS100571163000    05                                                  S
2611MAS10057116300703  00   00
2611FRAL1-0710N65W26   0GRASSLAND-COWCHIP
2611MAS1005711600020200003E02.1        E01.9       101.9038   201.7037
2611MAS11057115150002000 5                         302.1040   402.0042
2611MAS110571151500020105102.6040      202.7040
2611MAS1205711435  020105                          303.6042   403.4042
2611MAS1205711435  020205104.5044      204.3044
2611MAS1305711650  020204                          305.3047   405.7948
 611MAS1305711650  020304107.9052      207.6052
2611MAS150571                                                              C
26ONE YOUNG DEAD IN NEST, ALL HAD ANTS ON THEM - DESERTED
2611MAS1705711600  00   05                                                 C
26YOUNG DEAD IN NEST                                                       S
2611MAS17057116500504  04   00
2611FRAL1-0810N66W21   0GRASSLAND-SNAKEWEED
2611MAS110571123003    05
2611MAS120571135003    04E02.9      E03.0      E03.1
2611MAS170571130003    05
2611MAS18057112450201000 3
2611MAS19057111300102  05                                                  C
26TWO YOUNG DEAD IN NEST-EGG COLD-RAIN LAST NIGHT                          S
2611MAS19057111300603  02   00
2611FRAL1-0210N66W23   0GRASSLAND-RED THREE-AWN
2611MAS030571130001    01
2611MAS040571131500    05                                                  S
2611MAS040571131507
2611FRAL1-0310N66W23   0GRASSLAND-COWCHIP
2611MAS030571143002    02
2611MAS060571131503    05
2611MAS120571124503    05E02.4      E02.3      E02.2
2611MAS150571131503    04
2611MAS17057115000030000 3
2611MAS1805711345  0301051     044   2    045   3    048
 611MAS1905711330  0302041     049   2    048   3    049
2611MAS2005711510  0303051     054   2    052   3    056
2611MAS2505710820  020804            2    0630153    064018
2611MAS2605711430  00   05                                                 S
```

```
2611MAS2605711430040З  03  03
2611FRAL1-0410N66W21    0GRASSLAND-BLUE GRAMA
2611MAS040571124003     02
2611MAS060571124303     02
2611MAS100571140001     05
2611MAS110571124000     05                                              S
2611MAS11057112400703  00  00
2611FRAL1-0510N65W26    0GRASSLAND-BLUE GRAMA
2611MAS040571140003     02
2611MAS100571160503     05
2611MAS120571145003     05E01.9        F02.2       F02.2
2611MAS1305711640000300З4103.3044     203.0043    302.3040
2611MAS1505711115  030205107.0052    206.5049    305.5048
2611MAS1705711615  030405113.8060009213.6060038311.1056006
2611MAS1805711105  030505114.7062011215.1064011313.6060010
2611MAS1905711530  030604117.6067018218.4071019316.1065016
2611MAS2005711700  030704119.2075025221.8077025318.9072023
2611MAS2405711615  00  05                                               S
2611MAS24057116150403  03  03
2611FRAL1-0910N66W22    0GRASSLAND-RED THREE-AWN
2611MAS110571130003     02
2611MAS130571130003     04E03.0        F03.0       F02.9
2611MAS170571140003     05
2611MAS1805711300000300005102.5040    202.8043    302.4040
2611MAS1905711150  030103103.6043    204.1045    303.5042
2611MAS2005711345  030203106.0049    207.0050    305.9047
2611MAS2405711400  00  05                                               S
2611MAS24057114000703  03  00
2611FRAL1-1010N65W27    0GRASSLAND-WNW RABBITBRUSH
2611MAS110571142003     02E02.8        F02.7       F02.6
2611MAS150571114503     05
2611MAS17057115300201000510?.5042
2611MAS18057111550101000 5            202.3043
2611MAS1805711155  010105103.1044
2611MAS1905711405  010105             204.8047
2611MAS1905711405  010205106.3049
2611MAS2005711540  010204             208.1054
2611MAS2005711540  010304110.2056
2611MAS2405711455  010605             219.3069016
2611MAS2405711455  010705120.8072018
2611MAS2505711420  010705             220.9075021
2611MAS2505711420  010805122.9076025
2611MAS2605711500  010804             222.8078027
2611MAS2605711500  010904124.1085031
2611MAS2705711505  010905             224.5086036
2611MAS2705711505  011005126.1088037
2611MAS2905711410  00  05                                               S
2611MAS29057114100403  021002
2611FRAL1-1110N65W27    0B.GRASSLAND-ENE-COWCHIP
2611MAS11057114450003  04                                               C
 5YOUNG ARE 7-8 DAYS OLD-TRIED TO LEAVE NEST
2611MAS12057114050000  05                                               S
```

Avian Diet Data

Avian diet data collected in 1971 at the Pawnee Site is Grassland Biome data set A2U205B. Data were reported on forms NREL-2A, NREL-28, and NREL-29. Copies of these forms and an example of the data follow.

GRASSLAND BIOME

U.S. INTERNATIONAL BIOLOGICAL PROGRAM

LAB DATA SHEET--AVIAN DIET, PLANT FOODS

Card Code	Sample Type and Number	Genus and Species of Bird	Collector's Number	Family	Subfamily	Genus	Species	Type of Fruit	Length (mm)	Estimate Percent	Number Fruits	Individual Dry Weight	kcal/g Dry Weight	Date			Period	Season	Site	Data Type
														Day	Month	Year				
1-5	7-12	14-17	19-25	26-28	29-31	32-34	35-36	37-38	39-43	44-46	47-49	50-55	56-60	68-69	70-71	72-73	74-75	76	77-78	79-80
																				2A