Papers

Foods Eaten by Tree Sparrows in Relation to Availability During Summer in Northern Manitoba

GEORGE C. WEST[1]

ABSTRACT. The amount of animal matter in the stomach contents of tree sparrows (*Spizella arborea*) collected at Churchill, Manitoba, increased from June until the middle of July but quickly dropped off in August. Chief food items were seeds of 6 species of *Carex;* seeds, flowers and fruits of *Empetrum* and *Vaccinium;* adult Diptera and Araneida; and larvae of Coleoptera and Lepidoptera. From available foods tree sparrows selected several species of *Carex* and ignored others. Snails though abundant were not eaten, and several larval insect forms were selected out of proportion to their occurrence in availability samples. The gross caloric value of the average summer diet was 5211 cal./g. dry weight and the average metabolized energy requirement was estimated to be between 20 and 25 kcal./day or the equivalent of 5.06 and 6.33 g. dry wt. of diet items. On the basis of food supply it is doubtful that gross energy of available foods limits the breeding density of tree sparrows at Churchill.

RÉSUMÉ: *Nourriture consommée par les Pinsons hudsoniens, par rapport à sa disponibilité, en été, dans le nord du Manitoba.* La proportion de matière animale dans le contenu stomacal des Pinsons hudsoniens (*Spizella arborea*) capturés à Churchill, Man., augmente de juin jusqu'au milieu de juillet, puis diminue rapidement en août. Les aliments principaux sont: les graines de 6 espèces de *Carex*; des graines, des fleurs et des fruits d'*Empetrum* et de *Vaccinium*; des Diptères et des *Araneida* adultes; enfin, des larves de Coléoptères et de Lépidoptères. Parmi les aliments disponibles, les Pinsons hudsoniens choisissent plusieurs espèces de *Carex* et ignorent les autres. Les limaces, bien qu'abondantes, ne sont pas consommées, et plusieurs formes larvaires d'insectes sont choisies hors de proportion avec leur présence dans les échantillons de disponibilité. La valeur calorique brute du régime estival moyen est de 5211 cal/g de poids à sec, la demande moyenne d'énergie à métaboliser est estimée entre 20 et 25 kcal/jour ou l'équivalent de 5.06 et 6.33 g de poids à sec d'éléments du régime. Sur la base de la nourriture disponible, il est douteux que l'énergie brute de cette nourriture limite la densité de reproduction des Pinsons hudsoniens à Churchill.

РЕЗЮМЕ. *О соотношении доступного и потребляемого корма лесных воробьев в северной Манитобе летом.* Количество животной пищи, содержащейся в желудках лесных воробьев (Spizella arborea), которые были пойманы в районе Черчилля, Манитоба, возрастало с июня до середины июля, но уже в августе быстро снижалось. Рацион воробьев состоял, в основном, из семян шести видов *Carex;* семян, цветов и плодов *Empetrum* и *Vaccinium;* взрослых мух и пауков, а также личинок жуков и бабочек. Из тех видов пищи, которые были фактически доступны, воробьи потребляли несколько видов *Carex,* игнорируя другие; они совсем не ели улиток, несмотря на их изобилие, и были столь же разборчивы в личинках насекомых, отдавая явное предпочтение их определенным видам, что явствует из сравнения содержания последних в желудках и в валовых пробах, взятых в поле. Общая калорийность среднего летнего рациона составляла 5211 кал на 1 г сухого веса, тогда как средняя потребность энергии обмена веществ оценивается величиной от 20 до 25 ккал в день, что эквивалентно 5,06 - 6,33 г сухого веса летней пищи. Судя по настоящим наблюдениям, размножение лесных воробьёв в районе Черчилля вряд ли лимитируется суммарной энергией доступных для них кормовых ресурсов.

[1]Institute of Arctic Biology, University of Alaska, Fairbanks, U.S.A.

INTRODUCTION

In 1937, Baumgartner summarized her observations of the summer food of adult and juvenile tree sparrows (*Spizella arborea arborea*) in the immediate vicinity of Churchill, Manitoba (50°47′N., 94°11′W.). Her series of 19 adults indicated a gradual shift from vegetable to animal food at the peak of the breeding season and a slow return to a vegetable diet by the time of migration.

In the course of a study on the bioenergetics of the tree sparrow (West 1958, 1960) collections of foods eaten by adult tree sparrows and foods available in the environment where the tree sparrows fed were made at Churchill. The present study extends the winter program of food relations and of migration already published (West 1967; West and Peyton 1972).

METHODS

Foods Used

Tree sparrows arrive at Churchill at the end of May or in the first week of June having left their wintering grounds by the first of April. When they arrive on the shores of Hudson Bay, the sparrows find themselves in an early spring habitat as much snow remains on the ground. But melting occurs rapidly in the open areas and birds can be found singly or in pairs around the margins of partially melted ponds feeding primarily on sedge (*Carex sp.*) seeds of the previous year's production.

Tree sparrows were shot while they were feeding from late May through late August 1956 and 1957. Collections were made from Fort Churchill east along the road to the rocket launch site and Twin Lakes, 12.4 miles (20 km.) from Fort Churchill and also along the railroad tracks to Goose Creek, 10 miles (16 km.) south of Churchill Village. Habitats where tree sparrows nested were chosen for collection; these included the spruce-tundra ecotone, pond margins with alder and willow, and the dense willow thickets bordering the Churchill River (West, unpublished data).

The collected birds were weighed, sexed and aged; the esophagus, proventriculus and gizzard were removed and their contents washed into a Petri dish. Food in the mouth which could have been collected for feeding young was not included in the analyses. Whole invertebrates were preserved in 70 per cent ethanol and sorted into families. The identifiable seeds were allowed to air dry and were separated by hand into species. Both invertebrates and seeds were subsequently dried at 80°C. and weighed to 0.1 mg. The remaining crushed material was separated from the grit, dried and weighed and the percentage of plant and animal matter in the crushed contents was visually estimated under a binocular dissecting scope. Since the crushed material was physically separable only with great difficulty, it was assumed that the visual estimate of plant and animal matter was proportional to dry weight. Grit was weighed separately and not included in the weight of the total stomach contents. The dry weights of each food species were recorded for each individual bird and the percentage of each item was calculated. These percentages were then averaged by approximately half-month intervals

TABLE 1. Average per cent composition based on dry weights of stomach contents of tree sparrows during summer at Churchill, Manitoba.

	28 May to 15 June	*16 June to 30 June*	*1 July to 15 July*	*16 July to 31 July*	*1 Aug. to 15 Aug.*	*16 Aug. to 24 Aug.*	*Summer[1] Average*
NUMBER EXAMINED	10	20	8	10	16	5	69
PLANTS[2]							
Picea glauca, *P. mariana*	—	0.55[3]	—	—	—	—	0.09
Eriophorum sp.	0.85	0.91	—	1.91	4.76	—	1.41
Scirpus sp.	—	—	—	—	0.23	—	0.04
Carex sp. D	8.74	10.22	0.36	1.43	3.40	2.73	4.48
sp. E	—	—	—	tr	—	—	tr
sp. F	0.01	0.91	0.73	—	1.59	—	0.54
sp. I	—	0.73	0.36	0.24	9.30	21.38	5.34
sp. J	0.64	0.18	—	—	3.18	0.97	0.83
sp. K	2.77	0.18	—	—	0.45	0.48	0.65
Amaranthus sp.	—	0.18	—	—	—	—	0.03
Caryophyllaceae	—	—	—	—	1.13	1.77	0.48
Brassica sp.	—	—	—	—	tr	—	tr
Draba sp.	—	—	—	—	1.13	4.02	0.86
Cruciferae (?)	—	tr	—	—	2.27	—	0.38
Empetrum nigrum	—	—	—	1.91	7.03	2.09	1.84
Vaccinium uliginosum, *V. vitis-idea*: seeds	—	—	—	—	1.13	18.49	3.27
: flowers	—	—	—	0.48	—	—	0.08
Crushed plant matter	51.59	55.29	10.14	44.86	35.60	35.69	38.87
Total plant	64.60	69.15	11.59	50.83	71.20	87.62	59.17
ANIMALS							
Homoptera	—	—	—	0.01	—	0.32	0.06
Hymenoptera: adults	—	0.18	—	—	0.23	—	0.07
: pupae	—	0.91	—	—	—	—	0.15
Diptera: adults	0.21	0.18	1.81	1.19	0.23	0.32	0.66
: larvae	—	1.46	—	—	—	—	0.24
Coleoptera: adults	0.01	0.37	0.36	—	0.45	—	0.20
: larvae	—	—	3.62	—	0.68	—	0.72
Lepidoptera: adults	—	—	—	—	tr	—	tr
: larvae	—	0.73	—	7.88	—	—	1.44
Araneida	—	0.18	2.17	0.48	—	—	0.47
Acarina	—	tr	—	—	—	—	tr
Mollusca	—	tr	0.73	—	—	—	0.12
Unidentified eggs	—	—	—	—	5.22	—	0.87
Crushed animal matter	35.18	26.84	79.72	39.61	21.99	11.74	35.84
Total animal	35.40	30.85	88.41	49.17	28.80	12.38	40.84

[1]Average of the average per cent composition in each collection interval.
[2]Seeds unless otherwise indicated.
[3]Use of 2 decimal places does not imply this order of accuracy in measurement but is used to show relative amounts of minor components.

from the first date of collection on 28 May until the last date of collection on 24 August. The numbers of individuals analyzed are given for each interval in Table 1.

Foods Available

Tree sparrows pair and begin nesting in early June at Churchill and they form territories of varying sizes in which they gather their food (Baumgartner 1968). Nesting habitats, as noted above, included the majority of ecological types locally available with the exception of seacoast, continuous spruce woods and arid *Dryas* fellfield tundra. Water or wetness seemed to be an important constituent of each territory as tree sparrows were found mostly along the borders of small ponds, lakes, marshes, streams and rivers.

Food availability samples were taken in conjunction with the collection of a feeding bird and therefore are representative of the food available in the specific locality where tree sparrows were feeding. Two methods were employed to determine the foods available to summer feeding adult tree sparrows. First, ground samples covering 0.1 $m.^2$ each were taken in areas where tree sparrows were feeding. The method of ground sample collection followed that described by Davison *et al.* (1955) and used in the winter study (West 1967). A 0.1 $m.^2$ collapsible frame was opened up and placed over the area. All overlying vegetation, whether standing or recumbent, was quickly removed to a paper sack. Then a cut was made around the inner edge of the frame and the surface was scraped to a depth of about 1 cm. and placed in the bag. As tree sparrows did not scratch beneath the soil surface, the top 1 cm. included all seeds available to them. Samples were stored in closed paper sacks and either allowed to air dry and then be sifted through a 200 mesh/in. (8 mesh/mm.) screen, or were washed with water through the same screen to remove extraneous soil particles. The remainder of the sample was sorted by hand into animal or seed groups. The vegetation was checked and all seeds removed, since the tree sparrows fed not only on the ground but also directly from the standing vegetation.

TABLE 2. Number of samples of available foods collected by approximately half-month collection intervals during summer at Churchill, Manitoba.

Date	*Ground Samples*	*Sweep-net Samples*
28 May to 15 June	7	—
16-30 June	18	2
1-15 July	11	7
16-31 July	19	17
1-15 Aug.	17	17
16-24 Aug.	5	7
Total	77	50

After sorting, the seed samples were oven dried at 80°C. and weighed to the nearest 0.1 mg. The number of ground samples gathered in each half-month collection period is given in Table 2. Owing to the paucity of samples taken over the 2-year period and in many locations in the Churchill area, it was not practicable to attempt a comparison among collection periods. Therefore the total amount of each species in each sample was averaged for each period; then the average amounts for all periods during the summer were summed to obtain the total standing crop of seeds in grams dry wt./hectare per summer collecting season. This is given in Table 3, column 1. The percentages were then determined on these totals and are given in Table 3, column 2.

TABLE 3. Dry weight and percentage of plant food items available to tree sparrows during summer at Churchill, Manitoba, in relation to those actually eaten. Items are seeds unless indicated otherwise.

	Standing Crop grams/hectare for period 28 May to 24 Aug.	*Per cent of total (plant & animal)*	*Foods utilized (modified from Table 1)*[1] *(Av. per cent)*
Picea glauca, P. mariana	2882	4.33[2]	0.36[2]
Potamogeton sp.	5	0.01	
Scirpus sp.	4	0.01	0.15
Carex capitata (sp. A)	120	0.18	
C. paupercula (sp. B)	130	0.20	
C. limosa (sp. C)	263	0.40	
C. sp. D	4530	6.81	17.72
C. sp. E	848	1.28	tr
C. sp. F	58	0.09	2.13
C. sp. G	465	0.70	
C. sp. H	262	0.39	
C. sp. I	663	1.00	21.09
C. sp. J	152	0.23	3.27
C. sp. K	2859	4.30	2.56
Eriophorum sp.	3	tr	5.56
Juncus sp.	tr	tr	
Salix sp.	26	0.04	
Myrica gale	1289	1.94	
Alnus crispus	14	0.02	
Polygonum viviparum: bulbils	120	0.18	
Amaranthus sp.	1	tr	0.12
Brassica sp.	140	0.21	tr
Draba sp.	61	0.09	3.40
Rubus chamaemorus	2192	3.30	
Potentilla sp.	2	tr	
Geum sp.	44	0.06	
Umbelliferae	21	0.03	
Empetrum nigrum: seeds	14718	22.14	7.27
: berries	18890	28.41	
Andromeda polifolia	304	0.46	
Vaccinium uliginosum, V. vitis-idea: seeds	555	0.84	12.92
: berries	2629	3.95	
: flowers	1523	2.29	0.32
Arctostaphylos rubra	175	0.26	
Ericaceae (?)	99	0.15	
Menyanthes trifoliata	154	0.23	
Compositae sp. A	3	tr	
sp. B	tr	tr	
sp. C	3	tr	
Unknown No. 1	41	0.06	
No. 2	8	0.01	
No. 3	8	0.01	

[1]Percentages recalculated from identifiable items only (see text).

[2]Use of 2 decimal places does not imply this order of accuracy in measurement but is used to show relative amounts of minor components.

The second method of estimating available food was the insect sweep net. According to Shelford (1951), 48 1-metre sweeps of an insect net with a diameter of 33 cm. each through an unswept area of the vegetation results in a collection of insects equivalent to one that would have been obtained by covering 1 m.^{2} of ground and vegetation with an inverted can, adding a killing agent and gathering the dead insects. There is no question that errors in calibration could be involved in applying to the tundra and taiga the method Shelford designed for the Illinois prairies and woodlands. However, the technique provided an easy and consistent method of sampling insects that were abundantly available to feeding birds.

Sweeps were made in areas where birds were feeding, i.e. in sedge meadow, through the heath covering the tundra, among spruce and larch branches, and in willow and alder thickets. As with the ground samples, sweep samples were taken when collecting a feeding bird.

The number of sweep net samples collected in each interval are given in Table 2. The interval samples were pooled for both years and averaged to give the average grams dry weight per hectare of animals collected from the vegetation exactly as for the seeds (see above).

Seeds were identified by referring to the seed collection of the author and that at the University of Alaska. Charles R. Gunn identified a few species not determined by the author. Nomenclature follows Hultén (1968).

Insects were identified by Armi C. Salo from the family keys in Borror and de Long (1964) and nomenclature follows their system.

RESULTS AND DISCUSSION

Marked annual differences in phenology may cause changes in feeding habits of sparrows that depend on seeds covered by the winter's snow, new seeds produced during the current year, and the emergence of insects. My phenological records for the two summers are very similar and indicate approximately the same times of snow melt and insect emergence each year. The daily temperature readings from the Fort Churchill weather station were comparable between the two years and the average temperature for the 3 summer months in 1956 was 10.4°C. and for 1957, 10.1°C. On this basis, I believe it is proper to combine the data on foods used and foods available for the two summers.

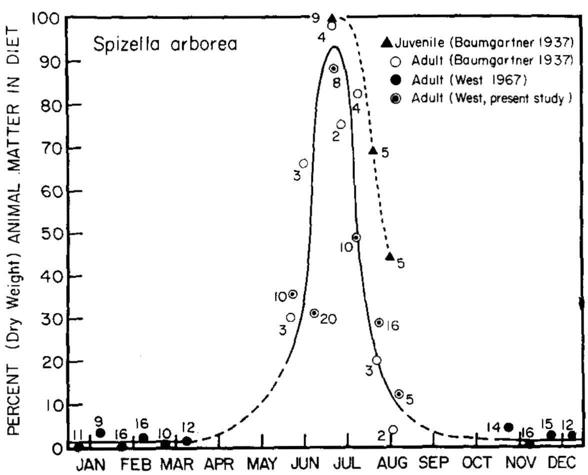

FIG. 1. Proportion of animal matter in the diet of tree sparrows during summer and winter. Data from Baumgartner (1937) and West (1967) in addition to the present study (Table 1). Dashed lines indicate times of migration. Food habits of tree sparrows during spring migration are now under study. Numbers beside data points indicate the number of stomachs analysed. Vertical lines in the horizontal axis indicate the middle of the month.

Foods Used

Eighteen identifiable taxa of plants (from family to species) and 12 taxa of animals (orders) were found in the gizzards of the 69 tree sparrows examined (Table 1). In this paper, a taxon is considered to be a recognizable taxonomic unit and is not used to denote different life forms of the same unit (e.g. flower and seed, or larva and adult). Plant materials made up from a minimum of 11.6 per cent of the total food in the first 2 weeks of July to 87.6 per cent in late August with animals making up the remainder (Table 1, Fig. 1). There was an increase in the proportion of animal food eaten by birds from their arrival in late May until the first weeks of July and a steady decline until collection stopped in August as Baumgartner (1937) had shown with her earlier collections (Fig. 1).

Crushed and unrecognizable plant and animal remains made up a large part of the total gizzard contents other than grit. It had to be assumed that the proportions of the various taxa recognized in the gizzard existed in the same relative proportions in the crushed miscellaneous matter, although it was realized that the softer items may have been ground while the harder items remained recognizable in the gizzard. However, most collections were made while the bird was feeding, and soft insects or seeds just ingested would not have had a chance to have been ground. The last column in Tables 3 and 4 represents the proportions of each taxon in the diet exclusive of crushed material.

TABLE 4. Dry weights and percentages of animals available to tree sparrows during summer at Churchill, Manitoba, in relation to those actually eaten.

Animal orders	*Families*	*Life form*	*Standing crop grams/hectare for period 28 May to 24 Aug.* by family	*by group*	*per cent of total (animal & plant)*	*Animals utilized (modified from (Table 1)*[1] *Av. per cent*
Collembola	all			822	1.24[2]	
	Poduridae		822			
Hemiptera	Unidentified		1	1	tr	
Homoptera	all			47	0.07	0.22[2]
	Cicadellidae		43			
	Aphididae		4			
Coleoptera	all	adult		669	1.01	0.79
	Cicindelidae	adult	49			
	Carabidae	adult	2			
	Omphoronidae	adult	68			
	Dytiscidae	adult	245			
	Silphidae	adult	19			
	Staphylinidae	adult	8			
	Cantharidae	adult	2			
	Dermestidae	adult	240			
	Tenebrionidae	adult	2			
	Phalacridae	adult	4			
	Scarabaeidae	adult	tr			
	Chrysomelidae	adult	10			
	Curculionidae	adult	3			
	Scolytidae	adult	tr			
	Unidentified	adult	17			
	Unidentified	larvae	167	167	0.25	2.84
	Unidentified	pupae	tr	tr	tr	

(*continued on following page*)

Table 4 (continued)

Animal orders	Families	Life form	Standing crop grams/hectare for period 28 May to 24 Aug. by family	by group	per cent of total (animal & plant)	Animals utilized (modified from (Table 1)[1] Av. per cent
Lepidoptera						
	Unidentified	adult	10	10	0.02	tr
	Unidentified	larvae	206	206	0.31	5.67
	Unidentified	pupae	7	7	tr	
Diptera	all	adult		2082	3.13	2.60
	Chironomidae	adult	839			
	Simuliidae	adult	698			
	Culicidae	adult	22			
	Bibionidae	adult	3			
	Cecidomyiidae	adult	9			
	Tabanidae	adult	270			
	Empididae	adult	tr			
	Bombyliidae	adult	5			
	Dolichopodidae	adult	7			
	Phoridae	adult	tr			
	Pipunculidae	adult	tr			
	Syrphidae	adult	1			
	Sciomyzidae	adult	30			
	Psilidae	adult	3			
	Chloropidae	adult	tr			
	Tachinidae	adult	7			
	Calliphoridae	adult	5			
	Anthomyiidae	adult	144			
	Ephydridae	adult	1			
	Unidentified	adult	38			
	Unidentified	larvae	221	221	0.33	0.96
	Unidentified	pupae	8	8	0.01	
Hymenoptera	all	adult		122	0.18	
	Tenthredinidae	adult	19			
	Ichneumonidae	adult	9			
	Braconidae	adult	1			
	Diapriidae	adult	tr			
	Formicidae	adult	57			
	Cephidae	adult	7			
	Torymidae	adult	4			
	Apidae	adult	25			
	Unidentified	adult	tr			
	Unidentified	larvae	17	17	0.03	
	Unidentified	pupae	345	345	0.52	0.60
Acarina	Unidentified		11	11	0.02	tr
Araneida	Unidentified		420	420	0.63	1.87
Mollusca	all			5045	7.59	0.48
	Zonitidae		278			
	Pupillidae		680			
	Succineidae		2216			
	Cochlicopidae		265			
	Planorbidae		132			
	Physidae		145			
	Lymnaeidae		1139			
	Sphaeriidae		190			
Annelida			16	16	0.02	

[1]Percentages recalculated from identifiable items only (see text).

[2]Use of 2 decimal places does not imply this order of accuracy in measurement but is used to show relative amounts of minor components.

Six recognizably different species of sedge (*Carex*) made up almost 47 per cent of the identifiable items in the average summer diet (Table 3). None of the 6 *Carex* species could be positively identified from the seeds since many species having similar seeds occur in the Churchill region.

Other than *Carex,* ericaceous plants made up much of the remainder of the diet: *Empetrum* seeds 7.3 per cent and *Vaccinium* seeds and flowers 13.2 per cent. These ericaceous plants were represented in the diet only after the middle of July and therefore the birds took only the fresh flowers and berries and not those berries left on the bushes or ground from previous years. Sedge seeds (*Carex* and *Eriophorum*), however, were taken all summer and therefore in the early summer consisted of seeds left from the previous year (Table 3).

It was not possible to identify much of the animal material in the gizzard to family since the bulk of it consisted of parts rather than whole individuals and therefore only orders are given in Table 1. Adult Diptera were taken consistently throughout the summer with the peak occurring in July. Araneida, adult Coleoptera, the larvae of Coleoptera, Diptera, and Lepidoptera and unidentified insect eggs made up most of the remainder (Table 1).

TABLE 5. Total stomach content and amount of grit present in tree sparrow stomachs from late May through August at Churchill, Manitoba.

Date	*No.*	*Total less grit* *Dry wt. (g)* ± *S.D.*	*No.*	*Grit* *Dry wt. (g)* ± *S.D.*
28 May - 15 June	10	0.0469 ± 0.0251	11	0.0802 ± 0.0405
16-30 June	20	0.0547 ± 0.0324	19	0.0594 ± 0.0439
1-15 July	8	0.0276 ± 0.0089	5	0.0263 ± 0.0173
16-31 July	10	0.0419 ± 0.0148	10	0.0394 ± 0.0363
1-15 Aug.	16	0.0440 ± 0.0192	15	0.0469 ± 0.0363
16-24 Aug.	5	0.0623 ± 0.0257	3	0.0590 ± 0.0370
Average of all samples	69	0.0466	63	0.0533

The total amount of food less grit in the gizzard was significantly less at the 0.05 level of probability during 1 to 14 July than in either the preceding or the following half month collection interval (Table 5). During this period, the birds were eating predominantly insect matter (88 per cent) as opposed to roughly one half that proportion both before and after (Table 1, Fig. 1). The reason for the lower amount of food in the gizzard may be related to the possibility that the efficiency of energy extraction from insects is higher than that from a similar weight of seeds. It is doubtful if energy requirements were lower at that time since the adults were feeding young (West 1960).

Except for the first collection interval, the amount of grit in the gizzard was in proportion to the amount of food in the gizzard (Table 5). The ratio of grit to food varied from 1.71 to 0.94 and averaged 1.12. In the winter, the ratio varied from 1.37 to 0.36 and averaged 0.64 (West 1967).

The average amount of food in the gizzard (0.0467 g.) was lower than that found in the winter (0.0866 g.) but the amount of grit was about the same in summer (0.0542 g.) as in winter (0.0584 g.) according to a previous report (West 1967).

Foods Available

Plant material: 41 recognizably different taxa were found in 77 ground samples collected over 2 summers in specific areas where tree sparrows were feeding (Table 3). Only 9 taxa were represented by a value of 1 per cent or more of the dry weight of the total taxa (seeds and animals) available. Seeds of *Empetrum nigrum* (22.1 per cent) and berries (28.4 per cent) made up half of the total food available. Eleven species of *Carex* accounted for 15.6 per cent, *Picea* for 4.3 per cent, *Myrica gale* for 1.9 per cent, *Draba* for 3.3 per cent, and *Vaccinium* seeds, berries, and flowers for 7.1 per cent of the total.

Animal material: Individual family data for the animals available are given in Table 4 along with a summary by order to permit comparison with the foods eaten. The data for the animals (mainly molluscs and beetles) which were found in the 77 ground samples as well as in the 50 sweep net samples were summed to give the weight of food available in each taxon. Only 4 orders contained 1 per cent or more of the dry weight of the total taxa (plant and animal) available: Molluscs 7.6 per cent, adult Diptera 3.1 per cent, Collembola 1.2 per cent, and adult Coleoptera 1.0 per cent (Table 4). Of these, the families Succineidae, Lymnaeidae, and Pupillidae (Mollusca); Chironomidae and Simuliidae (Diptera); and Poduridae (Collembola) were the most important (Table 4). Contrary to expectation, mosquitoes (Culicidae) were relatively insignificant whereas horse-flies (Tabanidae) made up a relatively large proportion of the total, perhaps due to their large individual size. Other important families of animals were the diving beetles (Dytiscidae), carpet beetles (Dermestidae), spiders (Araneida), and the several other families of snails. Larvae of beetles, flies, butterflies and moths, and pupae of wasps were also important available items.

Correlation of Foods Used to Those Available

Of the 53 taxa of available items, tree sparrows used 22 (41.5 per cent); see Tables 3 and 4. This is precisely the ratio of seeds used to those available during winter in Illinois where the birds had 82 taxa to choose from (West 1967). Selection of the 22 taxa was not based solely on availability since many groups were abundant and not used and other groups selected were poorly represented in the field samples. Those taxa of plants that were abundant but seldom or not used for food were seeds of spruce (*Picea glauca, P. mariana*), 1 species of sedge (*Carex sp.* E.), sweet gale (*Myrica gale*), cloudberry (*Rubus chamaemorus*), crow berry (*Empetrum nigrum*) seeds but especially the berries, and berries of blue-berries and cranberries (*Vaccinium uliginosum, V. vitis-idea*). The sedge taxa (*Scirpus sp.* and *Carex sp.* K), mustard seeds (*Brassica sp.*), and pigweed seeds (*Amaranthus sp.*) were used roughly in proportion to their availability. Tree sparrows appeared to prefer certain plant foods that were not as readily available in the habitat: 4 species of sedge (*Carex sp.* D, F, I, and J), mustard seeds (*Draba sp.*), blueberry and cranberry seeds (*Vaccinium uliginosum, V. vitis-idea*), and cottongrass seeds (*Eriophorum sp.*); see Fig. 2.

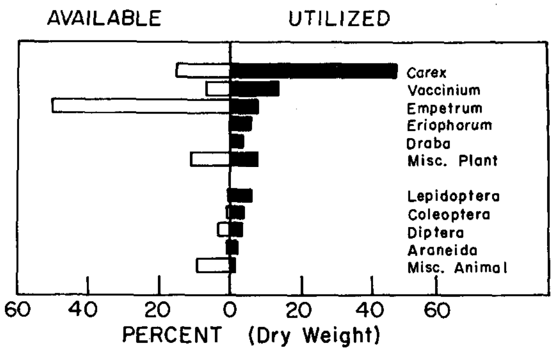

FIG. 2. Comparison of major taxa used by feeding tree sparrows in relation to their availability.

That certain items were preferred and others excluded may have been due to a number of factors such as size, palatability, hardness of the seed coat, difficulty in removal of the seed coat, some nutritional component, or gross energy content. Willson (1971) concluded that tree sparrows and the other small-billed species of sparrows she tested in the laboratory selected smaller rather than larger seeds and those that could be husked quickly. These included seeds with high caloric yield although that did not appear to be the reason for their selection. Likewise, seeds were not selected for their protein or fat content.

The wild tree sparrows at Churchill also selected relatively small seeds such as the smaller *Carex* species, mustards (*Draba* and *Brassica*), pigweed (*Amaranthus*) and the very small seeds of *Vaccinium*. On the other hand, spruce seeds (*Picea*) which have relatively hard seed coats and are large as are the seeds of *Rubus chamaemorus* were not selected.

The reason for not consuming the abundant snails may also be related to difficulty in extracting the animal although, at least for the smaller pupillids, the shells could have been as easily crushed in the gizzard as some seed coats.

The sparrows were also selective of animal taxa (Table 4). Abundant items such as spring tails (Collembola), and the many groups of snails (Mollusca) were seldom eaten. Scarce items such as beetle larvae (Coleoptera) and moth and butterfly larvae (Lepidoptera) were selected, whereas the majority of other insects and spider groups were taken roughly in proportion to their availability (Fig. 2).

Caloric Values of Foods and Energy Requirements of Tree Sparrows

There were sufficient amounts of 17 plant materials to permit determination of their caloric values (Table 6). Determinations were made using 10 to 30 mg. dry weight, crushed and pelleted samples burned in a Phillipson microbomb calorimeter (Phillipson 1964). It was possible to determine caloric values only on the plant parts since they had been stored in a dry condition. The animals, unfortunately, had been preserved in 70 per cent ethanol which extracted an undetermined amount of soluble products from the invertebrate tissue and any caloric value determined from these specimens would be meaningless. The bulk of the stomach content was finely ground plant and insect material and was stored dry. This was pooled from all stomachs and the caloric value determined on the aggregate. The resulting values (5171 ± 276 cal./gm. ash free dry wt., n = 3)

TABLE 6. Caloric values of plant materials collected at Churchill, Manitoba. Items are seeds unless indicated otherwise.

Classification	*Number of determinations*	*Average gram calories ± S.D. per gram ash free dry weight*
Pinaceae		
Picea alba, P. mariana	3	5408 ± 30
Cyperaceae		
Carex sp. D (oval)	3	5026 ± 47
E (△ yellow)	2	5092 ± 47
F (△ brown)	1	5335
G (flat olive-gray)	2	5328 ± 1
I (△ ochre)	3	5470 ± 28
J (flat yellow)	1	5139
K (flat red-brown)	3	5234 ± 41
Myricaceae		
Myrica gale	3	4959 ± 53
Cruciferae		
Draba sp.	1	6247
Rosaceae		
Rubus chamaemorus	3	4727 ± 47
Ericaceae		
Empetrum nigrum: seeds	3	4973 ± 44
: berries	4	5123 ± 81
Andromeda polifolia	1	5500
Vaccinium vitis-idea,		
V. uliginosum: seeds	2	5830 ± 16
: flowers	2	4527 ± 4
: berries	3	5042 ± 30

represent about the average of determinations on identified material (5233 cal./gm.; Table 6).

The average energy content per gram dry weight of the average summer stomach content of tree sparrows at Churchill can be calculated by multiplying the caloric value of each item by its relative proportion in the diet. However, the caloric equivalent of every plant item and of the animal items could not be determined. Caloric values were determined for 92.68 per cent of the average diet and the resulting caloric equivalent was 5211 cal./gm. dry wt. I also filled in the missing values for the remaining 7.32 per cent with values for seeds and animals from closely related items reported in the literature. Since this resulted in an average value (5217 cal./gm.) so close to that based on the values determined in this study, I will use the former value.

The existence energy requirements of captive tree sparrows were determined at Churchill, Manitoba, during the summer months when temperatures averaged 9.8°C. and the photoperiod was 19 hours of light per day (West 1960). "Existence energy" is defined as the amount of metabolizable energy required in caged birds for basal metabolism, maintenance of body temperature, taking food and drink, and the specific dynamic action of digestion and assimilation (Kendeigh 1949). Under the above-cited environmental conditions, tree sparrows required an average of 17.84 kcal./bird/day for existence at Churchill. Tree sparrows have additional energy requirements for reproduction (egg production and incubation) in June and part of July and the annual postnuptial moult in August. The added cost of these activities would raise the energy requirement by about 5.05 kcal./bird/day (West 1960). We do not yet know the real cost of free existence, i.e. the energy cost of flight in searching for food for the bird itself and for young and in defence of territories, but the maximum measured energy cost of activity in caged tree sparrows was determined during spring periods of nightly unrest. At this time the actual increased energy cost may be more than that required in the field. The added cost averaged 3.92 kcal./bird/day (West 1960). Adding these three energy requirements together yields a total of about 25 kcal./bird/day (40 per cent increase over existence) as the average daily energy requirement of tree sparrows at Churchill during summer.

However, Kendeigh (1972) has calculated that house sparrows *(Passer domesticus)* normally require only a 12 per cent increase for free existence above cage existence energy requirements (which includes moult and reproduction). If the extra energy requirement for short-term increases, such as for days of extreme cold in summer or excessive activity, is also added, the increase is 38 per cent above existence (Kendeigh 1972). If we assume a figure of 20 per cent, the average daily requirement becomes 21.4 kcal./bird/day for the tree sparrow.

The average energy value of the summer diet was determined to be 5211 cal./gm. dry weight. However, tree sparrows probably cannot use the total calories available and, in laboratory experiments, it was determined that tree sparrows, under the conditions of temperature and photoperiod at Churchill in summer, were able to extract 75.8 per cent of the caloric value contained in their diet (in that case, prepared baby chick mash, a mixture of ground seeds). Assuming the same percentage of energy extraction from the seeds eaten by the wild birds, 75.8 per cent of 5211 calories or 3950 cal./gm. dry wt. would be available to the bird.

With a requirement of 20 to 25 kcal./bird/day, and an availability of 3950 cal./gm., the dry weight of food required would be from an average of 5.06 to 6.33 grams/bird/day. In the early summer, tree sparrows eat a great deal of *Carex*. The standing crop of *Carex* totalled for the whole summer was 10,350 grams/hectare (Table 3). This amount could support 18 to 23 tree sparrows/hectare for the 90 days of summer at Churchill. *Empetrum nigrum* seeds are also abundant and accumulated to a total of 14,718 grams/hectare in the summer (Table 3). This could support 26-32 tree sparrows per hectare. However, these values are calculated on the basis of the standing crop, and not the total production of seeds over the summer, which would be greater. Therefore, more birds theoretically could be supported than that indicated above.

Weeden (1965) has studied tree sparrow (*S. a. ochracea*) population densities at Eagle Creek, Alaska, an alpine area ecologically similar to the tundra-taiga latitudinal ecotone at Churchill and generally with the same species of plants in the habitat. For 3 years, her calculations yielded densities of from 21 to 35 pairs/100 acres. If we assume a range of 20 to 40 pairs/100 acres, this is equivalent to 0.5 to 1.0 pair/hectare. From the calculations made above, we see that several species of seeds could support greater densities than 2 adult birds/hectare.

But the question remains as to whether there is enough insect food to support more than one pair of adults plus the young they raise per hectare in summer. My data are insufficient to tackle this question.

It is realized that not all species of food available are used (and therefore may not really be considered available, see Tables 3 and 4), and there are many other species of birds (and mammals and insects) which may compete for the same seed (and insect) food supply during the summer months. Other sparrows such as Gambel's white-crowned (*Zonotrichia leucophyrs gambelii*), white-throated (*Z. albicollis),* Harris' *(Z. querula),* fox *(Passerella iliaca),* and slate-colored junco (*Junco hyemalis*) and four species of warblers, yellow (*Dendroica petechia*), myrtle (*D. coronata*), blackpoll (*D. striata*) and orange-crowned (*Vermivora celata*) also may have overlapping territories or may feed in tree sparrow territories.

As I concluded from a study of the winter population (West 1967), my hypothesis from the present study is that the breeding population of tree sparrows in summer is not limited chiefly by food supply. However, further research is necessary in order to reach a firm conclusion.

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