

POPULATIONS AND ENERGETICS OF TAIGA BIRDS NEAR FAIRBANKS, ALASKA

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IN their annual breeding cycle, birds remove quantities of nutrients and energy from the taiga ecosystem each summer. A major portion of these nutrients and energy are returned to the system directly in the form of excrement, molted feathers, eggshells, and in the dead bodies of individuals that fall to the ground or are eaten by predators. Some portion of the annual production leaves the taiga ecosystem, as most of the species nesting in the taiga migrate south in fall. As breeding populations are maintained at about the same level from year to year, the amount of energy and nutrients equivalent to the annual production of young is transported south and deposited through mortality and predation in other ecosystems each year.

As a part of an initial assessment of the structure and function of the taiga ecosystem in interior Alaska, the populations and energetics of wild birds were investigated in summer 1971 on a biological research preserve adjacent to the developed portion of the University of Alaska campus near Fairbanks (65° 54' N, 147° 50' W). Some studies on the composition of vegetation, small mammal populations (Grodzinski 1971a, 1971b; Whitney 1973), and the decomposer organisms of this preserve have been made. Further studies to complete our understanding of this complex system are planned and in progress.

The objective of the present study was to estimate the amount of energy removed by the avian element of the consumer group in taiga forest of interior Alaska in summer by (a) censusing the bird populations throughout the summer, and (b) measuring the resting metabolic rate of selected species at the prevailing daytime summer temperatures and converting these measurements to the requirements of free-living birds.

METHODS

Census.—Two census trails were selected on the ski trail system northwest of the developed portion of the University of Alaska campus (Fig. 1). Trail A, 3.8 km in length, traversed taiga forest, edges of ponds and cultivated fields, and dirt roads. Trail B, 2.2 km long, covered more uniform taiga woods. The distances were measured with a pedometer calibrated against an automobile odometer. The censused sites are designated areas A and B respectively.

Taiga in the Fairbanks region is characterized by its heterogeneity in habitat type, which is a result of discontinuous permafrost, directional exposure of hill-sides, a variety of geological structures, nutrient characteristics and water content of the soil, and other features. Birds appear to respond primarily to vegetation type,

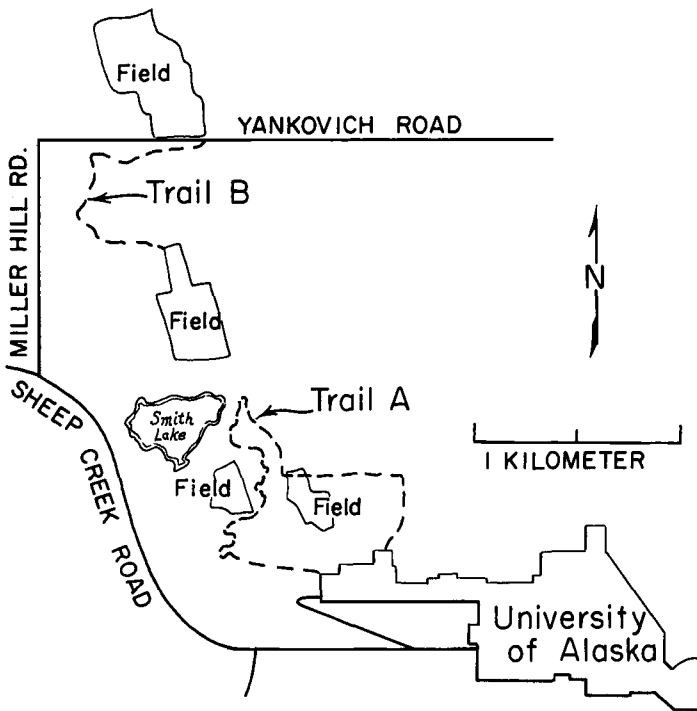


Fig. 1. Two trails northwest of the developed portion of the University of Alaska campus that were censused for bird populations during summer 1971.

which in turn depends on the mosaic of abiotic factors just mentioned. The principal tree species of taiga forest on the census sites are white and black spruce (*Picea glauca* and *P. mariana*), paper birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), tamarack (*Larix laricina*), quaking aspen (*Populus tremuloides*), green alder (*Alnus crispa*), and several species of willow (*Salix* spp.).

The understory consists of younger members of the tree species, additional species of shrubby willows, lower shrubs such as Labrador tea (*Ledum groenlandicum* and *L. decumbens*), blueberries (*Vaccinium uliginosum*) and cranberry (*V. vitis-idaea*), highbush-cranberry (*Viburnum edule*), and others. The herb layer contains a seasonal growth of horsetail (*Equisetum sylvaticum*), bunchberry (*Cornus canadensis*), grasses (chiefly *Calamagrostis canadensis*), other herbs and a large number of lichens and mosses (Anderson 1970).

We determined the frequency of different vegetation types along the two trails by traversing each trail at the same rate with a stopwatch and recording the time it took to pass through each vegetation type. Area A was more diverse in habitat type than was area B. In the following descriptions, the percent of the census site of trail A occupied by each vegetation type is given as (A-%) followed by the percent of the same type noted for trail B (B-%). Pure stands of mature white spruce were infrequent (A-9, B-0) as were pure stands of mature paper birch (A-13, B-0). Mixed stands of

closed canopy mature white spruce and paper birch with a shrub and herb understory occupied over one-half of the site traversed by trail B (A-9, B-54); a younger closed canopy spruce and birch mixture with some alder but no herbaceous understory except for mosses was more important on trail A (A-23, B-5). Mixed stunted black and white spruce with scattered tamarack, ericaceous shrubs, and lichens and mosses, the typical acid muskeg taiga with underlying permafrost, was more frequent along trail B (A-19, B-28). Stands of balsam poplar and aspen with scattered birch and alder were present on both trails (A-9, B-13). Only area A contained infrequently used dirt roads (A-10, B-0), cultivated fields that produced a mixed grass crop during the summer season (A-8, B-0), and proximity to small ponds.

Trail A was traversed for censusing 49 times over a 99-day period from 24 May through 30 August 1971, and trail B was traversed 13 times over a 76-day period from 12 June through 26 August 1971. All censuses were taken in the early morning.

We made transect counts using a modification of Emlen's (1971) method of detectability. The census area, 820 feet (250 m) wide with the trail as midpoint was divided into eight parallel strips, according to distance on either side of the trail as follows: 0-50, 50-100, 100-200, and 200-410 feet. Unlike Emlen, we did not subdivide the 0-50 foot strip into five 10-foot strips. For each species we recorded common name, lateral distance from trail when first detected (i.e. we located the bird in one of the strips listed above), number of individuals, age and sex when distinguishable, how detected (seen and/or heard), and the time when first detected. We walked slowly but steadily, pausing only long enough to identify and record species. Trail A was traversed in opposite directions on successive census days. Trail B was traversed both directions each census day, a total distance of 4.4 km.

A plot of numbers detected vs. distance from the midpoint of the census trail shows an increase to a peak, then a sharp decrease (Emlen 1971). The "critical distance" (our term) is the distance from the trail to the point at which the maximum number of detections were made. In our study the critical distance was usually 50 feet or less. In a few cases the critical distance fell between 50 and 100 feet.

We divided the census period into three intervals of about 1 month each. Period 1 (24 May-30 June) corresponds generally to the end of spring migration, establishment of territories, egg-laying, and incubation of most species censused. Period 2 (1-31 July) includes hatching and fledging of young, feeding of fledged young, and, for some individuals of certain species, initial movement away from the census sites. Period 3 (1-30 August) comprises fall molt and beginning of fall migration, with much premigratory flocking and local movements.

We totaled all detections, including birds heard but not seen, of each species for each of these three periods according to locations in the four parallel strips, whose distances are given above, on either side of the trail. Assumptions were made that (a) 50 feet is the critical distance in which all individuals of this species are detected, and (b) the population is randomly distributed in the whole band out to 410 feet on both sides of the trail. Using the total number of individuals detected within 50 feet of the trail as the base, we extrapolated to obtain the projected number present in the 410-foot bands on either side of the trail (see Emlen 1971, step 3 on p. 331). In a few cases the critical distance was 100 feet. For these we used the totals detected, 0-100 feet, as a basis for calculating projected numbers.

A census plot 250 m (820 feet) wide with a central trail 4.0 km long covers 100 ha. To determine the number of 4.0-km trips made during each period we multiplied the number of census days by total length of the trail and divided by 4.0. To determine the density of each species per 100 ha we divided the total number

TABLE 1A
SPECIES DETECTED ON TRAIL A, 24 MAY-30 AUGUST 1971

Species	Span between first and last detection (days)	Total detection in census (N)	Coefficient of detectability			
			Period			Over span ¹
			1	2	3	
Red-necked Grebe, <i>Podiceps grisegena</i>	58	8	²	²	²	²
Mallard, <i>Anas platyrhynchos</i>	84	7				
Pintail, <i>A. acuta</i>	86	18				
Goshawk, <i>Accipiter gentilis</i>	1	1				
Sharp-shinned Hawk, <i>A. striatus</i>	1	1				
Ruffed Grouse, <i>Bonasa umbellus</i>	65	3				
Sandhill Crane, <i>Grus canadensis</i>	1	17				
Common Snipe, <i>Capella gallinago</i>	82	3				
Solitary Sandpiper, <i>Tringa solitaria</i>	44	4				
Lesser Yellowlegs, <i>T. flavipes</i>	34	13	0.20	0.14		0.16
Northern Phalarope, <i>Lobipes lobatus</i>	35	23	0.22	0.33		0.23
Mew Gull, <i>Larus canus</i>	11	5				
Hawk Owl, <i>Surnia ulula</i>	1	1				
Short-eared Owl, <i>Asio flammeus</i>	1	1				
Belted Kingfisher, <i>Megaceryle alcyon</i>	60	2				
Common Flicker, <i>Colaptes auratus</i>	69	7				
Hairy Woodpecker, <i>Dendrocopos villosus</i>	1	1				
Alder Flycatcher, <i>Empidonax alnorum</i> ³	70	44	0.45	0.24	0.15	0.33
Hammond's Flycatcher, <i>E. hammondi</i> ³	94	67	0.23	0.15	0.27	0.22
<i>Empidonax</i> flycatchers, <i>E. hammondi</i> and <i>alnorum</i> ⁴	94	149	0.30	0.16	0.23	0.23
Western Wood Pewee, <i>Contopus sordidulus</i>	14	6				
Olive-sided Flycatcher, <i>Nuttallornis borealis</i>	41	13				
Bank Swallow, <i>Riparia riparia</i>	1	300+				
Gray Jay, <i>Perisoreus canadensis</i>	84	32				
Common Raven, <i>Corvus corax</i>	71	11				
Black-capped Chickadee, <i>Parus atricapillus</i>	81	61	0.16	0.24	0.23	0.22
Boreal Chickadee, <i>P. hudsonicus</i>	80	3				
American Robin, <i>Turdus migratorius</i>	99	223	0.21	0.17	0.24	0.22
Varied Thrush, <i>Ixoreus naevius</i>	99	94	0.53	0.17	0.61	0.44
Swainson's Thrush, <i>Catharus ustulatus</i>	96	398	0.37	0.18	0.33	0.32
Gray-cheeked Thrush, <i>C. minimus</i>	92	74	0.43	0.24	0.25	0.26
Ruby-crowned Kinglet, <i>Regulus calendula</i>	99	129	0.35	0.13	0.15	0.24

¹ Calculated for entire period; not a mean of periods 1, 2, and 3.

² Number of detections too few or irregular to calculate a coefficient of detectability.

³ Distinguished by voice.

⁴ Includes both *alnorum* and *hammondi* plus all sight records where species could not be identified.

TABLE 1A (cont')

Species	Span between first and last detection (days)	Total detections in census (N)	Coefficient of detectability			
			Period			Over span ¹
			1	2	3	
Bohemian Waxwing, <i>Bombycilla garrulus</i>	9	2				
Orange-crowned Warbler, <i>Vermivora celata</i>	96	119	0.28	0.20	0.16	0.24
Yellow Warbler, <i>Dendroica petechia</i>	99	249	0.29	0.17	0.20	0.24
Yellow-rumped Warbler, <i>D. c. coronata</i>	99	246	0.23	0.23	0.16	0.22
Townsend's Warbler, <i>D. townsendi</i>	87	54	0.33	0.12	0.12	0.22
Blackpoll Warbler, <i>D. striata</i>	98	6				
Northern Waterthrush, <i>Seiurus noveboracensis</i>	7	4				
Wilson's Warbler, <i>Wilsonia pusilla</i>	87	46	0.41	0.12	0.15	0.26
Rusty Blackbird, <i>Euphagus carolinus</i>	92	71	0.34	0.33	0.35	0.35
Pine Grosbeak, <i>Pinicola enucleator</i>	71	29				
Common Redpoll, <i>Acanthis flammea</i>	96	312	0.16	0.13	0.19	0.16
Savannah Sparrow, <i>Passerculus sandwichensis</i>	87	27	0.26	0.20	0.13	0.23
Dark-eyed Junco, <i>Junco h. hyemalis</i>	99	358	0.21	0.15	0.16	0.17
Chipping Sparrow, <i>Spizella passerina</i>	57	2				
White-crowned Sparrow, <i>Zonotrichia leucophrys gambelii</i>	99	312	0.31	0.17	0.20	0.22
Fox Sparrow, <i>Passerella iliaca</i>	96	246	0.24	0.17	0.16	0.20
Lincoln's Sparrow, <i>Melospiza lincolni</i>	87	16	0.21	0.13	0.25	0.21

projected by the number of 4.0-km census trips. For example, as the total number of Dark-eyed Juncos projected for area A during period 1 was 566, and the number of 4.0 km trips was

$$\frac{24 \text{ census days} \times 3.8 \text{ km}}{4.0 \text{ km}} = 22.8,$$

then $566/22.8 = 24.8$ Dark-eyed Juncos per 100 ha in area A during period 1. Calculations involving these three periods are shown in Tables 1A, 1B, 2, and 3.

Note: Emlen (1971) used a different method of calculating densities, involving the coefficient of detectability (total N detected/total N projected = coefficient of detectability). This coefficient, which is an attribute of the species in a stated situation and season, is useful when it can be established with extensive data in lieu of restricted data for a single locality censused only a few times. Our method, which is simpler and gives the same results, would normally be used when a substantial set of records for one locality and season is available (Emlen, pers. comm.).

We calculated the coefficient of detectability for each species regularly detected on the census trails (Tables 1A and 1B).

For 10 of the species common on trail A our observations permitted a refinement of the above method. Our data on fledged and independent young permit calcula-

TABLE 1B
SPECIES DETECTED ON TRAIL B, 12 JUNE-26 AUGUST 1971

Species	Span of detections by species (days)	Total detections in census (N)	Coefficient of detectability			
			Period			Over span ¹
			1	2	3	
American Kestrel, <i>Falco sparverius</i>	1	1	²	²	²	²
Ruffed Grouse, <i>Bonasa umbellus</i>	1	2				
Common Flicker, <i>Colaptes auratus</i>	1	1				
Alder Flycatcher, <i>Empidonax alnorum</i> ³	60	10	0.50	0.19	0.13	0.24
Hammond's Flycatcher, <i>E. hammondi</i> ³	76	7				
Gray Jay, <i>Perisoreus canadensis</i>	49	3				
Black-capped Chickadee, <i>Parus atricapillus</i>	48	21				
Boreal Chickadee, <i>P. hudsonicus</i>	1	2				
American Robin, <i>Turdus migratorius</i>	76	26	0.25	0.18	0.27	0.21
Varied Thrush, <i>Ixoreus naevius</i>	68	16	0.50	0.13	0.24	0.26
Swainson's Thrush, <i>Catharus ustulatus</i>	69	68	0.50	0.21	0.29	0.33
Ruby-crowned Kinglet, <i>Regulus calendula</i>	76	14	0.50	0.14	0.15	0.16
Orange-crowned Warbler, <i>Vermivora celata</i>	53	20	0.40	0.14	0.12	0.21
Yellow-rumped Warbler, <i>Dendroica c. coronata</i>	76	49	0.28	0.14	0.12	0.16
Townsend's Warbler, <i>D. townsendi</i>	69	38	0.33	0.25	0.50	0.33
Wilson's Warbler, <i>Wilsonia pusilla</i>	76	3				
Rusty Blackbird, <i>Euphagus carolinus</i>	1	1				
Pine Grosbeak, <i>Pinicola enucleator</i>	1	1				
Common Redpoll, <i>Acanthis flammea</i>	69	17	0.12	0.12	0.12	0.12
Savannah Sparrow, <i>Passerculus sandwichensis</i>	20	6				
Dark-eyed Junco, <i>Junco h. hyemalis</i>	68	89	0.20	0.13	0.16	0.15
White-crowned Sparrow, <i>Zonotrichia leucophrys gambelii</i>	62	8				
Fox Sparrow, <i>Passerella iliaca</i>	55	8				

¹ Calculated for entire period; not a mean of periods 1, 2, and 3.

² Number of detections too few or irregular to calculate a coefficient of detectability.

³ Distinguished by voice.

tion of density per 100 ha for intervals (phases A, B, C) that coincide more closely with stages of the nesting cycle than do periods 1-3 (Table 4). Phase A begins with the census date the species in question was first detected and ends with the last census date prior to detection of fledged young. Phase B begins with the first date fledged young of the species were detected and ends with the last census date prior to detection of independent young. Phase C begins with the latter event, includes the annual molt, and ends with the last census date individuals of the species were detected. Median dates for beginning and end of each phase for all 10 species are as follows: phase A: from 24 May through 22 June (30 days), phase B: from 24 June through 2 July (9 days), and phase C: 5 July through 30 August (57 days).

TABLE 2
POPULATIONS AND ENERGY REMOVED BY BIRDS DETECTED REGULARLY IN
TWO AREAS OF TAIGA WOODS NEAR FAIRBANKS, ALASKA

Species	Population in period ¹ n/100 ha			Energy removed in period ¹ Mcal/100 ha ²			99-day summer total Mcal/100 ha ²
	1	2	3	1	2	3	
TRAIL A:							
Dark-eyed Junco	24.8	70.6	62.9	14.2	32.9	28.3	75.4
White-crowned Sparrow	17.3	55.7	33.9	13.2	34.6	20.4	68.2
Fox Sparrow	25.2	31.4	24.7	20.0	20.3	15.5	55.8
Common Redpoll	37.8	64.3	35.8	17.6	24.4	13.1	55.1
American Robin	24.5	31.4	16.0	21.1	22.1	10.9	54.1
Swainson's Thrush	37.8	29.0	6.2	24.1	15.1	3.1	42.3
Yellow-rumped Warbler	33.8	15.7	14.8	16.5	6.3	5.7	28.5
Yellow Warbler	24.8	28.2	12.9	9.2	8.5	3.8	21.5
Ruby-crowned Kinglet	10.4	9.4	16.0	3.7	2.8	4.5	11.0
Varied Thrush	3.9	6.3	4.3	3.4	4.4	2.9	10.7
Orange-crowned Warbler	13.3	9.4	6.8	5.3	3.1	2.2	10.6
Hammond's Flycatcher	7.3	13.7	5.5	2.8	4.2	1.7	8.7
Rusty Blackbird	4.9	1.1	6.2	3.7	0.7	3.7	8.1
Black-capped Chickadee	2.5	7.8	10.5	1.1	2.9	3.8	7.8
Gray-cheeked Thrush	5.6	7.1	0.6	3.5	3.6	0.3	7.4
Lesser Yellowlegs	1.1	5.5	0	1.2	4.9	0	6.1
Alder Flycatcher	4.9	9.1	3.7	1.9	2.8	1.1	5.8
Townsend's Warbler	5.2	6.3	4.3	2.0	2.0	1.3	5.3
Wilson's Warbler	3.4	3.2	5.0	1.3	1.0	1.5	3.8
Northern Phalarope	3.9	1.2	0	2.8	0.7	0	3.5
Savannah Sparrow	3.6	2.4	0.6	2.1	1.1	0.3	3.5
Lincoln's Sparrow	2.5	0.8	0.9	1.3	0.3	0.4	2.0
TOTAL	298.5	409.6	271.6	172.0	198.7	124.5	495.2
PERCENT				34.7	40.1	25.1	99.9
TRAIL B:							
Dark-eyed Junco	7.6	47.6	55.1	4.3	22.2	24.8	51.3
Yellow-rumped Warbler	17.3	26.9	19.5	8.4	10.7	7.5	26.6
Swainson's Thrush	22.4	16.4	7.5	14.3	8.5	3.8	26.6
Townsend's Warbler	28.5	2.2	1.5	10.8	6.8	4.5	22.1
American Robin	2.4	13.5	7.5	2.1	9.5	5.1	16.7
Common Redpoll	12.4	6.0	12.0	5.8	2.3	4.4	12.5
Varied Thrush	3.6	2.9	6.0	3.1	2.0	4.1	9.2
Orange-crowned Warbler	7.6	8.9	4.5	3.1	2.9	1.4	7.4
Ruby-crowned Kinglet	1.2	8.9	6.0	0.4	2.6	1.7	4.7
Alder Flycatcher	3.0	2.9	2.9	1.1	0.9	0.9	2.9
TOTAL	106.0	136.2	122.5	53.4	68.4	58.2	180.0
PERCENT				29.7	38.0	32.3	100.0

¹ Period 1 = 38 days (24 May–30 June); 2 = 31 days (1 July–31 July); 3 = 30 days (1 August–30 August).

² Mcal = megacalorie = 10⁶ calories.

Metabolic measurements.—We captured 47 individuals of 11 species of birds and determined their resting metabolic rates during the day for periods up to 1 hour at prevailing daytime summer temperatures (17.5 to 19.5°C, mean 18.8°C). An open circuit system was employed in which oxygen consumption of up to four individuals

TABLE 3
NUMBER PER 100 HA FOR 10 SPECIES IN AREAS
A AND B FOR MATCHED PAIRS OF DATES¹

Species	Area	N/100 ha		
		Period 1	Period 2	Period 3
Common Redpoll	A	37.5	76.0	54.0
	B	12.4	6.0	1.8
Dark-eyed Junco	A	34.4	77.7	69.0
	B	7.6	47.6	61.6
Fox Sparrow	A	37.5	25.9	23.7
	B	0	1.5	13.0
Orange-crowned Warbler	A	5.6	13.9	10.8
	B	7.6	8.9	5.7
Yellow-rumped Warbler	A	34.4	12.0	17.4
	B	17.3	26.9	16.8
Townsend's Warbler	A	4.2	12.0	4.2
	B	28.5	2.2	0
Ruby-crowned Kinglet	A	11.6	12.0	15.0
	B	1.2	8.9	7.5
Swainson's Thrush	A	28.8	31.2	5.5
	B	22.4	16.4	9.3
American Robin	A	31.6	25.9	15.0
	B	2.4	13.5	7.5
Varied Thrush	A	8.8	7.0	10.8
	B	3.6	2.9	3.6

¹ Trail A, period 1: 11, 21, 25 June; period 2: 1, 13, 16, 21, 28 July; period 3: 2, 9, 12, 25 August. Trail B, period 1: 12, 20, 26 June; period 2: 2, 12, 17, 21, 27 July; period 3: 3, 10, 13, 26 August.

could be determined in sequence (Morrison and West 1974). Oxygen consumption rates were calculated by the appropriate formula in Depocas and Hart (1957) and corrected to STP. Carbon dioxide production was not measured. As the birds were captured during the day and tested within 1 to 2 hours of capture, we assumed an RQ of 0.75 to 0.80 and therefore used the caloric equivalent of 4.85 kcal per liter of oxygen consumed (Kleiber 1961) in order to convert resting oxygen consumption values to their caloric equivalents on a 24-h basis.

The resting metabolic rate does not take into account the energy required for obtaining food, for reproduction (territory formation and defense, courtship, nest building, egg-laying, incubation, and feeding of young), for molt, or for free existence. Therefore to the measured resting caloric requirements measured here, these additional costs must be added in the appropriate period. Most studies that have estimated the costs of reproduction, molt, and free existence have been made using the food consumption method, i.e. determination of food (energy) intake, excrement, and the resultant metabolizable energy difference over a period of several days. The base line value in these studies is called "caged existence." The cost of caged existence, which includes hopping about in the cage and obtaining food and drink, amounts to about 24% above that required at rest (basal rate, specific dynamic action, any additional costs for thermoregulation) (Kendeigh 1969, West 1972). In caged birds, reproductive energy has been estimated to add from almost nothing to up to 30% over caged existence values (West 1960, 1968; El-Wailly

1966; Brisbin 1969), but over the whole breeding season, the added cost is much lower and probably is not greater than 10 to 12% (Kendeigh 1973). Above the cost of reproduction would be an additional cost for free existence in nature. Although this parameter is perhaps the most difficult to determine, Kendeigh (1973) has shown that in the House Sparrow (*Passer domesticus*) the normal increment is near 12%. West (1973) also used this figure for Tree Sparrows (*Spizella arborea*).

The added cost of molting above that of caged existence has been estimated to be up to 25% for 1 week (West 1960), but Blackmore (1969) suggested that the cost of molt is almost completely compensated for by the savings resulting from increased feather insulation (in House Sparrows). Over the whole molt period, which lasted some 112 days, the increased cost was only 3.9% above existence at 22°C (Blackmore 1969). For this study, we have assumed that the cost of molt is equivalent to that of reproduction (10%) on a daily basis because the molt period in subarctic passerines is probably shorter than that in the caged House Sparrows Blackmore studied in central Illinois.

Therefore, by multiplying the resting requirement by 124%, we obtained the caged existence requirement (at the average temperature of 18.8°C), that figure multiplied by 110% yielded the cost of caged existence plus reproduction in periods 1 and 2 and of molt in period 3, and that times 112% gave the estimated requirement of a free living individual. The accumulative increase over the resting rate is 153%. We used this number to calculate total daily requirements from the resting rate (Table 5).

Because the temperature-metabolic rate curve for each species was not determined, it was not possible to predict the magnitude of increase in metabolic rate with temperatures lower than those used in the metabolic tests. The test temperatures represent daytime values in midsummer. Therefore one could expect an increase in energy requirement especially earlier and later in the season when temperatures are cooler at night. This would tend to increase the total energy removal from the system in periods 1 and 3 over the estimates shown in Table 2.

The total daily individual requirement when multiplied by the number of birds per 100 ha and the number of days per period yielded the total metabolizable energy requirement of the species population per period (Table 2).

RESULTS

Populations.—Area A: We recorded 48 species on the census plot traversed by trail A. Of these 22 were regular inhabitants, defined as species detected on the majority of census days during a period of at least a month. The other 26 species were recorded irregularly in area A, and the pattern of detection dates varied with the species (see Discussion). Table 1A gives scientific names, number of detections, span of detection dates, and coefficients of detectability during three periods comprising the 99-day census for all species recorded in area A.

The number of individuals per 100 ha of the 22 species regularly detected in area A and the energy they removed is given in Table 2. With respect to the population calculations, no consistent pattern of change is manifest with advance of the season; 13 species showed higher calculated population levels in period 2 than in period 1, 6 showed highest numbers in period 1, and 3 showed highest numbers in period 3.

TABLE 4
POPULATIONS AND ENERGY REMOVED BY COMMON SPECIES IN AREA A FOR THREE PHASES¹ OF THE NESTING CYCLE

Species	Phase A			Phase B			Phase C			(Mcal/100 ha)			Total, phases A-C
	Incl. dates	N/100 ha	Incl. dates	Incl. dates	N/100 ha	Incl. dates	Incl. dates	N/100 ha	Phase A	Phase B	Phase C		
Rusty Blackbird	23V-12VI	2.90	14VI-1VII	6.96	2VII-30VIII	3.60	1.2	2.5	4.2	7.9			
White-crowned Sparrow	24V-20VI	10.15	21VI-30VI	34.59	1VII-30VIII	43.49	5.7	7.0	53.2	65.9			
Dark-eyed Junco	24V-15VI	11.73	16VI-2VII	44.56	5VII-30VIII	67.55	4.1	12.0	57.8	73.9			
Fox Sparrow	23V-1VI	18.95	3VI-30VI	25.74	1VII-27VIII	27.62	4.0	15.0	33.4	52.4			
Orange-crowned Warbler	23V-28VI	12.40	30VI-16VII	14.08	21VII-27VIII	6.73	4.9	2.5	2.7	10.1			
Yellow Warbler	24V-30VI	24.82	1VII-15VII	31.58	16VII-30VIII	15.27	9.2	4.6	6.8	20.6			
Yellow-rumped Warbler	24V-17VI	27.50	20VI-28VI	40.75	30VI-30VIII	17.93	8.8	4.2	14.3	27.3			
Swainson's Thrush	24V-28VI	36.80	30VI-5VII	56.05	10VII-27VIII	11.00	22.2	5.7	9.0	36.9			
American Robin	24V-25VI	23.54	28VI-2VII	34.47	5VII-30VIII	21.78	17.6	3.9	28.2	49.7			
Varied Thrush	24V-28VI	3.39	30VI-5VII	10.79	10VII-30VIII	3.92	2.8	1.5	4.6	8.9			
TOTAL							80.5	58.9	214.2	353.6			
PERCENT							22.8	16.7	60.5	100.0			

¹ See text for definition of phases.

One reason for the lack of consistency in the calculated population densities given in Table 2 is the fact that periods 1-3 are arbitrarily defined, without regard to variation in timing of events in the nesting cycles of different species. We had enough data for 10 of the species regularly detected in area A to divide the census period into phases which agree more closely with events in the nesting cycle (Table 4). Inclusive dates for phases A, B, and C vary with the species. Table 4 shows that the calculated population levels of all 10 species showed the expected increase in phase B over phase A, caused by production of young. Seven of these species showed a decline in numbers per 100 ha in phase C, as would be expected if molting individuals became inconspicuous, and or if some birds moved out of area A and were not replaced by others moving in. The three species that reached maximum calculated population levels in phase C, rather than in phase B, are all fringillids. Their habit of foraging at the edge of clearings would make them conspicuous from the census trail, especially after they had left their breeding territories. As discussed more fully below, the Emlen method results in high figures for calculated population densities of species that, instead of being spaced at random to the limit of the census area, tend to flock near the trail. It is of course possible that an actual increase in numbers of fringillids may have occurred in phase C, owing to immigration of individuals that had bred outside area A.

Area B: The total number of species recorded in area B was 23; the number of species regularly detected from trail B was 10. Table 1B gives the scientific names and summarizes the data on detections for area B.

Data on the 10 species regularly detected in area B, presented in Table 2, show that for four species the calculated population level was highest in period 1, for four others the level was highest in period 2, and for one species the number per 100 ha was highest in period 3. We have too few data on nesting birds in area B to analyze population levels and energy removal according to phases of the breeding cycle, as we did for area A.

Metabolic rates.—Table 5 gives the metabolic rates of the 11 species tested. The values for males, females, and full grown juveniles of unknown sex were averaged to give mean body weights and resting metabolic rates. The caloric equivalents were calculated as stated under Methods. Metabolic rates of 11 species of birds that were regularly detected in the census but were not captured for determination of metabolic rate were taken from values of species of the same weight and family where possible; otherwise, values were calculated from the daytime (α) equation for the appropriate group of birds in Aschoff and Pohl (1970). No calculations of food energy removed from the ecosystem to feed nest-

TABLE 5
NUMBERS, SEX, AND AVERAGE WEIGHT OF BIRDS TESTED FOR RESTING METABOLIC RATE

Species	N indiv. tested	N tests	Sex ¹	Ave. Wt. g \pm 1 SD	Test T °C	ml O ₂ /hour \pm 1 SD	kcal/hour ²	Total energy ³ cost kcal/24 hours
Alder Flycatcher	5	8	3 ♂, 1 ♀, 1 u	13.6 \pm 0.8	18.5	54.6 \pm 17.0	0.265	10.05
Swainson's Thrush	3	3	3 u	26.8 \pm 1.6	19.1	91.1 \pm 4.8	0.442	16.76
American Robin	1	2	1 u	47.3	17.5	123.6	0.599	22.71
Ruby-crowned Kinglet	3	3	1 ♂, 1 ♀, 1 u	6.6 \pm 0.3	18.4	51.3 \pm 12.8	0.249	9.44
Orange-crowned Warbler	2	3	1 ♀, 1 u	8.3	18.4	57.6 \pm 14.8	0.279	10.58
Yellow-rumped Warbler	2	3	1 ♀, 1 u	12.3	19.4	69.8 \pm 3.7	0.339	12.85
Yellow Warbler	7	12	5 ♂, 1 ♀, 1 u	9.4 \pm 0.6	19.3	52.8 \pm 17.9	0.256	9.71
Wilson's Warbler	4	8	2 ♂, 2 ♀	7.5 \pm 0.3	18.5	54.4 \pm 12.8	0.264	10.01
White-crowned Sparrow	8	9	2 ♂, 2 ♀, 4 u	25.0 \pm 1.6	19.5	109.1 \pm 25.7	0.529	20.06
Fox Sparrow	5	9	1 ♀, 4 u	34.4 \pm 2.3	19.2	113.5 \pm 15.6	0.550	20.86
Dark-eyed Junco	7	7	3 ♂, 1 ♀, 3 u	18.5 \pm 0.9	19.4	81.7 \pm 21.6	0.396	15.02

¹ u = juvenile birds, sex could not be determined externally.

² ml O₂/h \times 4.85 kcal/liter O₂ consumed (see text).

³ kcal/h \times 1.53 (153% over resting rate, see text).

ling young were made. This might double the total amount used by adults from the time the young hatched until they became independent and were included in the population census. With the uncertainties of estimation of added costs for reproduction, molt, and free existence (see Methods), the values given for energy removal in Tables 2 and 4 should therefore be considered only as approximations. Nevertheless, they indicate the relative removal by species, period, and census site. Also irregularly detected species are not included in Table 2 and could only increase the total energy removal.

Comparison of areas A and B.—Both the total number of species recorded and the number regularly detected were more than twice as great in area A than in area B. In addition, the number per 100 ha of a given species was in most cases much higher in area A than in B. Of the species regularly detected on both trails, the population density of 9 out of the 10 species on area A was greater than on area B in period 1. In period 2, 9 out of 10 species on area A also had greater numbers than on area B, and in period 3, 7 out of 10 had greater numbers (Table 2). In these two adjacent sites the population totals and resultant total energy removal per 100 ha was in the ratio of about 3:1 (Table 2). Identical species showed different patterns of change in abundance with season at the two sites. Of the 10 species regularly detected in area B, only Swainson's Thrush showed highest and lowest numbers per 100 ha during the same periods in both sites.

Because some of the differences just described could be due to the discrepancy in the number of days that the census was taken at the two sites, we calculated population densities of 10 species detected on both trails, using matched pairs of census dates. We selected 3 pairs of dates in period 1, 5 pairs in period 2, and 4 pairs in period 3. All these censuses were taken under weather conditions comparable for each matched pair of dates. The resulting calculations of population densities for the two sites are given in Table 3. Equalizing the number of census days and choosing pairs of dates with similar weather did not eliminate differences in calculated number per 100 ha of identical species. Table 3 shows that for 18 of the 30 comparisons population level differences of a given species between areas A and B are greater than those shown in Table 2.

Another contrast concerns the number of young birds counted at the two sites. For nine common species we calculated the number of fledglings actually detected per 4.0-km trip along each trail in periods 2 and 3. The totals for trail A were higher in both periods for the young of six species, and higher in one period for the young of two others. Only one species showed higher totals for young on trail B for both periods.

The calculated energy requirements for each species population in periods 1, 2, and 3 corresponded generally with the population census numbers because the calculation of individual energy costs remained constant over the summer (Table 2). The calculation remained constant because of the sequential arrangement of energy demanding activities throughout the summer season from territory formation and defense, courtship, egg-laying, incubation, brooding and feeding of young, and finally molt (West 1960, 1968). In both areas A and B, the total energy removal was slightly higher in period 2 than in 1 or 3 because of the production of young, and it then diminished in period 3 due to emigration or death of individuals, probably mostly young birds. Note that the rate of energy removal remained almost stable throughout the 3 summer months.

A comparison of the amounts of energy removed in phases A, B, and C by the 10 species whose activities could be divided this way (Table 4) reveals that almost 60% of the energy removal occurred in phase C, which includes postbreeding wandering of fledged young, flocking, and the annual molt. The variations in energy removal by phase are largely dependent on the length of the phase, which averaged 30 days in A, 9 days in B, and 57 days in C. The short interval of phase B was compensated for in part by increased numbers of individuals in that phase so that the resulting energy removal in phase B was not one-third (as the date span would indicate), but nearer three-fourths of that in phase A. The slight (average 6%) deviations in the species energy removal totals between Tables 2 and 4 are due largely to gaps in the dates between events that delimited the three phases in Table 4.

DISCUSSION

Probably several different reasons caused the irregular detections of numerous species on both trails (26 species on trail A, 13 species on trail B). Some, like the Sandhill Crane seen once in area A, were transients. Others, like the Ruffed Grouse, may have been present continuously in both census tracts, but, owing to their secretiveness, were detected irregularly. The aquatic species detected from trail A, such as the Red-necked Grebe, Mew Gull, and Bank Swallow, remained in the immediate vicinity of Smith Lake (a 7.2-ha lake with one side 200 m from one point of trail A) for much of the census period, and only rarely approached near enough to the census trail to be included in census data. Another group of species irregularly detected were those known to be resident in the vicinity, but which may have had foraging ranges larger than the specific census sites. Examples are the Gray Jay and Pine Grosbeak. Hence no generalization can be made concerning the species

irregularly detected, and calculation of the amounts of energy removed by them from the census sites must be based on assumptions that differ with the species. A thorough knowledge of the natural history of each species would be necessary before we could assess accurately the impact of such species on the census sites, but in any case, they would act to increase the total energy removal from the ecosystem.

In our calculations of the projected number of birds present on either side of the census trail, we used the number of individuals detected within the critical distance (usually 0–50 feet), based on Emlen's assumptions that (a) all individuals will be detected within the critical distance, and (b) the birds are randomly distributed out to the boundary line (which we set at 410 feet on either side of the trail). We are reasonably confident that the first assumption was valid for our field conditions. Counts of a given species on successive census dates fluctuated little. When a substantial increase in numbers was recorded it was almost always due to the first appearance of fledged young. Even on wooded sections of the trails it was possible to see to the edge of the 50-foot strip; the understory was not dense, the conifers were scattered, and the deciduous trees were sparsely leafed beneath the canopy. In the early morning the environment was quiet except for bird sounds. Emlen's second assumption was probably not valid for our census situation. Random distribution of birds is more likely in a uniform habitat. Taiga includes irregularly distributed patches of open ground among intermixed stands of spruce, birch, and other tree species, and hence does not constitute a uniform habitat. This is especially true of the census plot traversed by trail A, which included fields and proximity to ponds. Trail B passed through more uniform woods. Even at places where the woods were uniform we believe that the assumption of random distribution is not equally valid for all species. The census trail itself constituted an opening along which ground-foraging species (fringillids such as juncos) congregated, especially after fledging their young. We think that the numbers of individuals of such species were actually greater within the 0- to 50-foot strips bordering the trail than in the strips farther away. Thus, assumption of random distribution would result in falsely high projected numbers for edge-frequenting species, and hence the calculated densities per 100 ha would be greater than the actual densities. The Emlen method is probably more reliable during the period when pairs are restricted to territories, and as Emlen (1971) states, is not designed for species that occur in flocks.

The greater variety of species recorded, as well as the greater number of those regularly detected, in area A compared with area B can be explained by the greater diversity of habitats present in area A.

The greater numbers per 100 ha in area A than in area B for identical species, and the greater number of young detected per 4.0-km trip on trail A, indicate that even those species regularly detected on both trails nested more abundantly in area A. Again, the greater habitat diversity traversed by trail A probably explains this. The varied plant communities, ponds, and cultivated fields in area A may have yielded more food for the young.

We calculated the total biomass in each of the periods 1, 2, and 3 for the population of birds in the more uniform taiga habitat, area B. The total biomass present in the three periods was 1854, 2703, and 2379 g/100 ha respectively. Subtracting the biomass of period 1 from that of period 3 (525 g/100 ha) yields the total amount of biomass actually removed from the system (assuming that all birds in period 3 departed). Neither the total bird biomass in each period nor the amount exported are very impressive in comparison to the minimum energy loss through respiration calculated for each period (Table 2). At about 5 kcal/g, the 180,000 kcal summer total for area B is equivalent to 36,000 g, 68 times the amount exported.

These calculations also assume that the birds that arrived in period 1 remained to breed, and that in period 3 all individuals produced that did not die remained at the census sites to be counted. This is more likely to be the case for area B than for area A, which as indicated above had both a concentration of certain species along roads and edges of fields and emigration of certain species (phalarope and yellowlegs) out of the locality (to ponds) after breeding. The corresponding biomass totals for the three periods on area A were 6573, 9194, and 5749 g/100 ha, which indicate that actually 824 g/100 ha were added to the system. If this were actually the case over several years, the locality would soon be devoid of many bird species.

The 99-day summer total of 495 Mcal/100 ha of energy removed from area A (Table 2) represents the metabolic or respiratory energy lost from the system by the adult population. The energy removed from the system by nestling young was not estimated. If we assume that the adult birds were in energy balance throughout the summer (maintaining constant body weight) and that the efficiency with which they converted the gross energy (GE) in their food to metabolizable energy (ME) was near 70%, then the total calories in foods removed approximates 700 Mcal/100 ha with the difference of 205 Mcal (700-495) returned as excrement. The average caloric value of foods consumed by small birds (insects and seeds) is 5200 cal/g dry wt (West 1973). The 700 Mcal/100 ha of GE can then be converted to 135 kg/100 ha of dry food re-

moved. Assuming that the amount of water approximates 70% in the foods, the total wet weight of fresh food removed from the system would be near 193 kg/100 ha for the 99-day summer season. At this time there is no estimate of the production of either insect or seed species used for bird food in the taiga. It would be interesting to determine the availability of food and the proportion of the annual production removed by the birds as Grodzinski (1971a, 1971b) estimated for small mammals.

Carbyn (1971) censused the breeding birds in boreal forest habitats near Great Slave Lake, N.W.T. from May to July. In five habitat types that did not differ greatly from many habitats encountered on our census trails, he found an average of 524 individuals per 100 ha representing 17 species of passerines over the breeding season. The average biomass calculated for the same period was 10,260 g/100 ha. Our periods 1 and 2 compare to his census period and we found considerably less numbers and biomass in the 20 passerines on our area A and especially area B.

Kendeigh (1956) conducted a trail census in northern Minnesota through a mixed deciduous-coniferous forest. He found the highest densities of males in aspen-birch-pine stands and the lowest (200 males/100 ha, or something less than 400 breeding individuals/100 ha) in tamarack-black spruce habitat. This value is higher than breeding adult values seen in period 1 of either of our two sites. Kendeigh (1947) also censused birds in the spruce-fir habitat of southern Ontario and found a density of 1595 individuals/100 ha in the breeding adult population.

The habitat types in the vicinity of Great Slave Lake, N.W.T. where Carbyn (1971) estimated bird populations correspond more closely to those of the taiga of interior Alaska than do the habitats farther south and east studied by Kendeigh (1947, 1956). Bird species encountered by Kendeigh in Minnesota and Michigan included many native to the eastern deciduous forest that extend their range into ecotonal localities to the north: Red-eyed Vireo, (*Vireo oliveceous*); Scarlet Tanager (*Piranga olivacea*); several warblers in the genera *Dendroica*, *Vermivora*, *Seiurus*, *Geothlypis*, *Wilsonia*, *Parula*, *Setophaga*, *Oporornis*, and other species that do not occur in Alaska. Habitats in those southern localities perhaps have more available space since the trees, especially the pines (*Pinus strobus*, *P. resinosa*, *P. banksiana*), are considerably taller.

As we measured populations for only 1 year, we do not know if the numbers we counted are representative of an average year. It would be instructive to continue the census over several years in order to make this test and to correlate the populations with other ecosystem parameters such as annual production of seed crops and invertebrates.

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SUMMARY

The birds present in two adjacent areas of taiga in interior Alaska were censused from late May to the end of August using a modification of the trail census method of Emlen (1971). On area A we found 48 species, 22 of which were regular inhabitants and on area B, 23 species, with 10 regular inhabitants. Area A was characterized by greater habitat diversity than area B. The resting metabolic rate during daytime was measured on 11 species of regular inhabitants and the total amount of energy needed for existence, reproductive activities, and molt were estimated.

At both census sites the population and estimated energy removal increased in July and decreased again in August. In general the higher numbers in July were a result of production of young; the decrease in August was a result of mortality and emigration from the census area. The total numbers of breeding birds and their biomass were less on the two sites censused than those reported in other localities within the boreal forest from Northwest Territories, southern Ontario, or northern Minnesota.

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