MODEL ESTIMATION OF ENERGY FLOW IN NORTHWESTERN CONIFEROUS FOREST BIRD COMMUNITIES[1]

JOHN A. WIENS AND RONALD A. NUSSBAUM[2]

Department of Zoology, Oregon State University, Corvallis, Oregon 97331 USA
and
Forest Research Laboratory, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. A simulation model developed in the Grassland Biome Program of the US/IBP is applied to data gathered in the Coniferous Forest Biome Program to estimate the magnitudes and patterns of energy flow in breeding bird populations in Northwestern coniferous forests. Six stands along a moisture-temperature gradient in the central Oregon Cascades supported breeding avifaunas of 7–15 species, with standing crops of 223–526 g/ha. Total energy flow through these avifaunas during the April–October breeding season was estimated at roughly 10 kcal m⁻² season⁻¹ in the low-elevation, moderately xeric stands; 12 kcal m⁻² season⁻¹ in the high-elevation stands; 17 kcal m⁻² season⁻¹ in a mesic floodplain stand; and 21 kcal m⁻² season⁻¹ in a midelevation "transitional" stand. About 1% of the seasonal energy flow was channeled into production, while reproduction-related processes accounted for 15%–16% of the total energy intake. Thermoregulation required 13%–19% of the seasonal total, with the higher relative costs associated with the cooler, higher elevation stands. Foliage-gleaning bird species accounted for the greatest proportion of the energy intake at most stands, but within this "guild" the importance of granivorous "opportunistic" species generally increased through the stand sequence as the growing season became shorter and environmental conditions more severe.

Key words: *Bird community*; *coniferous forest*; *energy flow*; *IBP*; *simulation model.*

INTRODUCTION

Coniferous forests occupy roughly one-third of the land area of the western United States and attain perhaps their greatest development in the Pacific Northwest. Here the maritime coastal climates, with heavy winter precipitation, summer dry seasons moderated by frequent fog or cloudy weather, and relatively small seasonal temperature variations, favor the development of forests of massive proportions. Such forests support a diverse and distinctive bird fauna (Udvardy 1963). These bird populations have received little quantitative study, although some species (notably woodpeckers) are known to respond both functionally and numerically to insect outbreaks (Baldwin 1968, Koplin 1969, Koplin and Baldwin 1970) and may at times inhibit the spread of epidemics.

The role of bird populations in the energy dynamics of coniferous forest ecosystems is less clear. Information on energy flow through bird populations, however, is essential to efforts to analyze or model complete forest ecosystems, such as are currently being conducted as part of the US/IBP Coniferous Forest Biome Studies. Determination of energy flow magnitudes and patterns requires knowl-

edge of the energy demands of populations and their positions in the trophic web. Recently, attempts have been made to approximate these relationships in several ecosystem types, either through indirect calculations (e.g., Karr 1971, Holmes and Sturges 1973) or by computer simulations (Wiens and Innis 1974, Wiens and Scott, *in press*). Here we appraise the patterns and magnitudes of energy flow through the breeding avifaunas of six plant community types in Northwestern coniferous forests, using a simulation modeling approach. This examination represents a joint effort of the Grassland Biome and Coniferous Forest Biome Studies of the U.S. International Biological Program (IBP). The field studies were conducted as part of the Coniferous Forest program, while the analyses were undertaken within the Grassland program.

METHODS

Field studies

In June 1972, populations of breeding birds were sampled in relation to several reference stands established as part of the environmental grid of the US/IBP Coniferous Forest Biome. Each stand was sampled at one time period, and census estimates were derived from values for 6–12 census plots within each stand. A variable, circular plot method of censusing was devised in order to contend with the special problems of sampling birds in old-growth coniferous forests where the canopy is extremely

tall. The method will be described in detail elsewhere, but briefly the procedure was as follows. Random points were established in each habitat type to determine plot locations. Two observers stood at each point and recorded the location of each singing male by distance and direction from the point. In most cases, all singing males within a plot could be recorded in less than 15 min. Detectability of individuals decreases with distance from the observer. The shape of the detectability curve varies with species, habitat, and the nature of the observation (whether visual or auditory). By determining the detectability function, we could estimate the densities of the individual species within a circular plot of a given radius. Emlen (1971) used similar principles for strip censusing of bird populations.

The vegetational features of the reference stands were sampled and described by other biologists in other phases of research within the Coniferous Forest Biome studies. We have drawn freely from unpublished data made available by Jerry Franklin, Ted Dyrness, William Moir, and Glen Hawk.

The phenological data, taken from unpublished reports of the IBP Coniferous Forest Biome, were gathered by regular monitoring of individual plants in the different reference stands. Air temperature was measured by continuous recording devices established within the reference stands. The data are available in complete form in Internal Report 127 of the Coniferous Forest Biome (unpublished report).

Model analysis

To estimate the magnitudes and patterns of energy flow through the breeding bird populations of these forest stands, we utilized the simlation model described by Wiens and Innis (1974). The details of the structure and assumptions of the model are given in that paper and will be only briefly summarized here.

There are two basic submodels in the model. In one, information on various life history attributes of a population (e.g., clutch size, hatching success, immigration and emigration timings and patterns, reproductive phenology) is coupled to the field values of breeding population density to generate estimates of the density of adults and of each age class of offspring of each species at any given point during the breeding season. Our analyses began on 1 April and ended on 7 October for all stands. Migrant or transient individuals were not included in the density estimations.

The second submodel estimates the energy demands placed upon the ecosystem by these populations through time. Information on ambient temperature regimes is coupled with values of body weight of adults or of growing young to estimate individual existence energy demands (M), according to the equations of Kendeigh (1970) for passerines:

$$M_0 = 4.337\, W^{0.53} \text{ at } 0°C \qquad (1)$$

$$M_{30} = 1.572\, W^{0.62} \text{ at } 30°C \qquad (2)$$

where W = body weight (grams). Through these functions, the existence energy demands of individuals of different age classes of different species may be calculated for any given date and ambient temperature. The demands are adjusted to reflect the additional energy costs of growth (for young), activity, and egg production. These adjusted individual metabolic energy demand estimates are then multiplied by 1.43 (assuming a 70% digestive or assimilation efficiency) to provide an estimate of the energy demands (kcal bird^{-1} day^{-1}) placed upon the system by individuals. Integrating these estimates with those of the population dynamics submodel permits calculation of the energy demand of the entire population of a species on any given day. The model thus generates daily estimates of population density, total biomass, and the bioenergetic demands placed upon the food resources, by each age class, for all of the species occupying a stand.

The calculations of existence energy requirements include the energy costs of thermoregulation at ambient temperatures below thermoneutrality. A variation in the model structure, introduced subsequent to the description of Wiens and Innis (1974), permits separation of thermoregulation costs from the other elements of existence energy in a very general manner. If the existence energy demand of an individual of body weight W is determined for the lower critical temperature (the lower boundary of the thermoneutral zone) using Eq. (1) and (2), then the difference between this energy demand and the requirements calculated by these equations at lower ambient temperatures is a measure of the energy allocation to thermoregulation. Determinations of lower critical temperatures are lacking for most of the species we considered, and we assumed a value of 25°C for all species (S. C. Kendeigh, *unpubl. data*). Sensitivity tests indicated that errors of ±5°C had relatively minor effects on the measures of energy flow reported here.

The model requires as data input specifications of some 30 variables for each species considered. Most of these relate to population phenology (timing of arrival, departure, onset of nesting, incubation periods, etc.), while others quantify features of survivorship (hatching success, fledging success, etc.) or growth (hatching weight, logistic growth constant, etc.). We have used values obtained from field studies in western Oregon coniferous forests, augmented by literature data. Altitudinal variation may
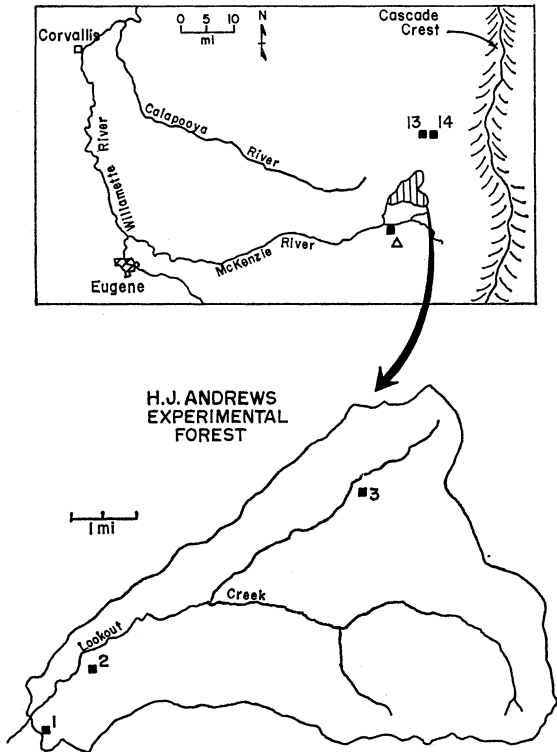
FIG. 1. Locations of the six coniferous forest stands on the western slope of the Cascades in central Oregon.
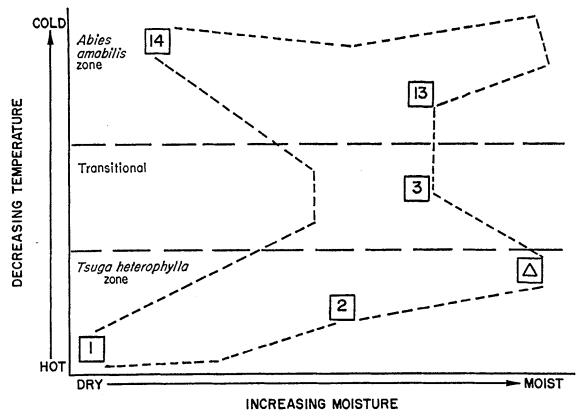

FIG. 2. Relative positions of the six stands in an ordering of central Oregon Cascade plant community types by moisture and temperature levels. Dashed line encompasses the range of community types represented in the ordination. Generalized from Dyrness et al. (1974).

influence these values, but in the absence of data on this, standard (mainly lowland) values were used. The input variables are described in detail in Wiens and Innis (1974), and a listing of the values used in our present analyses is available from the authors upon request.

STUDY SITES

The six forest stands are located in the McKenzie River drainage on the western slope of the Cascade

Range in west-central Oregon (Fig. 1). Three of the stands are located in the H. J. Andrews Experimental Forest of the U.S. Forest Service, two more in the Wildcat Mountain Research Natural Area (described in Franklin et al. 1972). All stands except Delta are reference stands of the Coniferous Forest Biome studies. The stands were selected, from among a larger series upon which avifaunal studies were conducted, to include a broad elevational span and to represent a relatively even sampling of the spectrum of plant community types occurring in the coniferous forests of the Pacific Northwest (Fig. 2, Dyrness et al. 1974). General features of the stands and their vegetation are given in Table 1 and Fig. 3 and 4. Here we have ordered the stands according to generally decreasing temperatures (Fig. 3), although other stand orderings are of course possible. Species code designations are defined in the legend to Fig. 4.

Stand 1. The tree overstory of this stand was

TABLE 1. General features of the coniferous forest stands considered in this study

Site code	Community type (Tree dominant[s]/shrub dominant/ herbaceous understory dominant[s])	Elevation (m)	Phenology (Date of vegetative bud break, 1972)	
			Understory conifers[a]	*Linnaea borealis*
1	*Pseudotsuga menziesii/ Holodiscus discolor*	488	19 May	15 March
2	*Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa*	488	7 June	29 March
Δ	*Tsuga heterophylla/Acer circinatum/ Polystichum munitum–Oxalis oregana*	360	13 May	absent
3	*Tsuga heterophylla–Abies amabilis/ Linnaea borealis*	945	17 June	16 May
13	*Abies procera/Clintonia uniflora*	1,311	7 July	19 June
14	*Abies amabilis–Tsuga mertensiana/ Xerophyllum tenax*	1,433	13 July	absent

[a] Includes *Pseudotsuga menziesii, Tsuga heterophylla, Abies amabilis,* and *Abies grandis*; individuals < 3 m tall.
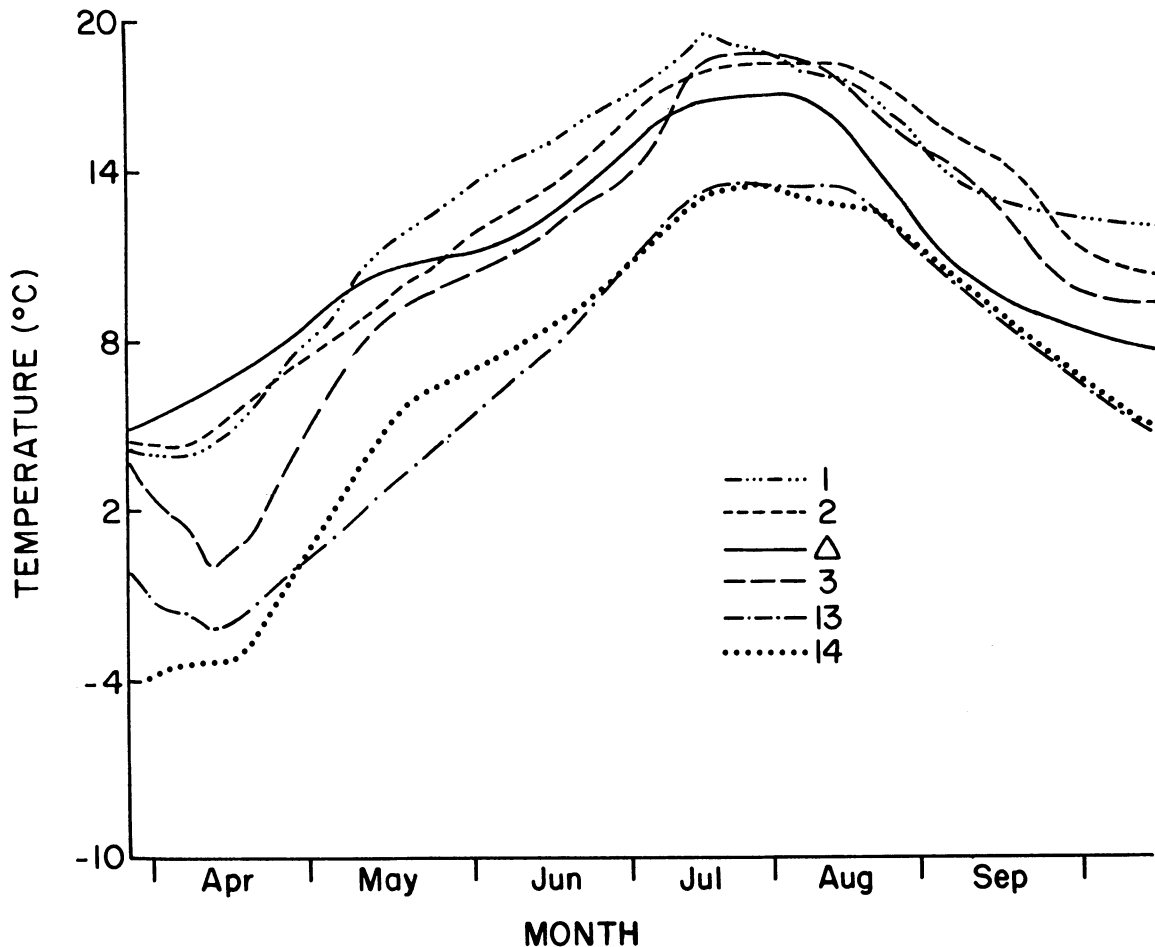
FIG. 3. Ambient temperature regimes for the six coniferous forest stands. The curves represent model output generated from monthly mean temperatures.

dominated by Douglas-fir (PSME), while the major understory species were vine maple (ACCI), ocean spray (HODI), Oregon grape (BENE), and sword fern (POMU). This was the hottest and driest of the sites, occupying a southwest-facing slope at a low elevation in the H. J. Andrews forest. Total canopy coverage (45%) was lower than in the other stands, and shrub coverage was relatively high. Initial bud-break of twin-flower (LIBO), a phenological indicator species whose spring activity closely follows snow-melt (A. McKee, *pers. comm.*), was earlier in this stand than in any of the others in which this species occurred, and understory conifer phenology was nearly 3 wk advanced over that in Stand 2, which was located at the same elevation a short distance away.

Stand 2. This stand occupied a north-facing slope in the Andrews forest and, consequently, was somewhat more mesic than Stand 1. The tree overstory was composed of Douglas-fir (PSME) and western

hemlock (TSHE) in equal coverage, and the understory was dominated by Oregon grape (BENE), vine maple (ACCI), and rhododendron (RHMA) in the shrub layer and twin-flower (LIBO) and sword fern (POMU) in the herbaceous ground cover.

Stand Delta (Δ). This stand was not part of the system of reference stands used in the IBP studies, but did not receive close study by Hawk (1972); see also Hawk and Zobel (1974). It was included in our analysis because of its location, in the floodplain of the McKenzie River below the Andrews forest. The most mesic as well as the lowest of the stands, Delta supported the most diverse overstory, with western hemlock (TSHE) dominating, but Douglas-fir (PSME), big-leaf maple (ACMA), western red cedar (THPL), and grand fir (ABGR) also contributing to the canopy. Shrubs, chiefly vine maple (ACCI) and Oregon grape (BENE), formed a moderately dense ground cover, and herbaceous vegetation was dense, largely because
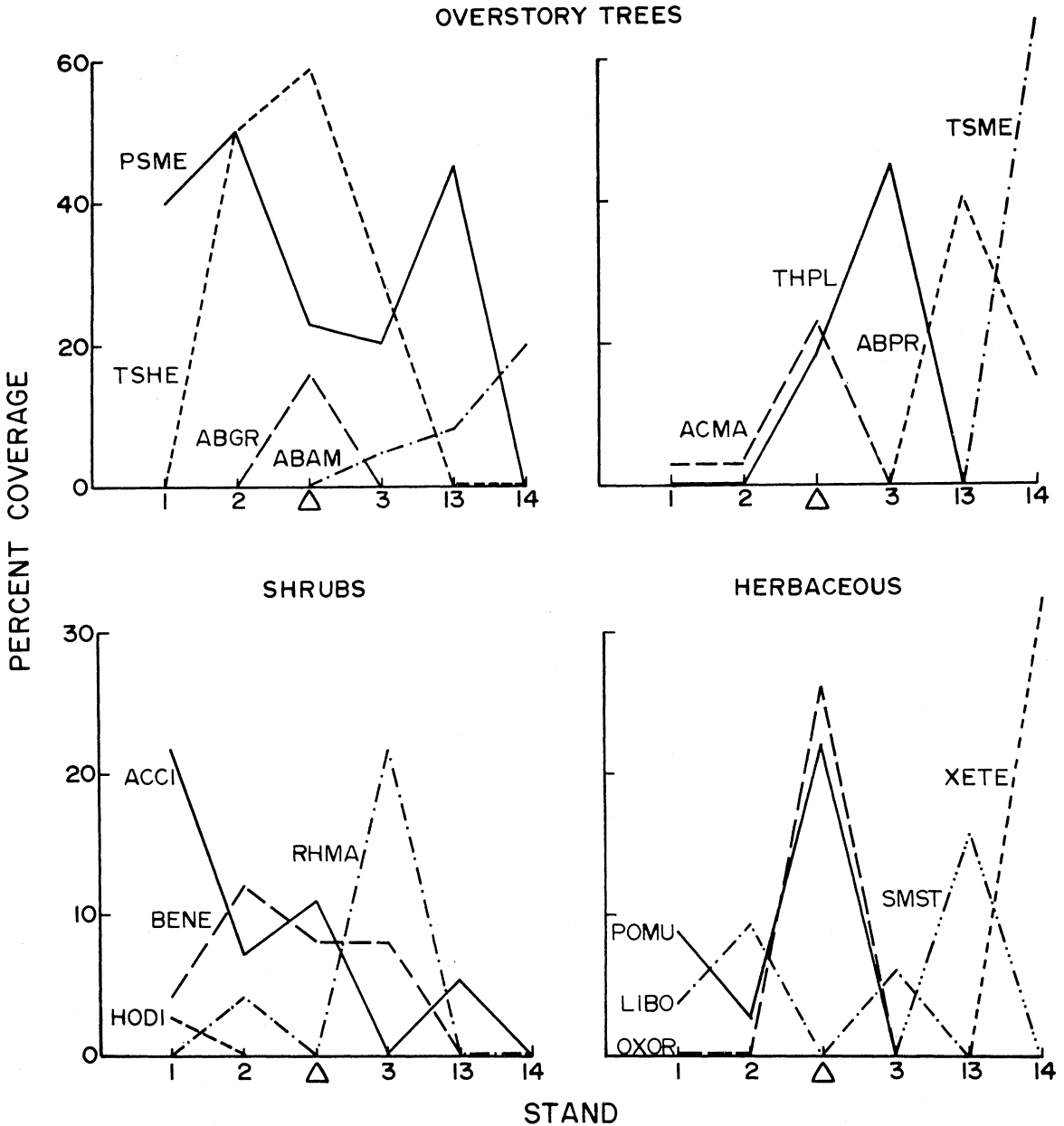
OVERSTORY TREES

FIG. 4. Coverage of major tree, shrub, and herbaceous species in relation to a sequence of the six coniferous stands based upon generally decreasing temperature (Fig. 2). ABAM = *Abies amabilis*, ABGR = *Abies grandis*, ABPR = *Abies procera*, ACCI = *Acer circinatum*, ACMA = *Acer macrophyllum*, BENE = *Berberis nervosa*, HODI = *Holodiscus discolor*, LIBO = *Linnaea borealis*, OXOR = *Oxalis oregana*, POMU = *Polystichum munitum*, PSME = *Pseudotsuga menziesii*, RHMA = *Rhododendron macrophyllum*, SMST = *Smilacina stellata*, THPL = *Thuja plicata*, TSHE = *Tsuga heterophylla*, TSME = *Tsuga mertensiana*, XETE = *Xerophyllum tenax*.

of the relatively high coverage by Oregon oxalis (OXOR) and sword fern (POMU). Understory conifer phenology was most advanced in this stand.

Stand 3. This stand represented the set of community-types transitional between hemlock-dominated and true fir-dominated communities. Located on a northwest-facing slope at an inter-

mediate elevation in the Andrews forest, it supported a canopy composed chiefly of western red cedar (THPL), western hemlock (TSHE), Douglas-fir (PSME), and Pacific silver fir (ABAM). Rhododendron (RHMA) dominated the understory shrubs, while the herbaceous layer was comprised largely of twin-flower (LIBO), but in relatively low coverage.

TABLE 2.   Ecological attributes and population densities of the breeding bird species of the six coniferous forest stands

Species	Body weight (g)	Residency[a]	Ecological category[b]	Population density (individuals/km^2)					
				1	2	Δ	3	13	14
Yellow-bellied Sapsucker (Sphyrapicus varius ruber)	45.9	P	TD	⋯	151	⋯	⋯	⋯	⋯
Hairy Woodpecker (Dendrocopos villosus)	68.0	P	TD	⋯	⋯	27	⋯	⋯	104
Hammond's Flycatcher (Empidonax hammondii)	9.5	S	AI	⋯	46	⋯	⋯	⋯	⋯
Western Flycatcher (Empidonax difficilis)	10.0	S	AI	212	175	367	25	⋯	54
Steller's Jay (Cyanocitta stelleri)	106.6	P	FO	7	7	83	39	⋯	⋯
Gray Jay (Perisoreus canadensis)	74.6	P	FO	⋯	⋯	⋯	68	⋯	⋯
Chestnut-backed Chickadee (Parus rufescens)	10.0	P	FI	399	170	154	612	214	⋯
Red-breasted Nuthatch (Sitta canadensis)	10.3	P	TS	356	⋯	101	44	323	13
Brown Creeper (Certhia familiaris)	8.4	P	TS	⋯	125	541	680	348	⋯
Winter Wren (Troglodytes troglodytes)	8.9	P	GI	135	76	326	109	⋯	67
American Robin (Turdus migratorius)	81.2	P	GO	18	46	⋯	151	⋯	⋯
Varied Thrush (Ixoreus naevius)	79.3	P	FP	⋯	⋯	⋯	15	67	59
Townsend's Solitaire (Myadestes townsendi)	34.0	S	FO	⋯	⋯	⋯	⋯	⋯	7
Hermit Thrush (Hylocichla guttata)	26.3	S	FO	14	⋯	⋯	54	⋯	20
Swainson's Thrush (Hylocichla ustulata)	30.0	S	FO	145	⋯	91	54	⋯	⋯
Golden-crowned Kinglet (Regulus satrapa)	6.0	P	FI	135	135	539	680	439	255
Hermit Warbler (Dendroica occidentalis)	8.3	S	FI	75	78	113	134	344	120
Western Tanager (Piranga ludoviciana)	26.9	S	FI	86	113	50	⋯	⋯	⋯
Evening Grosbeak (Hesperiphona vespertina)	64.2	S	FI	⋯	⋯	⋯	⋯	⋯	127
Pine Siskin (Spinus pinus)	13.0	S	GO	⋯	⋯	⋯	108	⋯	152
Red Crossbill (Loxia curvirostra)	29.4	P	FP	⋯	⋯	⋯	⋯	⋯	226
Oregon Junco (Junco oreganus)	17.6	P	GO	196	290	226	116	175	26

[a] P = permanent, S = breeding season only.
[b] AI = air-insect feeding, FI = foliage-insect feeding, FO = foliage-omnivore, FP = foliage-seed or fruit-eating, TS = timber-searching, TD = timber-drilling, GI = ground-insect feeding, GO = ground omnivore; categories after Anderson (1970).

Stand 13.   Located at a relatively high elevation on a south-facing ridge in the Wildcat Mountain Research Natural Area, this stand was cool and wet. Understory conifer phenology was a month later than that in Stand 2, and lagged behind Delta and Stand 1 by more than 6 wk. Douglas-fir (PSME) and noble fir (ABPR) were the principal overstory tree species; shrub cover (chiefly vine maple (ACCI)) and herbaceous cover (primarily starry Solomon's-plume (SMST)) were low.

Stand 14.   Like Stand 13, this stand was located at a relatively high elevation in the Wildcat Mountain Research Natural Area. Despite its northwest exposure, it had a much drier microclimate, a result of wind patterns and soil characteristics of its exposed ridge location. Mountain hemlock (TSME), noble fir (ABPR), and Pacific silver fir (ABAM) were the overstory tree dominants, and common bear grass (XETE) attained high coverage in the herbaceous layer; shrub cover (3% overall) was the lowest among the six stands.

RESULTS

Avian community structure

Twenty-two breeding bird species were recorded in the censuses on the six stands, although 10 of these (45%) were encountered in only one or two of the stands (Table 2). Several of the species exhibited fairly well-defined changes in population density or distribution along the vegetational-environmental gradient represented by the six stands. Western Tanagers, for example, were recorded only in the lower elevation *Tsuga heterophylla*-zone communities of Fig. 2, and Western Flycatchers attained their greatest densities in these stands. Other species, such as Brown Creepers and Golden-crowned Kinglets, were most abundant in the middle range of Stands (Δ, *3*, *13*), while Varied Thrushes were found in the higher elevation, *Abies amabilis*-zone stands of Fig. 2, and Evening Grosbeaks and Red Crossbills were recorded only in Stand *14*. Of the 6 species recorded in only one of the six stands, 3 were found in Stand *14*.

Stand *14* differed avifaunally from the other stands in several other respects. It supported the lowest total density of breeding individuals (Table 3), although the total standing crop biomass was greater than that in three of the stands, despite the absence of any large-bodied (> 80 g) species (Fig. 5). Of the breeding species 46% were seasonal residents, a proportion elsewhere approached only in Stand *1*.

Stand *13* supported the lowest number of breeding species (7); Stand *3* contained more than twice that number (Table 3). Overall, breeding population densities were high relative to those recorded in forest communities elsewhere in the United States (Fig. 4 in Wiens 1973), although the number of breeding species was generally somewhat lower. Stands *3* and Δ supported the greatest avian biomass, more than twice that recorded in Stands *1* and *13*. In the latter stands, biomass was not appreciably greater than that recorded in some grasslands (Wiens 1973). Stands *2* and *14* supported the most diverse avifaunas, but diversity was low in Stand *3*, which

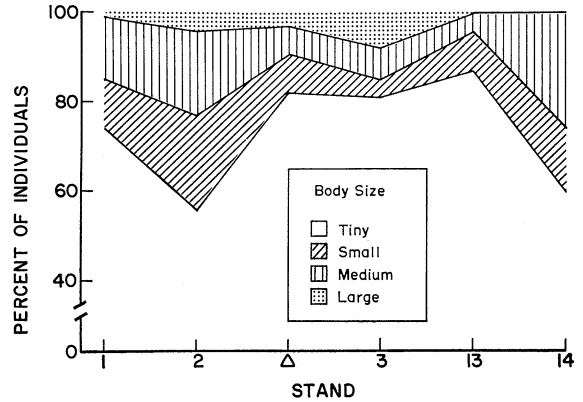FIG. 5. Distribution of breeding bird individuals among body size classes in the six coniferous forest stands. Tiny ≤ 10 g body weight, small = 11–25 g, medium = 26–80 g, large > 80 g.

contained the greatest number of species, individuals, and biomass (Table 3). This no doubt was due to the dominance of chickadees, creepers, and kinglets in this stand (Table 2). In fact, small species (≤ 10 g body weight) numerically dominated the avifaunas at all stands (Fig. 5). This is in marked contrast with the size composition of breeding communities in grassland or shrub-steppe communities, where such small species are totally absent; in shrub-steppe habitats, 11–25 g species tend to predominate, while in shortgrass prairies most individuals fall in the 26–80 g size class (Wiens 1974).

Patterns of ecological structure of these coniferous forest stands are discussed (following section) more fully in an energetic framework, while the avifaunal characteristics of these and other Northwestern coniferous forest communities are treated in more detail by Anderson (1970, 1972).

Energy flow patterns and magnitudes

Estimates of the total energy demand of the breeding avifauna over the entire breeding season (1 April–7 October) differed considerably between stands (Table 4). The two low-elevation, moderately

TABLE 3. Avifaunal characteristics of the six coniferous forest stands. Species diversity $(H') = -\Sigma p_i \ln_e p_i$, where p_i = the proportion of all individuals belonging to the ith species. Equitability $= H'/\ln S$, where S = number of species

Stand	Number of species[a]			Total density (individuals/km²)	Standing crop biomass (g/ha) on 1 July	Species diversity (H')	Equitability
	Permanent	Seasonal	Σ				
1	7	5	12	1,779	262.8	2.05	0.82
2	8	4	12	1,380	275.8	2.21	0.89
Δ	8	4	12	2,619	424.3	2.13	0.86
3	10	5	15	2,887	526.1	1.89	0.70
13	6	1	7	1,910	223.3	1.64	0.84
14	7	6	13	1,229	361.9	2.22	0.87

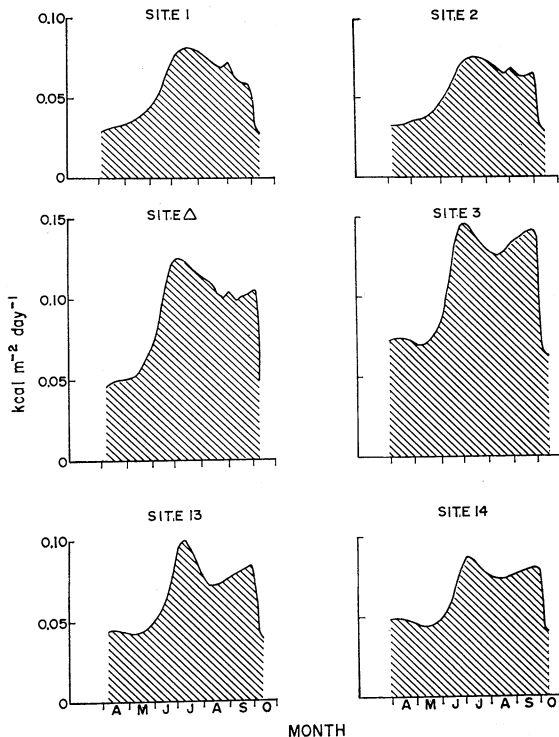[a] "Permanent" and "Seasonal" refer to residency.

FIG. 6. Model estimates of daily energy demand by the breeding avifaunas of the six coniferous forest stands.

xeric Stands (*1* and *2*) had the smallest seasonal flows, 10.6–10.9 kcal m^{-2} season^{-1}, while the bird populations of the two high-elevation Stands (*13* and *14*) processed roughly 17% more energy (12.5–12.7 kcal m^{-2} season^{-1}). Avian community energy demand was considerably higher in the transitional Stand (*3*), roughly twice that of the low-elevation communities. The mesic floodplain Stand (Δ) populations had a collective seasonal energy demand of 16.9 kcal m^{-2}, considerably greater than other stands supporting the same number of breeding species in more xeric locations.

The simulation model estimated energy demand on a daily basis, so we may examine the patterns of energy demand through the breeding season as well as the seasonal totals. There are well-defined peaks of community energy demand in all sites (Fig. 6). The patterns for Stands *1* and *2* were similar, with a single, rather broad peak in demand from 5 July–25 July. In Stands *3*, *13*, and *14* the patterns of variation in energy demand were similar in form although differing in magnitude, with one peak (ca. 1 July) coinciding with the production of nestlings by most species, the second (ca. 1 October) reflecting the effects of lower ambient temperatures in fall. Values of peak energy demands for the combined populations at each stand are given in Table 4.

The energy demands placed upon the system in each stand may be partitioned by employing some of the functions assumed in the model structure. Since we assume a digestive efficiency of 70%, then 30% of the total energy demand can be considered to be excretory (fecal) loss. Production involved energy allocated to biomass increase: in this case, production of eggs and the growth of nestlings and fledglings. Egg production costs are calculated directly in the model, while we assume that existence energy demands of nestlings are elevated by 20% to account for growth, those of fledglings by 5%. Combining these values, we can estimate the energy allocated to production in each stand. The energy remaining after production and excretory totals are subtracted from the estimated intake is used in self-maintenance or "respiration." Values for each of these flows for each stand are given in Table 4. In all stands the energy allocated directly to production was quite low, representing 0.9% to 1.1% of the total energy intake.

The energy allocation to production during the breeding season is of course one element of an overall energy commitment to reproduction (rather than self-maintenance) activities by the populations. The magnitude of energy allocation to reproduction is a central element of the reproductive "strategy" of a population (Gadgil and Solbrig 1972), but unfortunately few calculations of reproductive effort are available for bird populations. We can obtain a conservative estimate of the energy channeled into reproduction-related processes by combining the energy demands of nestlings and fledglings with the costs of egg production; such a calculation ignores the energy costs of reproductive behaviors by the adults. The average percentages of the total seasonal energy flow allocated to reproduction by the populations of each stand are listed in Table 4 and show little variation between stands. Overall, approximately 12% of the total energy intake was devoted to reproduction, as considered here.

Although this measure was relatively constant between stands, substantial variation existed in the energy allocation patterns of the different populations occupying a single stand. Winter Wrens and Steller's Jays, for example, apportioned a smaller percentage (roughly 12%) of their energy intake to reproductive functions than did any other species, while Hermit Warblers devoted on the average 30% of their total seasonal intake to reproduction. There was a consistent trend for the allocation percentage of a given species to increase from Stand *1* to Stand *14*. Thus Hermit Warblers in Stands *1*, *2*, and Δ channeled 27% of their energy intake into reproduction, in Stand *3* they used 31%, and in Stands *13* and *14* roughly 35%. In terms of the model,

TABLE 4. Magnitudes and patterns of energy flow through the breeding bird populations of the six coniferous forest stands, from model output

	Stand					
	1	2	Δ	3	13	14
Seasonal energy demand (kcal m^{-2})						
Egg production	0.01	0.01	0.02	0.02	0.01	0.01
Nestlings	0.27	0.23	0.35	0.43	0.27	0.21
Fledglings	1.10	1.10	1.66	2.03	1.23	1.02
Adults and juveniles	9.35	9.15	14.62	18.28	10.75	10.91
Total	10.73	10.49	16.65	20.76	12.26	12.15
Peak daily energy demand (kcal m^{-2} day^{-1})						
Amount	0.08	0.08	0.13	0.15	0.10	0.09
Dates	14 July	9–19 July	24–29 June	29 June–3 July	4–9 July	4 July
Seasonal energy allocation (kcal m^{-2})						
Production	0.11	0.10	0.19	0.23	0.14	0.12
Excretion	3.21	3.12	4.94	6.17	3.64	3.61
Respiration	7.49	7.28	11.54	14.39	8.49	8.43
Allocation to thermoregulation (kcal m^{-2})						
Amount	1.41	1.40	2.43	3.09	2.34	2.10
Percent of seasonal Σ	13.1	13.3	14.6	14.9	19.1	17.3
Percent of seasonal Σ allocated to reproduction						
Egg production	0.1	0.1	0.1	0.1	0.1	0.1
Nestlings	2.5	2.2	2.1	2.1	2.2	1.7
Fledglings	10.3	10.5	10.0	9.8	10.0	8.4
Total	12.9	12.8	12.2	12.0	12.3	10.2

this increasing energy allocation may represent a response to the lower ambient temperatures of the latter stands (Fig. 3).

The species also varied in the internal patterns of this energy allocation. Fledgling American Robins, for example, accounted for nearly three times the energy flow through nestlings, whereas Winter Wren fledglings required less than twice the energy used by nestlings. These differences were consistent between stands and were apparently associated with differences in nestling or fledgling mortality patterns or in growth rates between the species.

The breeding avifaunas of the stands also differed in the allocation of energy to thermoregulation (Table 4). Roughly 13%–19% of the total breeding season energy flow was required for thermoregulation, with the high proportions associated with the cooler, higher elevation Stands (13 and 14). Energy allocations to thermoregulation by individual species populations also followed this trend, but there were interspecific differences in thermoregulation costs in any one stand. In Stand 1, for example, 10% of the seasonal energy demand of Steller's Jays was devoted to thermoregulation, while Golden-crowned Kinglets channeled 14% of their seasonal energy demand into thermoregulation. In Stand 13, this value for kinglets was 20%, whereas Varied Thrushes

in that stand allocated only 16% of their seasonal energy flow to thermoregulation. These species differences are to a large degree associated with the higher relative thermoregulation costs at low temperatures for smaller sized species.

The estimations of population energy demands may also be useful as a measure of the importance or "dominance" of a species in a given segment of the vegetation-environment gradient represented by the six stands. Although relative density or relative biomass values have generally been used to measure ecological dominance (e.g., McNaughton and Wolf 1970), energy measures may also be appropriate, since they may relate more directly to ecosystem functioning. Relative values (percentages of community totals) for population density, standing crop biomass, and energy demand are given for several bird species in Fig. 7. In general, the three measures of dominance yield similar results. In some cases (Chestnut-backed Chickadee, Brown Creeper, Golden-crowned Kinglet), dominance measured by energy flow or density was considerably greater than biomass dominance, perhaps because all three species are quite small and thus have proportionately greater energy demands per gram body weight than have larger species (e.g., Oregon Junco, Western Tanager). However, Hermit Warblers, Western Flycatchers,
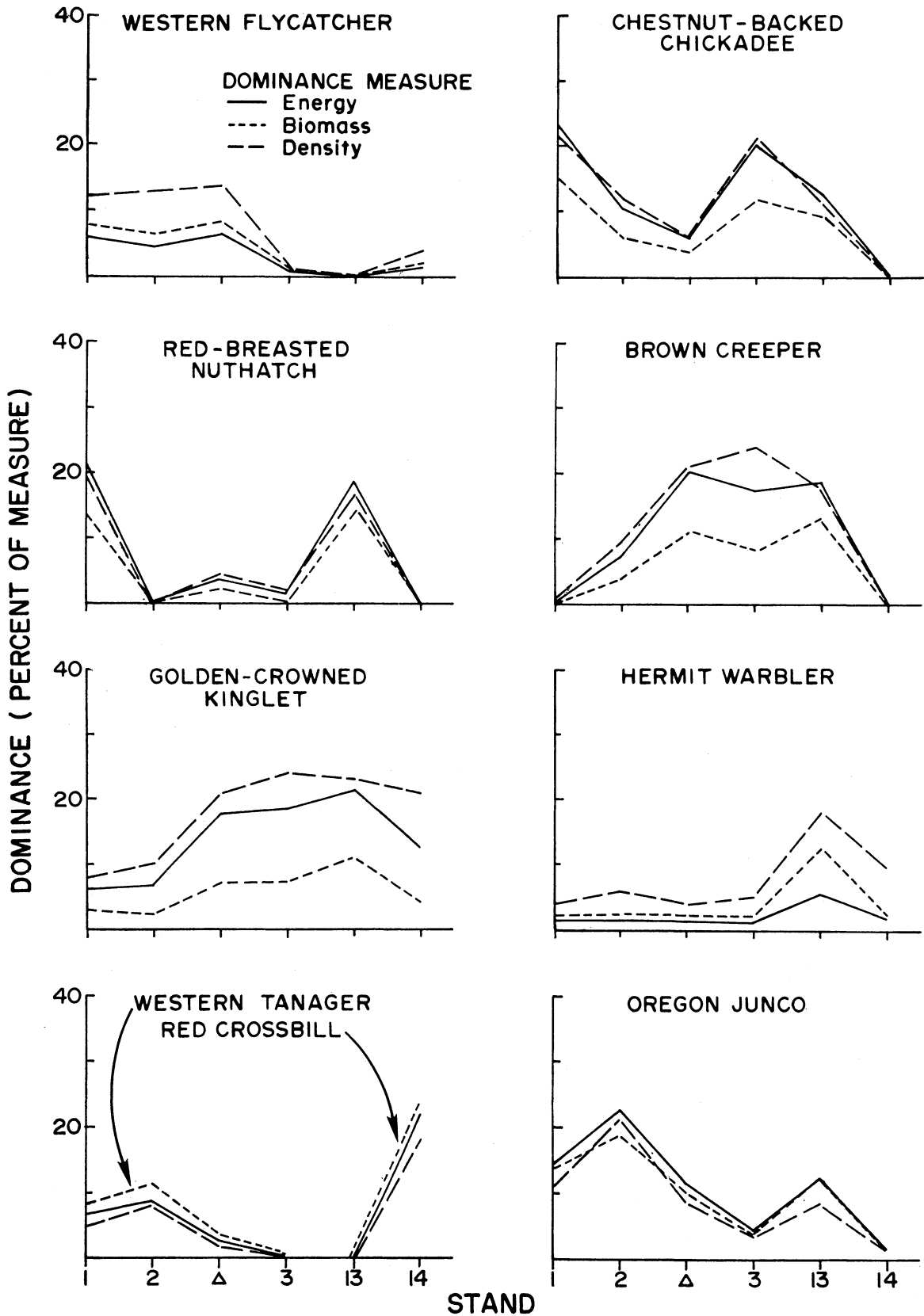
TABLE 5. Relative consumption (percent volume of gut contents) of animal and plant prey by coniferous forest species during the April–September breeding period. Asterisks used to indicate values estimated from sources

Species	Percentage of diet		Authority
	Animal	Plant	
Yellow-bellied Sapsucker	60	40	Bent 1939*, Martin et al. 1961*
Hairy Woodpecker	80	20	Martin et al. 1961
Hammond's Flycatcher	100	0	Martin et al. 1961
Western Flycatcher	100	0	Martin et al. 1961
Steller's Jay	40	60	Martin et al. 1961
Gray Jay	30	70	Martin et al. 1961*
Chestnut-backed Chickadee	97	3	Anderson 1970
Red-breasted Nuthatch	100	0	Anderson 1970
Brown Creeper	96	4	Anderson 1970
Winter Wren	95	5	Martin et al. 1961*
American Robin	30	70	Martin et al. 1961
Varied Thrush	10	90	Martin et al. 1961
Townsend's Solitaire	40	60	Martin et al. 1961*, Bent 1949*
Hermit Thrush	70	30	Martin et al. 1961
Swainson's Thrush	52	48	Bent 1949
Golden-crowned Kinglet	100	0	Martin et al. 1961*, Bent 1949*
Hermit Warbler	85	15	Martin et al. 1961*
Western Tanager	82	18	Bent 1958
Evening Grosbeak	75	25	Martin et al. 1961, Bent 1968
Pine Siskin	60	40	Martin et al. 1961
Red Crossbill	10	90	Martin et al. 1961
Oregon Junco	54	46	Anderson 1970

and Red-breasted Nuthatches are just as small, but exhibited a tendency for energy flow dominance to be the lowest of the three measures. The underlying reasons for these differences in species dominance patterns are unclear to us. In any event, no single species achieved a dominance value of 25% by any of the measures, which contrasts with the situation in simpler habitat types (Wiens 1973).

These analyses of energy flow patterns have been based upon species populations or total breeding avifaunas of stands. The patterns may also be viewed in terms of several ecological categorizations (species groups) to reveal elements of the structuring of the avian communities in the stands. One way of doing this is to categorize species by foraging station (air, foliage, timber, or ground) and general dietary habits (insect-feeding, ≥ 75% of diet animal prey; omnivore; or plant-eating, chiefly seeds or fruits, ≥ 75% of diet plant prey). Our categorizations were based upon those developed by Anderson (1970, 1972) and dietary information (Table 5); species categories are indicated in Table 2. Foliage-gleaning forms accounted for the greatest proportion of the energy intake at all stands except Stand 2 (Fig. 8), where ground-feeding forms consumed a slightly greater percentage of the total intake. Of the foliage-feeders, insectivorous species predomi-

nated at all stands except Stand 14. Plant-feeding species were restricted to the higher elevation Stands (3, 13, 14), accounting for the greatest proportion of the total energy flow in Stand 14. Conversely, air-feeding forms (flycatchers), although not a major element in the flow pathways of any stands, were virtually absent from the higher elevation stands. Ground-feeding species generally decreased in the proportion of the total community intake from Stands 2 to 14, with omnivorous forms making up the greatest share of this category in all stands except Δ, where omnivorous and insectivorous forms accounted for an equal proportion of the energy flow. Timber-associated species were relatively uniform in their overall proportion of the energy intake; drilling species (woodpeckers) were conspicuous elements of this group only in Stands 2 and 14.

Species may also be categorized according to their length of tenure in the stands, as seasonal (migratory) or permanent residents (Table 2). The proportion of the breeding species that were only seasonal occupants of the stands varied between 33% and 46% in all stands except Stand 14, in which only 14% of the species were seasonal. The proportion of the total community energy intake consumed by seasonal residents, on the other hand, decreased steadily from the drier, low-elevation stands to the more mesic

←

FIG. 7. Community dominance by several of the breeding bird species in the six coniferous forest stands, as measured by the proportions of total avian density (individuals), biomass, and breeding season energy flow for each stand.
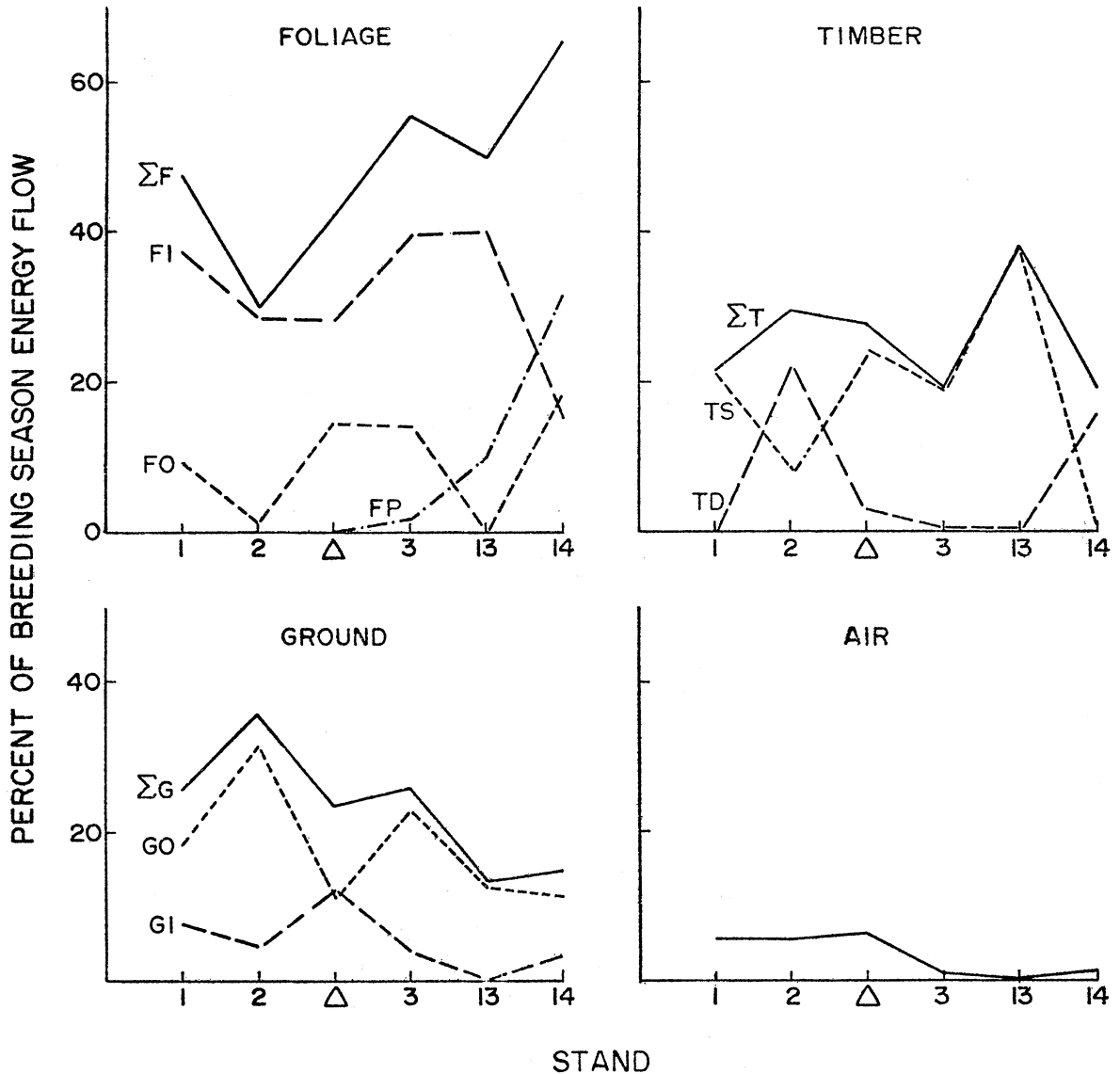
FIG. 8. Partitioning of the total avian breeding season energy flow in the coniferous forest stands among various ecologically defined segments of the avifauna. FP = foliage plant (seed) feeders, FO = foliage-feeding omnivores, FI = insectivorous foliage-feeders, TD = timber drillers, TS = timber searchers, GI = ground-feeding insectivores, GO = ground-feeding omnivores. Species assignments to these categories are given in Table 2.

and higher elevation stands (Fig. 9). The stand sequence reflects a shortening of the growing season, later persistence of low temperatures (and attendant retardation of insect emergence), and generally more severe environmental conditions persisting later into the breeding season. Under such conditions, the seasonal "flush" in insect abundance which is generally exploited by migratory species may become increasingly constrained in time, favoring the more flexible resident species. In the dry, highest elevation Stand (14), however, seasonal residents accounted for a greater proportion of the total energy

flow than in any other stands (Fig. 9). This was accompanied by a change from dominance by insectivorous forms to seed- and fruit-eating species among the foliage-feeding group (Fig. 8). These patterns suggest the possibility that as environmental conditions (especially insect prey availability) during the early portion of the breeding season worsen with increasing elevation and/or dryness, a point is reached at which even the resident species find it difficult to exploit the system, and highly opportunistic plant-feeders may be able to utilize the resources more effectively. Evening Grosbeaks and
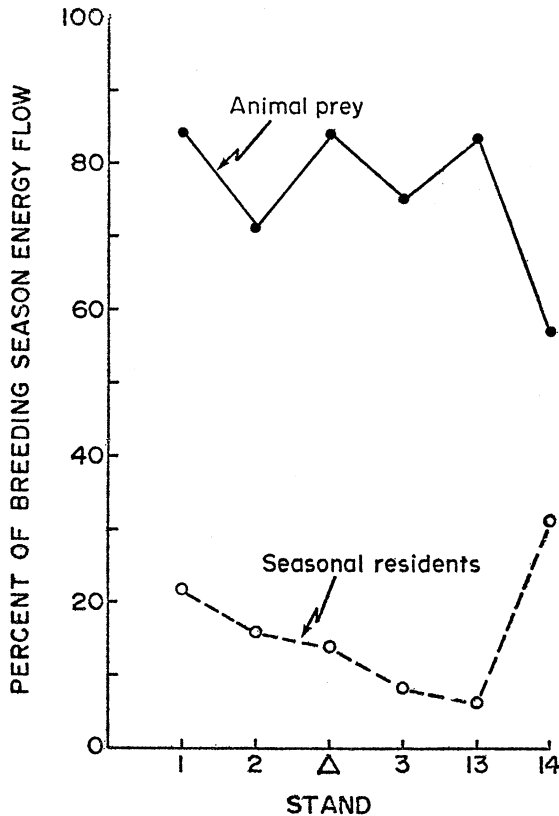
FIG. 9. Partitioning of total avian community breeding season energy flow in the six coniferous forest stands according to energy source (animal vs. plant prey) and residency of the bird populations (seasonal or migratory vs. permanent residents).

TABLE 6. Energy flow (kcal m^{-2} season^{-1}) from animal and plant (seed) resource pools into permanent and seasonal (migratory) resident bird populations in the six coniferous forest stands

Stand	Residency[a]		Energy source (percentages in parentheses)	
			Animal	Plant
1	P		7.21 (86)	1.19 (14)
	S		1.78 (76)	0.56 (24)
		Σ	8.99 (84)	1.75 (16)
2	P		6.02 (68)	2.82 (32)
	S		1.46 (88)	0.19 (12)
		Σ	7.48 (71)	3.01 (29)
Δ	P		12.00 (84)	2.37 (16)
	S		1.91 (84)	0.36 (16)
		Σ	13.91 (84)	2.73 (16)
3	P		14.44 (76)	4.59 (24)
	S		1.15 (66)	0.58 (34)
		Σ	15.59 (75)	5.17 (25)
13	P		9.63 (83)	1.95 (17)
	S		0.58 (85)	0.10 (15)
		Σ	10.21 (83)	2.05 (17)
14	P		4.32 (51)	4.10 (49)
	S		2.65 (71)	1.08 (29)
		Σ	6.97 (57)	5.18 (43)

[a] P = permanent, S = seasonal.

Red Crossbills, two seed-eating species known for their "irruptive" and opportunistic population movements, together accounted for 40% of the energy flow in Stand *14*. Such species were generally absent from the other stands.

All of these patterns relate to how energy demands are partitioned in various ways within the bird communities. From a systems point of view, it is more important to determine how these demands are partitioned among the resource units (prey) that must satisfy the demands. The details of this partitioning process rest upon the patterns of prey selection exercised by the species in relation to prey abundance and availability, but such information is available for very few species, much less entire breeding communities. We may obtain a very general view of the sources of the energy consumed by the bird populations by considering the composition of the diet in terms of either animal or plant prey (Table 5). These values provide only coarse approximations of the actual dietary composition of the birds occupying the stands. Avian diets usually exhibit consider-

able variation through a season and between localities, and the values presented here are averages for a 6-mo breeding period. In addition, while the values reported by Anderson (1970) were obtained in western Oregon coniferous forest stands, the other values were gathered from a broad variety of habitat types from many sections of the United States. Until more precise and accurate information is available, however, these estimates of dietary composition may be used to generate rough estimations of the magnitudes of energy flow from each of these food compartments into the bird populations of the stands. These values for permanent and seasonal residents of the stands are given in Table 6, while the overall pattern of energy extraction from plant and animal resource pools is shown in Fig. 9. The total amount of energy extracted from each of these compartments during the breeding season varied between stands, largely as a function of the differences in total energy intake (Table 4). There was, however, a general consistency in the percentage of the total seasonal energy intake in each stand which was derived from plant or animal sources, varying from 71% to 84% animal prey sources among all stands except Stand *14*. Here less than 60% of the energy was drawn from animal sources, again emphasizing the switch to seed- and fruit-eating habits already noted. Further, while seasonal residents in this stand obtained a greater proportion of their energy intake from plant sources than in any other stand except Stand *3*, permanent residents exhibited an even greater reliance upon plant prey, deriving almost half of their energy intake from seeds or fruits (Table 6).

CONCLUDING COMMENTS

Our application of simulation modeling analysis to these coniferous forest census data has revealed several distinctive patterns of energy flow and allocation among the breeding bird populations. Such energetic patterns have generally been ignored in considerations of avian community structure or organization and may add an important additional dimension. Within an ecosystem framework, however, it is of concern to establish the role, impact, or "importance" of the bird populations in system dynamics. The first step in assessing potential impact is to determine the relations between consumption of prey and prey availability or abundance. As noted, our categorization of prey types into animal and plant prey is coarse, but we can use the model estimations of energy flow from these categories to obtain general approximations of the biomass of material extracted from these compartments. Given caloric values of 2.32 kcal/g wet wt for invertebrate prey and 2.40 kcal/g wet wt for plant (conifer seed) prey (assuming wet wt = 0.4 dry wt) (Cummins and Wuycheck 1971), we can calculate the total biomass of these food types consumed during the breeding season from the total stand energy flow estimates given in Table 6. For invertebrate prey, the estimated consumption ranged from 3.1 (Stand 14) to 6.9 (Stand 3) g m^{-2} season^{-1}, and seed consumption varied from 0.7 (Stand 1) to 2.2 (Stands 3 and 14) g m^{-2} season^{-1}. Unfortunately, the coniferous forest ecosystem studies conducted to date have given little attention to documenting standing stocks of invertebrates or seeds. We thus lack quantitative information on food resource states against which these consumption rates may be compared to determine their potential significance in ecosystem dynamics.

We may, however, draw some comparisons between the magnitudes of total energy flow in these stands and those reported for some other biome types. Holmes and Sturges (1973) used a generally similar but less detailed approach than that used here in their analysis of the energy requirements of the avifauna of a Northeastern hardwood forest (Hubbard Brook). Correcting their estimate of metabolic demand for the period 1 April–7 October for activity and digestive efficiency, we obtain an estimate of 5.9 kcal m^{-2} for the roughly 25 breeding species (peak densities of 3,090–3,400 individuals km^{-2}, standing crop biomass of 640–667 g ha^{-1}). This estimate seems quite low. The correction factor of 2.5 applied to standard (not existence) metabolism by Holmes and Sturges to account for activity is probably slightly less than our overall adjustment of existence metabolism. The approach used by Holmes and Sturges, however, does not include the

production of offspring, and ignores the effects of ambient temperature, which in our model structure significantly affects estimates of energy requirements (Wiens and Innis, 1974). Such effects are especially pronounced at relatively low temperatures, such as characterized the coniferous stands for much of the season (Fig. 3).

Other estimates of avian community energy demands have been made by Karr (1971) for a variety of habitat types in Illinois and Panama. Karr simply estimated existence energy demands, using Kendeigh's (1970) equations and the mean ambient temperature for the 15 April–15 July period in central Illinois and Panama, so again direct comparisons with his values are difficult. If we expand his estimates to cover the 190-day period covered in our study and adjust existence metabolism for activity and digestive efficiency as is done in the simulation model, we can obtain seasonal values which probably represent slight overestimates of adult energy demands, but which also ignore the demands of the offspring produced. For the Illinois habitats, these estimates range from 1.1 kcal m^{-2} in a "bare ground" habitat to 16.0 kcal m^{-2} in a bottomland forest; the Panama estimates range from 1.4 kcal m^{-2} (dry, ungrazed grassland) to 16.5 kcal m^{-2} (moist forest). Our estimates for total seasonal energy flow for the coniferous stands thus approximate those for shrub or forest communities in the Midwest and in the tropics, despite the substantially smaller number of breeding species.

LITERATURE CITED

Anderson, S. H. 1970. Ecological relationships of birds in forests of western Oregon. Ph.D. Diss. Oregon State Univ., Corvallis. 124 p.

———. 1972. Seasonal variation in forest birds of western Oregon. Northwest Sci. **46**:194–206.

Baldwin, P. H. 1968. Woodpecker feeding on Engelmann spruce beetles in windthrown trees. U.S. For. Serv., Rocky Mt. For. Range Exp. Stn. Res. Note 105. 4 p.

Bent, A. C. 1939. Life histories of North American woodpeckers. U.S. Natl. Mus. Bull. 174. Washington, D.C. 334 p.

———. 1949. Life histories of North American thrushes, kinglets and their allies. U.S. Natl. Mus. Bull. 196. Washington, D.C. 454 p.

———. 1958. Life histories of North American blackbirds, orioles, tanagers, and their allies. U.S. Natl. Mus. Bull. 211. Washington, D.C.

———. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237, Part 1. 634 p.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Int. Ver. Theor. Angew. Limnol. No. 18. 158 p.

Dyrness, C. T., J. F. Franklin, and W. H. Moir. 1974. A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. Coniferous For. Biome Bull. No. 4, Seattle, Wash.

Emlen, J. T. 1971. Population densities of birds derived from transect counts. Auk **88**:323–342.

Franklin, J. F., F. C. Hall, C. T. Dyrness, and C. Maser. 1972. Federal research natural areas in Oregon and Washington: A guidebook for scientists and educators. USDA Forest Service, Pacific Northwest Forest Range Exp. Stn., Portland, Ore. 498 p.

Gadgil, M., and O. T. Solbrig. 1972. The concept of r- and K-selection: Evidence from wild flowers and some theoretical considerations. Am. Nat. **106**:14–31.

Hawk, G. M. 1972. Forest vegetation and soils of terraces and floodplains along the McKenzie River, Oregon. M.S. Thesis. Oregon State Univ., Corvallis.

Hawk, G. M., and D. B. Zobel. 1974. Forest succession on alluvial landforms of the McKenzie River valley, Oregon. Northwest Sci. **48**:245–265.

Holmes, R. T., and F. W. Sturges. 1973. Annual energy expenditure by the avifauna of a northern hardwoods ecosystem. Oikos **24**:24–29.

Karr, J. R. 1971. Structure of avian communities in selected Panama and Illinois habitats. Ecol. Monogr. **41**:207–233.

Kendeigh, S. C. 1970. Energy requirements for existence in relation to size of bird. Condor **72**:60–65.

Koplin, J. R. 1969. The numerical response of woodpeckers to insect prey in a subalpine forest in Colorado. Condor **71**:436–438.

Koplin, J. R., and P. H. Baldwin. 1970. Woodpecker predation on an endemic population of Engelmann spruce beetles. Am. Midl. Nat. **83**:510–515.

Martin, A. C., H. S. Zim, and A. L. Nelson. 1961. American wildlife and plants: A guide to wildlife food habits. Dover Publications, Inc., New York. 500 p.

McNaughton, S. J., and L. L. Wolf. 1970. Dominance and the niche in ecological systems. Science **167**:131–139.

Udvardy, M. D. F. 1963. Bird faunas of North America, p. 1147–1167. In XIII Int. Ornithol. Congr., Proc. Ithaca, N.Y.

Wiens, J. A. 1973. Pattern and process in grassland bird communities. Ecol. Monogr. **43**:237–270.

———. 1974. Habitat heterogeneity and avian community structure in North American grasslands. Am. Midl. Nat. **91**:195–213.

Wiens, J. A., and G. S. Innis. 1974. Estimation of energy flow in bird communities: A population bioenergetics model. Ecology **55**:730–746.

Wiens, J. A., and J. M. Scott. (in press). Model estimation of energy flow in Oregon coastal seabrid populations. Condor.