

BIRD COMMUNITIES ALONG A MONTANE SERE: COMMUNITY STRUCTURE AND ENERGETICS

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ABSTRACT.—We examined 11 of 24 ecosystem attributes that Odum (1969) proposed would change during succession in avian communities in meadow, aspen, fir, and spruce forests in northern Utah and southern Idaho. A total of 71 bird species was observed during the 30-month study, of which 43 were known to breed.

Yearly energetic relationships were calculated for the breeding bird populations using an avian community energetics model. In the different avian communities, the ratios of annual secondary production/community respiration, secondary production/biomass present, and secondary production/consumption all tended to decrease with increasing plant succession; biomass present/"unit energy flow" tended to increase. All of these trends are consistent with those postulated by Odum for the entire ecosystem. These energetics ratios differed in 1977 from those in 1976 and 1978 due to a severe drought. They also fluctuated greatly during the course of a year.

Avian species diversity was highest in the preclimax fir forest during the breeding season and fluctuated widely in the nonbreeding season. Species equitability tended to be relatively high in all avian communities, although it was slightly lower during the nonbreeding season. No trends were found in male body sizes, mean clutch size, and mean length of incubation period (a crude measure of parental investment). Thus, for the bird communities, we reject the postulated trends of increased species diversity, equitability, and organism size in the climax, quantity to quality production, and r- to K-selection. During the drought of 1977 the spruce avifauna appeared more stable, so we cannot reject Odum's hypothesized trend of increased stability in the climax.

We conclude that the vegetational characteristics of a given sere will in most cases determine the avian population response along that sere; this in turn will influence the correspondence of the avian communities to Odum's postulates. Incorporating these avian results with other studies within our subalpine sere, some of Odum's hypothesized trends are supported while others are not, suggesting that successional relationships are more complicated than would follow from Odum's relatively simple model. *Received 20 February 1980, accepted 9 June 1980.*

ODUM (1969: Table 1) proposed trends in 24 ecosystem attributes that change as succession proceeds from early (pioneer) to late (mature or climax) stages. He divided these ecosystem attributes into six groups: community energetics, community structure, life history, nutrient cycling, selection pressure, and overall homeostasis. The trends Odum proposed were based on the following premises concerning succession: "i) It is an orderly process of community development that is reasonably directional and, therefore, predictable; ii) It results from the modification of the physical environment by the community . . . ; iii) It culminates in a stabilized ecosystem in which maximum biomass (or high information content) and symbiotic function between organisms are maintained per unit available energy flow" (Odum 1969: 262; see also Odum 1971: 251–267). This viewpoint has been widely criticized (see review in Connell and Slatyer 1977). Connell and Slatyer stated that Odum's scheme is based on analogy, not evidence, and Engleberg and Boyarsky (1979) argued that even the analogy is a poor one. Few studies have attempted to test the proposed attributes simultaneously on an ecosystem-wide basis.

During 1975–1978 a study was undertaken to test empirically as many of Odum's 24 attributes as possible in a relatively simple subalpine sere. Data were collected on as many aspects of the plant and animal communities that were related to Odum's

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TABLE 1. Eleven attributes proposed by Odum (1969) that were tested by examining the spruce-fir avifauna along a subalpine sere.

Ecosystem attribute	Predicted trend (Odum 1969)
Community energetics	
Production/respiration	Approaches 1
Production/biomass	High to low
Biomass/unit energy flow	Low to high
Net community production	High to low
Community structure	
Total organic matter	Low to high
Species diversity—variety	Low to high
Species diversity—equitability	Low to high
Life history	
Size of organism	Small to large
Selection pressure	
Growth form	r- to K-selection
Production	Quantity to quality
Overall homeostasis	
Stability	Poor to good

postulates as possible. Preliminary results encompassing both plants and animals (including invertebrates) have been reported in MacMahon (1980), and a detailed study of the herbivorous mammals along the sere is reported by Andersen et al. (1980). Here we report a portion of the results concerning the subalpine avifauna (see also MacMahon 1980; Smith 1980, 1981). Historically, successional theory has focused on botanical characteristics of seres (see review in MacMahon 1980), and, although many studies have been conducted on avian communities in successional stages, few of these have addressed aspects other than species diversity and biomass. By incorporating results from 3 yr of field work with published values on avian life history characteristics, we are able to address 11 of the 24 proposed ecosystem trends (Table 1). Of the remaining 13 trends, some cannot be tested adequately by studying the avian community alone (e.g. food-web structure), some do not apply to the bird community (e.g. mineral cycles, role of detritus), and others are so nebulous that they may be inherently untestable (e.g. internal symbiosis, entropy, information).

METHODS

Study area.—The study was conducted in the Bear River Mountains of northern Utah and southern Idaho. The subalpine region is generally characterized by disturbance-created meadows initiating a four-stage successional sequence leading through stands dominated by aspen (*Populus tremuloides*) to subalpine fir (*Abies lasiocarpa*) forests and climaxing in Engelmann spruce (*Picea engelmannii*) or spruce-fir dominated forests. A detailed description of the successional pathways in this region of the Rocky Mountains can be found in Schimpf et al. (1980).

Study sites that maximized the vegetative distinctiveness of each seral stage were chosen. The meadow, aspen, and fir plots were within 1 km of each other in Franklin Basin (elevation = 2,550 m), Franklin County, Idaho (42°02'N, 111°38'W). The spruce plot was located 20 km to the south in the Utah State University School Forest (2,600 m), Cache-Rich Counties, Utah (41°52'N, 111°30'W). The meadow plot contained primarily grasses and forbs with a few isolated sagebrush (*Artemisia tridentata*) less than 0.5 m tall. The entire meadow was about 2 km² and contained some permanently flowing water. The aspen stand was composed almost entirely of aspen trees, with fewer than 20 fir trees and no spruce. During the summer the lush forbs and shrub understory grew to a height greater than 1 m. While the fir plot was dominated by fir, it also contained aspen, spruce, and an occasional Douglas fir (*Pseudotsuga menziesii*). The relatively sparse ground cover consisted mostly of grasses and forbs, reaching a height of less than 0.5 m. The spruce plot contained large, old (>300 yr) spruce trees with numerous firs and

only an occasional aspen. Little or no understory existed on this plot, but there were considerable numbers of dead and fallen trees. A more complete analysis of the vegetative characteristics of each plot is presented in Smith (1981) and the climatic, edaphic, and biotic aspects of the sere are summarized in Schimpf et al. (1980).

The years 1976 and 1978 were similar climatically; one of the worst droughts of this century occurred in 1977 (Richardson 1977). For example, snow pack in a meadow near the spruce plot was comparable between 1976 and 1978, but the ground was bare in April 1977 when more than 200 cm would have been expected. This drought had profound effects on the avian community (K. Smith MS) and provided a natural experiment that we used to make inferences about the stability of the ecosystem.

Field studies.—In early June 1976, four 10-ha study plots were established, one in each seral stage. Numbered and lettered wooden stakes (0.4 m) were placed within each plot in a grid system with a 50-m spacing. These plots were censused from June 1976 through December 1978, with some casual observations made between January 1976 and the start of censusing. A modified Williams spot-map technique was used during the breeding season (June–August) whereby the plots were censused by walking along the grid in a randomly determined direction from a randomly determined starting point and by stopping for 5 min at every other stake (100 m). All birds seen or heard during the course of the census within 25 m of the observer (always KGS) were recorded on a scale map of the plots. The international censusing guidelines (International Bird Census Committee 1970) were followed as closely as possible. Usually censuses were begun 0.5 h before sunrise and lasted 3.5 h; afternoon and evening censuses also were conducted during the breeding season. Approximately 10 censuses/plot were made during each breeding season.

During the nonbreeding season (September–May), the censuses consisted of approximately 2-h trips (usually on skis or snowshoes) around the plots in either late morning or early afternoon. Although few species are present in the winter, this technique was effective in determining the density of the species present, because the birds tended to be conspicuous and localized. The plots were censused in every month possible (~25 of 30 months). During some months, the plots were inaccessible due to weather, road conditions, and snowmobile failure.

The census results were supplemented during the summers of 1976 and 1977 by mist-netting birds in the three forested plots. Weights of most species were obtained in this manner. Census results were further supplemented with observations made while engaged in other research on the avian communities during which more than 100 h were spent on each forested plot during the three summers. Some supplemental observations also were made during the winter. By supplementing the census results, we hoped to reduce any bias due to employing different census methods and intraseasonal differences in bird detectability (e.g. Järvinen et al. 1977). A total of 71 species was observed on the plots over the course of the study, of which 43 were known to breed (see Appendix).

Data analysis.—The avian community energetics model (BIRD II) developed by Innis and Wiens (1977) was used to calculate various energetic relationships within each seral community. An earlier version of the model (Wiens and Innis 1974) has been used to determine avian community energetic relationships in northwestern coniferous forests (Wiens and Nussbaum 1975), coastal seabird communities (Wiens and Scott 1975), and the grasslands of North America (Wiens 1977). The model requires approximately 30 input variables and parameters, some based on field data (e.g. population sizes, times of arrival, times of departure) and others that were gleaned from the literature (primarily from the Bent Life History series) (e.g. average clutch size, number of clutches, length of incubation). A complete list of input values is available upon request. Details of the assumptions, structure, and input/output values used in the model are discussed fully in Wiens and Innis (1974) and will not be dealt with here (see also Wiens and Nussbaum 1975, Wiens 1977), except for the estimation of consumption.

One important change between the two BIRD models is the manner in which the estimate of consumption is obtained. In the earlier model, a weight of 0.40 existence energy was added to the estimate of existence energy to account for consumption due to various activities (Wiens and Innis 1974). In the model we used, the weight factor is variable and distributed according to a sine function (see Innis and Wiens 1977 for details). We used a minimum weight of 0.10 and a maximum weight of 0.25 existence energy, values used in Innis and Wiens (1977). We feel that this addition to our estimate of existence energy to account for activities is important, but it is impossible to assess the biological reality of our choice of weighting factors.

Two changes were made in BIRD II at the suggestion of Wiens (pers. comm.). The cost associated with molting was deleted from the model, because it is unclear what, if any, are the costs of molting (e.g. see Dolnik and Gavrilov 1979). Second, the equations that are used for estimating the energy demands were replaced by a set of equations (Kendeigh et al. 1977) that integrate photoperiod, ambient temperature, and body weight. From these equations, the energy requirements for passerines and non-

passerines were calculated at 0°C and 30°C for 10-h and 15-h days. Linear interpolation was then used to obtain the energy demand for the proper combination of temperature and day length. This procedure is documented in Innis and Wiens (1977), but the equations reported therein are incorrect. Weekly average temperatures (1976–1978) calculated from data obtained in a meadow near the spruce plot by a continuously recording hygrothermograph and maximum deviation from 12–12 h photoperiod at the study area latitude were entered as input variables for use in these energy demand equations.

A total of 43 species was included in the avian community energetics model (Appendix). An additional 28 species, each observed less than 5 times during the 3 yr of observation, were not included in this analysis. Because the model requires density expressed as individuals/km², census results on the 10-ha plots were multiplied by 10 for hummingbirds, woodpeckers, and passerines, which is justified because the plots were chosen to maximize the distinctiveness of the different seres. Numbers of raptors, owls, and grouse were estimated with consideration for territory size and population densities in general in northern Utah (pers. obs.). Few community energetics studies (e.g. Alatalo 1978) have included this nonpasserine component of the avifauna; we have included it in our analysis, because these species may be important in terms of avian community energetics.

Calculations of biomass, production, consumption, and respiration were made at 1-day intervals for each seral stage in each year. Production, of course, refers to secondary production, in this case the cost associated with egg production and the growth of nestlings and fledglings. Fledglings are defined as young birds that are out of the nest but still in the care of the parents; juveniles are self-sufficient. Within the constraints of the model, no production occurs outside of the breeding season within the adult component. Although this may not be realistic (e.g. fat deposition), it probably has little effect on the estimation of production.

Species diversity (H') and equitability (J') were calculated for each month based on census data collected from June 1976 through October 1978. All species observed during censusing were used in this analysis. Simpson's index, Hurlbert's index, and species diversity calculated as H all gave similar conclusions as those obtained with H' [see Peet (1974) for equations and discussion of indices]. Similarity of avifaunas between seral stages was calculated for each year, using Jaccard Analysis (MacMahon and Trigg 1972):

$$\text{Similarity} = \frac{2w}{a + b} \times 100,$$

where w is the number of species that the two seral stages share in common, and $a + b$ is the total number of species observed in both seral stages.

Total biomass and size of organisms were estimated based on the bird weight data obtained from mist-netting. In a few cases, weights of the rarer species, e.g. raptors, were obtained from the literature. Unless otherwise noted, average weights were calculated disregarding sex and the seral stage in which the birds were captured. Growth form and production quality were analyzed based on natural history data obtained from the literature.

RESULTS

Community energetics.—Results of the avian community energetics model estimations are summarized in Table 2. Annual consumption was very low in the meadow, because only three species bred there. In the predrought year of 1976, consumption by the aspen bird community was 78 and 97% of the fir and spruce communities, respectively. The drought of 1977 affected the aspen birds to a greater degree than it did the other two forested plots (see below): consumption by the aspen birds was reduced to about 30% in 1977 and about 40% in 1978 of both the fir and spruce communities. In the fir avian community, consumption was consistently higher than in the spruce for all 3 yr (24, 9, and 2%, respectively).

Respiration accounted for the greatest proportion of consumption, with more energy lost through excretion than was spent in production (Table 2). Note that production in the aspen was slightly less than that in the fir and greater than that in the spruce bird community in 1976, but much less than production in the other two in 1977 and 1978. Production was highest in the fir stage in 2 of the 3 yr. The

TABLE 2. Summary of distribution and allocations of avian community energetics for each seral stage for 1976 through 1978 generated by the bird community energetics model.

	Meadow			Aspen			Fir			Spruce		
	1976	1977	1978	1976	1977	1978	1976	1977	1978	1976	1977	1978
Minimal consumption (kcal/m ²)												
Eggs	<0.01	<0.01	<0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Nestlings	0.04	0.03	0.03	0.12	0.29	0.23	0.40	0.25	0.41	0.37	0.32	0.35
Fledglings	0.16	0.14	0.11	1.37	0.54	1.00	1.18	0.76	1.94	0.72	0.66	1.65
Adults-juveniles	0.40	0.32	0.27	5.22	1.33	2.31	7.25	5.50	6.30	6.02	4.99	6.53
Annual total	0.61	0.50	0.42	6.89	2.00	3.55	8.84	6.52	8.66	7.12	5.97	8.53
Annual allocation of consumption (kcal/m ²)												
Production	0.03	0.02	0.02	0.14	0.06	0.11	0.15	0.10	0.17	0.12	0.11	0.16
Excretion	0.18	0.15	0.12	2.07	0.60	1.06	2.65	1.96	2.60	2.13	1.79	2.56
Respiration	0.41	0.33	0.28	4.70	1.35	2.39	6.05	4.47	5.90	4.87	4.09	5.82
Percentage of consumption allocated to reproduction												
Eggs	0.33	0.41	0.24	0.18	0.25	0.28	0.16	0.14	0.14	0.13	0.13	0.11
Nestlings	6.28	6.40	6.32	4.24	6.06	6.43	4.50	3.89	4.44	5.19	5.28	4.06
Fledglings	26.60	27.89	27.49	19.93	26.90	28.19	13.30	11.67	22.40	10.08	10.98	19.35
Annual percentage allocated	33.21	34.70	34.05	24.35	33.21	34.90	17.96	15.70	26.98	15.40	16.39	23.52
Annual biomass present (g/m ²)												
Nestlings	<0.01	<0.01	<0.01	0.06	0.02	0.04	0.09	0.04	0.09	0.07	0.06	0.08
Fledglings	0.02	0.02	0.02	0.28	0.08	0.23	0.33	0.22	0.35	0.21	0.13	0.21
Adults-juveniles	0.26	0.21	0.18	5.75	0.90	2.75	10.00	5.72	7.80	7.22	3.47	7.57

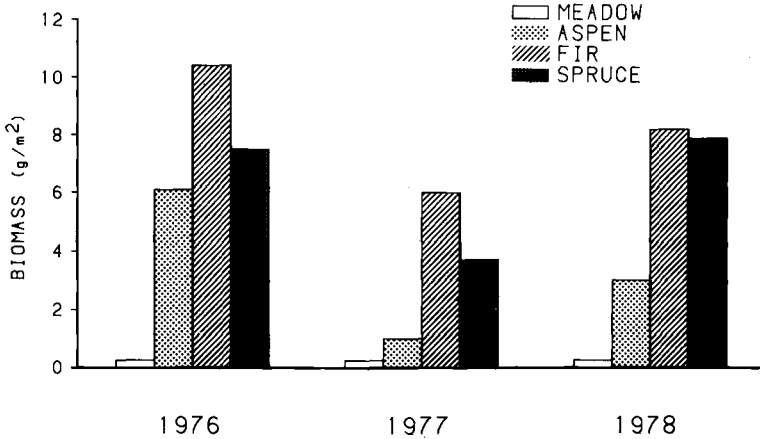


Fig. 1. Annual avian biomass present during 1976, 1977, and 1978 in four seral stages.

percentage of total annual consumption allocated to reproduction decreased along the sere, i.e. higher in the meadow and aspen and lower in the fir and spruce. Less than 0.5% of the total annual consumption was allocated to egg production, and about 5–6% was allocated to the nestlings. As expected, adults and juveniles accounted for most of the biomass present on the plots, with nestlings and fledglings contributing less than 5% of the total avian biomass present on the forested plots. The fir plots consistently supported more avian biomass (Fig. 1) than the climax spruce forest in all 3 yr (39, 63, and 5%). If we equate biomass present to total organic matter, the hypothesis that the climax forest supports the highest avian biomass does not appear to be correct.

Using data from Table 2, it is possible to examine the trends in community energetics listed in Table 1. Total annual secondary production/respiration (P/R) generally decreased from meadow to spruce in all 3 yr (Fig. 2A), as did total annual secondary production/annual biomass present (P/B) (Fig. 2B). Total annual biomass present/“unit energy flow” (= production + respiration, Odum 1969) (B/E) tended

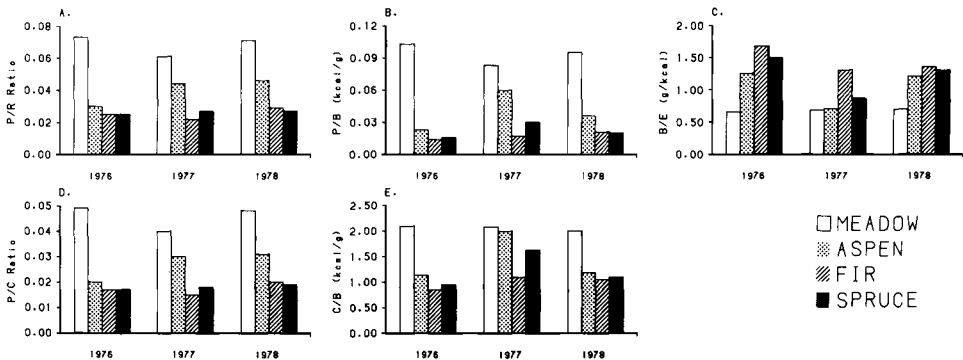


Fig. 2. Annual avian energetics relationships during 1976, 1977, and 1978 in four seral stages. A. Avian secondary production/avian community respiration; B. Avian secondary production/avian biomass present; C. Avian biomass present/unit energy flow; D. Avian secondary production/avian community consumption; E. Avian community consumption/avian biomass present.

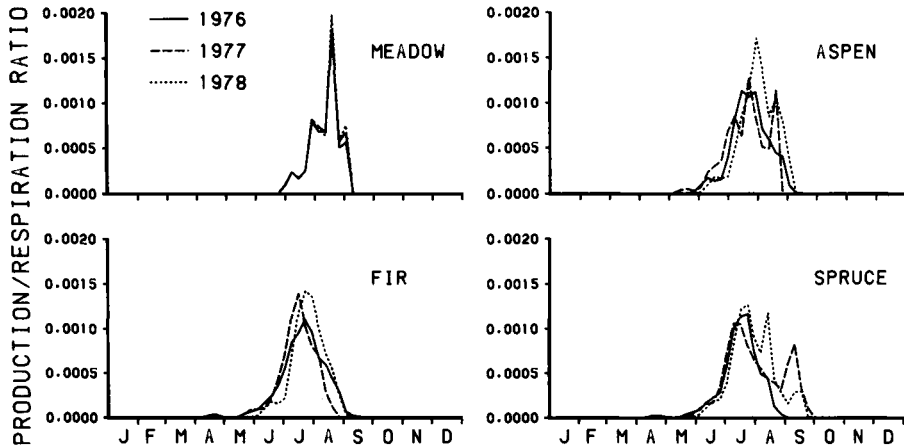


Fig. 3. Daily avian secondary production/avian community respiration during 1976, 1977, and 1978 in four seral stages.

to increase through the course of succession (Fig. 2C). All three of these trends generally are in accordance with those suggested by Odum (1969).

Another proposed trend was a decrease in net community production with successional development. It has already been shown that total secondary production did not follow this trend (Table 2), being low in the meadow and high in the spruce forest. This is merely a function of the increasing number of species and individuals. The percent of annual consumption allocated to production was greatest in the meadow and aspen (Table 2), which is in accordance with the hypothesized trend. Because Odum was more interested in net primary production, total annual secondary production/consumption (P/C) would seem to be the measure of net secondary production. The trend in this ratio is in agreement with that postulated (Fig. 2D). [Note the similarity between P/B and P/C (Fig. 2B and 2D).]

Salt (1957) argued that the climax should support more biomass on a given energy budget than could earlier seral stages and proposed using consuming biomass/standing crop biomass to examine this phenomenon. We have chosen to examine the ratio of annual consumption/biomass present (C/B), which should decrease with succession. This trend is generally supported (Fig. 2E). This relationship is the inverse of B/E (Fig. 2C).

Because more than 70% of the breeding species are migratory (see Appendix) and the number of species encountered on the study plot outside of the breeding season is quite low, an analysis of the above ratios on a daily basis is informative, as the values for most ratios fluctuate widely over the course of the year. Daily P/R (Fig. 3) peaked sharply in the early successional stages and tended to be relatively more spread out in the later seral stages. Within the constraints of the model, this ratio is zero outside of the breeding season. The second peak evident in some seral stages is due to production associated with second clutches. The spruce P/R distribution was significantly different from the aspen (Kolmogorov-Smirnov test, $P < 0.05$) and the fir ($P < 0.01$) only in 1977, and the meadow distribution was significantly different from all other stages in all years ($P < 0.01$) for this and all other daily energetics relationships (Figs. 3–6).

Daily P/B (Fig. 4) also peaked sharply in the meadow stage; other stages were

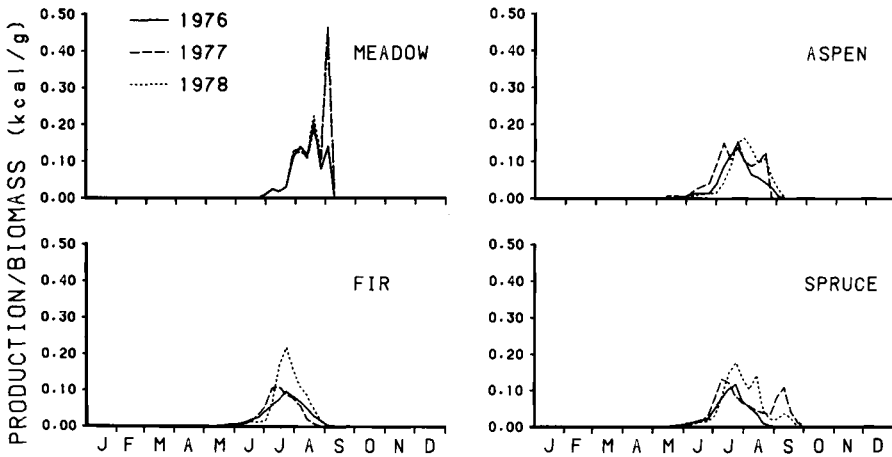


Fig. 4. Daily avian secondary production/avian biomass present during 1976, 1977, and 1978 in four seral stages.

fairly similar. Daily P/C showed the same pattern. The spruce P/B and P/C distributions were significantly different from the aspen and the fir ($P < 0.05$ for both) in 1977. Daily B/E (Fig. 5) was high during the nonbreeding season (provided that birds were present) and generally low during the breeding season. Daily C/B had the opposite trend, i.e. was higher in the breeding season than in the nonbreeding season. Note that the aspen B/E distribution was similar to that of the fir and spruce in the predrought year, 1976, but differed in 1977 and 1978 ($P < 0.01$ from fir and spruce in both years). This same pattern occurred in the amount of daily biomass present (Fig. 6).

Comparing the daily patterns between years (Figs. 3–6), it is evident that the breeding season was about 2 weeks earlier in 1977 than in 1976 due to the drought and about 1–2 weeks later in 1978, probably due to the late-lying snow pack.

Species diversity and equitability.—Species diversity was highest during the

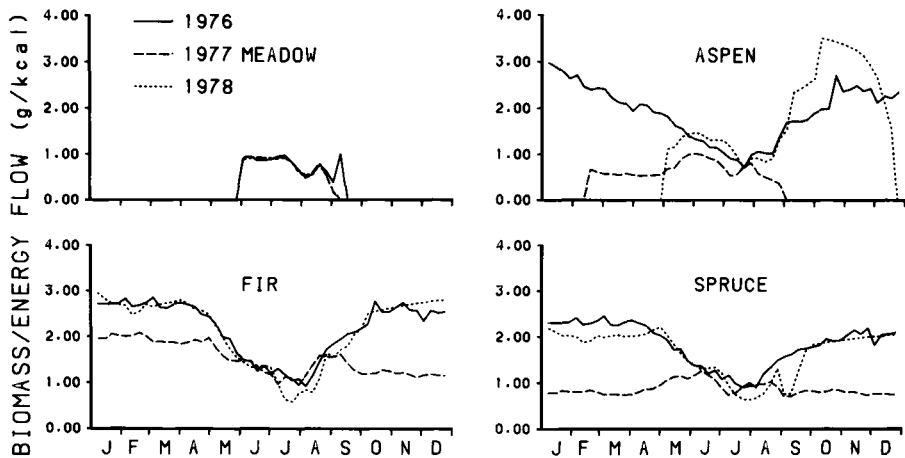


Fig. 5. Daily avian biomass present/unit energy flow during 1976, 1977, and 1978 in four seral stages.

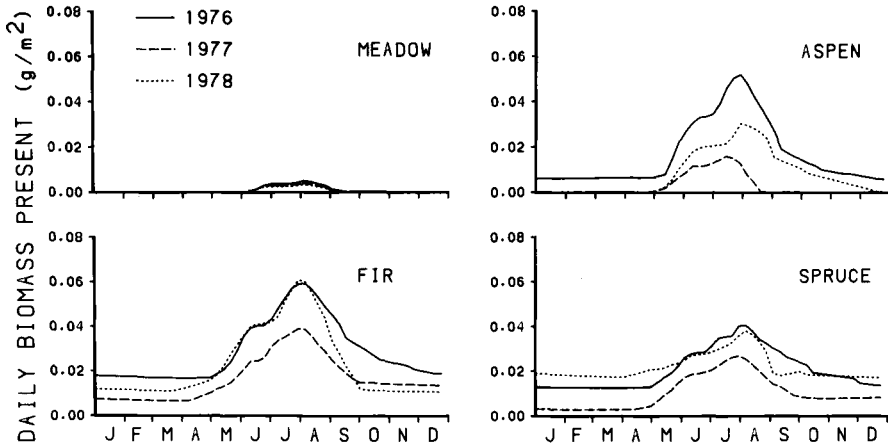


Fig. 6. Daily avian biomass present during 1976, 1977, and 1978 in four seral stages.

breeding season and lowest during the winter months (Fig. 7). This pattern was due to most species emigrating before winter with only a few species immigrating [e.g. cardueline finches, see Smith (1978, 1979)]. Although the number of species and their densities fluctuated greatly during the 3 yr of study (Appendix), the year-to-year species diversity remained similar, a trend also found by Järvinen and Väisänen (1976).

During the breeding season, diversity in the meadow was very low compared to other stages; no species occurred in the meadow from October to May due to snow cover. Aspen bird diversity was consistently less than fir and spruce after the first 2 months, and no species occurred on the aspen plot during the winter of 1977–1978. The fir plot generally had the highest bird species diversity; the climax does not support the highest diversity.

As might be expected, the meadow was quite distinct from the other forested stages, sharing no breeding species with the fir and only one of three species with the aspen (Fig. 8). During the breeding season, the aspen forest had about 50% similarity with the fir and spruce plots, although the similarity with these other

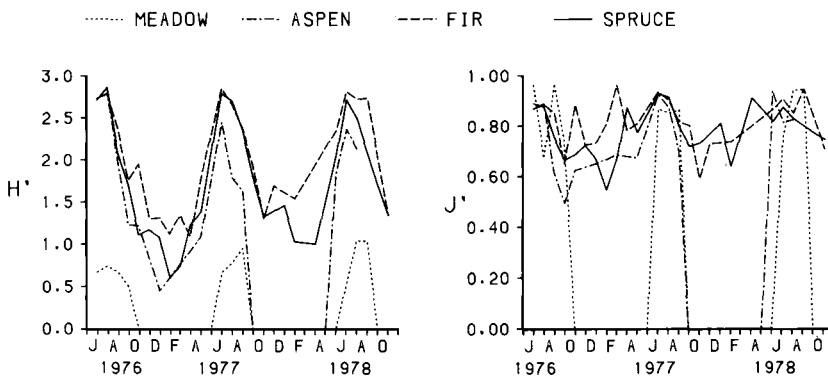


Fig. 7. Species diversity (H') and species equitability (J') from June 1976 through November 1978 calculated for each month from census data for meadow, aspen, fir, and spruce seral stages.

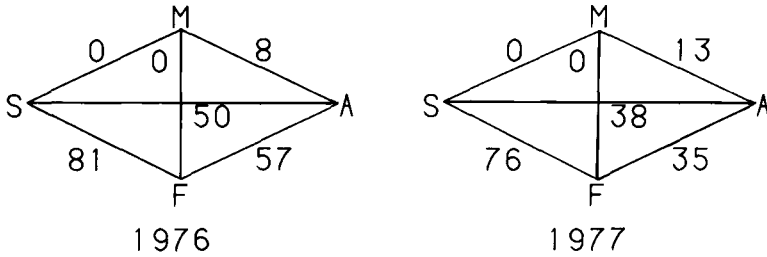


Fig. 8. Jaccard analysis of the avian communities in the four seral stages during the breeding seasons of 1976 and 1977 (drought year). Numbers refer to percent similarity between communities connected by line. The pattern in 1978 was similar to 1976.

avifaunas decreased during the drought year. The fir and spruce breeding avifaunas were quite similar in all 3 yr.

Species equitability remained relatively high throughout the study period (provided birds were present), although it was more variable in the nonbreeding season (Fig. 7). In some months, the avifaunas in early successional stages were at least as evenly distributed as those in the later stages, and the fir avifauna generally seemed to be more equitable than the spruce. At times, no species occurred in the two early seral stages, so that equitability was zero. Nonetheless, we reject the hypothesis that equitability tends to increase with successional stage.

Other trends.—The size of the organisms was postulated to increase from early to late successional stages. There are no large bird species in the meadow, and grouse are the only large birds found in the aspen. Several large raptorial species are found in the fir and spruce forests primarily during the breeding season (Appendix). Using adult male body weight as a measure of organism size (e.g. Karr 1968), the meadow had significantly smaller birds during the breeding season (Mann-Whitney U -test, $P < 0.05$) than did the other seral stages in all years (Table 3). Bird species in the aspen were significantly smaller than species in fir in 1977, but in no year was the aspen avifauna significantly different from that in spruce or the fir avifauna from that in spruce. Because the fir forest consistently supported species that averaged larger than those that the spruce forest supported, we conclude that the climax does not support the largest species. It should be noted that about 90% of the subalpine breeding avifauna is composed of relatively small species (Appendix), so that the average size of the birds present in all seral stages is quite similar if the four large nonpasserines are ignored.

Because the amount of energy channeled into production was greatest in the early successional stages (Table 2), one might expect that birds of the meadow and aspen forests are more r-selected and birds of the coniferous forest are more K-selected. However, mean size of birds was similar between forested plots, mean clutch size of species present did not decrease along the sere (Table 3), and mean length of incubation period (a very crude measure of parental investment) was longest on the fir plot, not in the climax spruce (Table 3). No significant differences existed in mean clutch size or length of incubation period between any seral stages in all 3 yr (Mann-Whitney U -test), and, if anything, mean clutch size tended to increase along the sere. We feel that a strong successional trend from r- to K-selection does not exist (see also Głowaciński and Weiner 1977) but realize that the concept itself is an oversimplification (e.g. Grime 1979, Whittaker and Goodman 1979).

TABLE 3. Mean (with standard error) adult male body weight (g), clutch size, and length of incubation period (days) for all birds breeding on the four study plots in 1976, 1977, and 1978. Most weight data were obtained by mist-netting. Some weight, all clutch size, and all incubation length data were taken from the literature.

Serial stage	<i>n</i>	\bar{x} Adult male weight	\bar{x} Clutch size	\bar{x} Length of incubation
Meadow				
1976	3	19.7 (3.9)	3.4 (0.3)	12.0 (0.0)
1977	3	19.7 (3.9)	3.4 (0.3)	12.0 (0.0)
1978	3	19.7 (3.9)	3.4 (0.3)	12.0 (0.0)
Average		19.7	3.4	12.0
Aspen				
1976	3	54.0 (21.3)	4.6 (0.4)	13.9 (0.7)
1977	12	20.1 (4.8)	4.3 (0.4)	12.7 (0.3)
1978	16	60.2 (31.5)	4.9 (0.5)	13.4 (0.7)
Average		44.7	4.6	13.3
Fir				
1976	25	115.9 (61.4)	4.4 (0.4)	14.5 (0.9)
1977	20	113.4 (57.2)	4.5 (0.5)	14.4 (1.0)
1978	24	160.2 (75.6)	4.4 (0.5)	14.7 (1.0)
Average		129.8	4.4	14.5
Spruce				
1976	20	98.3 (70.5)	4.4 (0.4)	13.7 (0.8)
1977	21	71.1 (45.5)	4.5 (0.4)	13.8 (0.8)
1978	22	144.1 (80.0)	4.3 (0.4)	14.5 (1.0)
Average		104.7	4.4	14.0

Stability of later stages of succession was hypothesized to be greater than that of earlier stages. By stability, Odum (pers. comm.) specifically meant short-term external perturbations that would stress the system, not catastrophic events (e.g. Borrmann and Likens 1979) that would have long-term effects and initiate succession *àe novo*. Fortunately, such an external perturbation occurred during the course of our study—the extreme drought of 1977. The number of species present on the spruce plot remained constant throughout the 3 yr, while decreasing 50% in the aspen and 17% in the fir in 1977 (Fig. 9). Total annual avian biomass decreased on all three forested plots during 1977, but avian biomass supported on the spruce plot increased 4.8% in 1978 over the predrought level, whereas the aspen and fir supported 50.4 and 20.9% less biomass in 1978 than in 1976, respectively (Fig. 1). Also the energetic ratios P/R and P/B (but not B/E) were more constant in the spruce forest during the 3 yr of study (Fig. 2). Thus, we conclude that the mature spruce forest was more resistant to the drought perturbation than either the aspen or the fir (see also K. Smith MS). It should be mentioned that the meadow avifauna changed little during the drought, but an extreme drought may not represent as severe a perturbation to those three meadow species, as the meadow is a dry habitat every summer.

DISCUSSION

Community energetics.—Comparisons among energy flows through the seral stages and other studies where avian community energetics have been estimated reveal some interesting relationships. The total energy demand (consumption) calculated for our subalpine meadow ($0.42\text{--}0.61 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) is apparently the lowest avian community energy demand reported, being $\frac{1}{3}$ less than any avian grassland

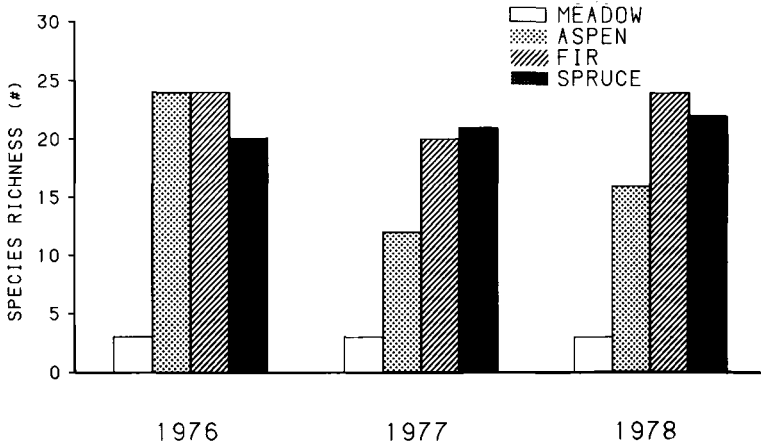


Fig. 9. Species richness during the breeding season in 1976, 1977, and 1978 in four seral stages.

community in North America (see Wiens 1977: Table 6). Annual demand values for the predrought aspen, fir, and spruce communities (Table 2) are comparable to those reported by Holmes and Sturges (1975) for a hardwood forest in New Hampshire ($7.39 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) and are somewhat less than the values estimated by Karr (1975) for the temperate deciduous forest in general ($10.4 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) and by Wiens and Nussbaum (1975) for the dry coniferous forests of the Northwest ($10.7\text{--}12.2 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{season}^{-1}$). Values for the forested plots, however, do not approach the values reported by Wiens and Nussbaum (1975) for the moist coniferous forests of the Northwest ($16.6\text{--}20.8 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{season}^{-1}$) and by Głowaciński and Weiner (1977) for forested plots ($17.6\text{--}23.4 \text{ kcal} \cdot \text{m}^{-2} \cdot \text{season}^{-1}$) in an oak-hornbeam (*Quercus robur-Carpinus betulus*) sere in Poland. Although our study contained nearly twice as many species as the Northwestern coniferous study, breeding densities of species both reported in Wiens and Nussbaum (1975: Table 2) and found in northern Utah (Appendix) were generally 5–10 times higher in Oregon. The highest breeding density in Oregon was nearly 2.5 times that of the highest density in Utah. One reason for this difference may be that all the Oregon study plots are more than 1,000 m lower in elevation than the Utah study plots. Also, the census technique used in Oregon was different from the one used in Utah.

In northern Finland, Alatalo (1978) reported an average annual consumption of 2.52 kcal/m^2 for several boreal coniferous forest habitats that appear very similar to the subalpine forests we examined (e.g. 59 vs. 71 species observed, 36 vs. 43 breeding species, several species in common). His estimate is near the value obtained in the aspen forest during the drought but is generally less than $\frac{2}{3}$ the value for the forested plots in northern Utah, primarily due to the total avian density on Alatalo's study areas being about half that found in Utah. Some discrepancy may be due to the different census technique employed: data collected along two 7-km transects were used to estimate densities in Finland.

Energetic relationships found among the seral avian communities basically agree with those proposed by Odum: generally P/R, P/B, P/C, and C/B decrease and B/E increases. During the breeding season in a Polish oak-hornbeam sere, Głowaciński and Weiner (1977) also obtained similar results for P/R, P/B, and P/C. They found,

as did we, that the preclimax avifauna, rather than the climax, often had the extreme value for a given ratio. Given the error associated with having to supply about 30 input values, we feel justified in stating that the trends in the estimates from meadow to aspen to coniferous forest that we depict above are realistic. There are probably few real differences between the preclimax fir and climax spruce values.

Trends in C/B and B/E fit the postulated trends poorly, with values for the preclimax fir quite different from spruce in 1977 and to a lesser degree in 1976. No trend in either of these ratios is evident in a Polish oak-hornbeam forest (Głowaciński and Weiner 1977), and Karr (1968) found no trend in existence energy/biomass present ($\sim C/B$) in strip-mined areas in Illinois. Also in Illinois, Blem and Blem (1975) found daily C/B was the same for avian communities in floodplain and upland forests. These results may reflect the use of existence energy, or in our case a weighted existence energy estimate, instead of actual consumption. If actual consumption measurements could be obtained, the values for consumption, respiration (and excretion), and unit energy flow might increase, the number and size of the species present determining the amount of increase over existence energy. Because production and biomass would remain the same, the relationships between P/R, P/C, C/B, and B/E would show steeper trends from meadow, aspen, to fir avifaunas. A slight reversal would be expected in the climax spruce avifauna, as this is the trend in species richness (Fig. 9) and average body size (Table 3). In practice, accurately estimating actual consumption is extremely difficult for an entire avian community, because each species (and probably each sex) has a unique consumption pattern (e.g. Holmes et al. 1978; Holmes, Black, and Sherry 1979).

Two other important conclusions emerge by comparing daily energetic relationships (Figs. 3–6). First, the relationships change as the avifaunas change due to movement of the summer residents. These changes should occur in most North American coniferous forests (*contra* Shugart et al. 1975), because the majority of these forests have many migratory species. Second, the relationships between seral stages for the various daily energetic ratios can vary dramatically from year to year due to changing environmental conditions. For example, it is clear that the number of bird species in the aspen avian community was low during the 1978 breeding season due to the drought of 1977. This means that three different conclusions concerning daily B/E (Fig. 5) could possibly be drawn, depending on which 1 of the 3 yr was examined. Changes in the daily ratio are reflected in the annual ratio as well: note how the position of the aspen B/E ratio changes in relation to fir and spruce in Fig. 2C. One should use caution in interpreting avian energetics results based on only one breeding season or even a 12-month period.

Although Odum (1969) was discussing ecosystem-wide relationships and was concerned with attributes such as primary production and community respiration, the spruce-fir avian energetic relationships follow the postulated trends fairly well. The mammalian communities of this sere also adhered to the hypothesized trends (Andersen et al. 1980), suggesting that energetic relationships at the consumer level exhibit the same patterns expected of the whole system. Although the magnitude of the ratios may vary widely between groups and trophic levels (Colinvaux and Barnett 1979), it should be remembered that in general vertebrates account for a very small portion of the energy flow in most terrestrial ecosystems (Wiens 1977). Preliminary results incorporating plant energetic relationships suggest that our ecosystem, as a whole, does not support the trends hypothesized by Odum (see MacMahon 1980).

Species diversity, equitability, and other trends.—The pattern of increasing species diversity through intermediate stages with a decrease in the climax was hypothesized by Johnston and Odum (1956) to occur when the climax becomes overaged or “senile” (see also Margalef 1968). Odum (1969) elaborated further that whether or not species diversity continues to increase during succession depends on the availability of potential niches, due to increasing biomass, stratification, etc. Because many studies of bird communities in succession show increasing trends in diversity with a decrease in the climax (e.g. Karr 1968, Ferry and Frochot 1970, Anderson 1972, Głowaciński and Weiner 1977) and many have found no decrease (e.g. Johnston and Odum 1956, Shugart and James 1973), the trend in species diversity must be dependent on the type of sere being considered (see also Odum 1950, Anderson 1972).

In our spruce-fir sere, we feel that three factors are accounting for the decrease in diversity in the climax. First, fewer hole-nesting species are found in spruce forests, as no woodpeckers, except the Northern Three-toed Woodpecker, drill into the relatively hard spruce wood (Haapanen 1965). Further, invasion by spruce into an earlier successional forest may cause a decrease in avian diversity (e.g. Haapanen 1965, Austin and Perry 1979). Thus, physical characteristics of the climax could limit the number of species in the avian community (see also Smith 1980). Second, fewer insects may be associated with spruce forests than with deciduous forests (e.g. Haapanen 1965). Wiens (1975) speculated that spruce forests in western North America have fewer associated insects than eastern spruce forests. Thus, a reduced food base in the climax may limit opportunities for avian exploitation. Third, the fir seral stage is an admixture of fir, aspen, and spruce, so that some birds found in either the aspen or spruce, but not in both, are found in the fir stage (see Appendix). In Great Britain, Lack and Lack (1951) found that more species occurred in the intermediate scrub habitat during afforestation, because it attracted species from both heath and forest. Our fir stage also represents a transition—from deciduous to coniferous vegetation—so that the fir stage should be more vegetationally heterogeneous, increasing the number of species using this stage (e.g. Bond 1957; Willson 1974; Theberge 1976; Winternitz 1976; Holmes, Bonney, and Pacala 1979).

Equitability remained relatively high during most of the study period, a pattern consistent with most studies of avian communities in general (e.g. Tramer 1969, Short 1979) and avian successional communities in particular (e.g. Anderson 1972, Głowaciński 1975, Adams and Barrett 1976, Głowaciński and Weiner 1977). In contrast, equitability values based on biomass rather than number of individuals for the mammalian communities of our sere are quite low (<0.40 ; Andersen et al. 1980).

Two hypotheses, not mutually exclusive, have been proposed to explain this pattern in avian community equitability. Tramer (1969) suggested that intraspecific territoriality would tend to cause high equitability during the breeding season in most terrestrial bird communities. One then expects more variance in equitability during the nonbreeding season (see also Rotenberry et al. 1979). Such a conclusion is consistent with our data (Fig. 7). In contrast, Austin and Tomoff (1978) argued that trophic diversity is more important than territoriality. Data concerning avian trophic diversity during succession tend to support this contention (Valiela 1971).

Of all the trends examined by us to date in the spruce-fir ecosystem, equitability

has fared the worst at all levels (MacMahon 1980); there appears to be no trend of increasing equitability with succession.

Also rejected on an ecosystem-wide basis was the postulated size increase of species along this sere (MacMahon 1980). For birds in succession, this trend has been supported by some (e.g. Karr 1968, Ferry and Frochot 1970, Blem and Blem 1975) and refuted by others (e.g. Turček 1957, Shugart et al. 1975, Głowaciński and Weiner 1977). We conclude that the trend in organism size, like that of species diversity, must be determined by the specific environment of the sere studied (see also Willson 1974).

The word stability has numerous meanings, but Odum (1969: Table 1) specifically meant "the resistance to external perturbations." Some authors (e.g. Kricher 1973, Głowaciński 1975) have equated this with persistence and have analyzed turnover rates of avian species without reference to any perturbation. Others have compared situations after catastrophic events that destroy rather than perturb the ecosystem, such as major forest fires (e.g. Bock and Lynch 1970, Roppe and Hein 1978) or clear-cut logging (e.g. Titterington et al. 1979). We believe that our results during the drought of 1977 more closely conform to the type of perturbation that Odum envisioned (see also Adams and Barrett 1976). Andersen et al. (1980) concluded that mammalian communities in later seral stages showed greater stability during the drought. Thus, it appears that in this subalpine ecosystem the vertebrate component, as a whole, supports Odum's hypothesis of greater stability in the climax. Our bird data may be somewhat anomalous, however, because the drought year also coincided with one of the best cone years in 30 yr in northern Utah (K. Smith MS) during which many cardueline finches were attracted to the spruce stage (Smith 1978, 1979).

Birds and succession.—The relationship of the avian community to plant succession may be quite complicated. In certain early successional situations, such as on dredge islands (Soots and Parnell 1975, Lewis and Lewis 1978) or in large bird colonies (Sobey and Kenworthy 1979), birds are capable of strongly affecting the progress of succession. Birds may also influence successional rates in intermediate stages that have many plant species that are dispersed by birds (Johnston and Odum 1956). Generally, birds are rather passive elements in seres (Kendeigh 1948), especially in the climax (Shelford and Olsen 1935). Further, there is no a priori reason to expect animal succession to correspond to plant communities (e.g. Kendeigh 1948, Drury and Nisbet 1971). Bond (1957) stated that most often ecological amplitudes of birds are broader within and between vegetation types than the amplitude of most plants within that type (see also Theberge 1976). Despite this, there is little doubt that birds are responsive to vegetational characteristics (e.g. James 1971, Smith 1977), but the magnitude (or threshold) of change needed for the avian response probably differs greatly among species. In this study, meadow and aspen avifaunas were distinct due to the unique configuration of the vegetation. The coniferous avifauna was also distinct, but little difference existed between avifaunas of the two coniferous types, fir and spruce. We conclude that the distinctiveness of the vegetation in various seral stages will determine the degree of avian population response along that sere and also the uniqueness of the avian communities compared to the plant successional communities (e.g. see Titterington et al. 1979), although other factors, such as fluctuations in reproduction, mortality, and dispersal rates,

may occasionally influence the distribution of a single species along a sere (Soikkeli and Salo 1979).

CONCLUSIONS

We conclude that trends in avian energetics parallel those postulated by Odum (1969) for the entire ecosystem. Trends other than those concerned with energetics are sere-dependent. Odum's postulated trend in species equitability does not obtain for avian communities.

Most succession studies have been concerned with plant communities and have focused on few of Odum's postulates. Relatively few studies of succession have centered on animal communities. Only a small number have attempted to combine plant and animal populations to examine the postulated trends within an entire ecosystem. It is, of course, difficult to study all aspects of an ecosystem simultaneously. In our sere, we are integrating many different types of studies, such as those of birds, herbs, trees, soil invertebrates, etc., in our attempt to test Odum's ideas empirically. Our preliminary results (this study, Andersen et al. 1980, MacMahon 1980) show that some predictions are supported while others are not. This is interesting, as all of Odum's hypotheses are deductions based on the same steady-state, mature community analogy (see Connell and Slatyer 1977: 1137). This suggests to us that successional relationships are more complicated than would follow from Odum's (1969) relatively simple model. An alternative model, based, in part, on the avian results presented here, is developed in MacMahon (1980).

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APPENDIX. A list of the 43 bird species that were used in the community energetics calculations. Status refers to whether species was migratory or permanent resident. Densities (in individuals/km²) entered were those used in bioenergetics model (see text for how values were obtained). Total breeding densities (in individuals/km²) and total species present are also given.

Species	Scientific name	Status ^a	1976			1977			1978				
			Meadow	Aspen	Fir	Spruce	Meadow	Aspen	Fir	Spruce	Meadow	Aspen	Fir
Goshawk	<i>Accipiter gentilis</i>	M											2
Red-tailed Hawk	<i>Buteo jamaicensis</i>	M						2					2
American Kestrel	<i>Falco sparverius</i>	M		10									
Ruffed Grouse	<i>Bonasa umbellus</i>	R		10	10		10					10	10
Great Horned Owl	<i>Bubo virginianus</i>	R			6		6					6	6
Pygmy Owl	<i>Glaucoedon groma</i>	R(?)			2								
Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>	M		60									10
Red-shafted Flicker	<i>Colaptes auratus cafer</i>	M		20				20				20	20
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	M		20									20
Williamson's Sapsucker	<i>S. thyroideus</i>	M		40	20			20				40	40
Hairy Woodpecker	<i>Picoides villosus</i>	R		20	20			20				20	20
Downy Woodpecker	<i>P. pubescens</i>	M		20									20
Northern Three-toed Woodpecker	<i>P. tridactylus</i>	R										40	
Dusky Flycatcher	<i>Empidonax oberholseri</i>	M		40				60				60	40
Western Wood Pewee	<i>Contopus sordidulus</i>	M		40				20				60	60
Olive-sided Flycatcher	<i>Notiallornis borealis</i>	M			40			80				40	20
Tree Swallow	<i>Iridoprocne bicolor</i>	M		20				20				20	20
Steller's Jay	<i>Cyanocitta stelleri</i>	R										40	20
Mountain Chickadee	<i>Parus gambeli</i>	R		20				20				20	20
White-breasted Nuthatch	<i>Sitta carolinensis</i>	M						80				160	120
Red-breasted Nuthatch	<i>S. canadensis</i>	R		20								40	60
Brown Creeper	<i>Certhia familiaris</i>	R										20	20
House Wren	<i>Troglodytes aedon</i>	M		20								60	60
American Robin	<i>Turdus migratorius</i>	M		100	40			60				60	40

APPENDIX. Continued.

Species	Scientific name	Status ^a	1976				1977				1978			
			Meadow	Aspen	Fir	Spruce	Meadow	Aspen	Fir	Spruce	Meadow	Aspen	Fir	Spruce
Hermit Thrush	<i>Catharus guttatus</i>	M		40	20	40	20	40	20			40	20	
Mountain Bluebird	<i>Sialia currucoides</i>	M										20		
Golden-crowned Kinglet	<i>Regulus satrapa</i>	R		40		20		20				20	100	
Ruby-crowned Kinglet	<i>R. calendula</i>	M			80	40		40	60			40	40	
Warbling Vireo	<i>Vireo gilvus</i>	M		40	20	20		40				60	40	
Orange-crowned Warbler	<i>Vermivora celata</i>	M		20								40		
Audubon's Warbler	<i>Dendroica coronata auduboni</i>	M		60	80	80		20	20			60	60	
Western Tanager	<i>Piranga ludoviciana</i>	M		60	60	20		20	20			40	20	
Lazuli Bunting	<i>Passerina amoena</i>	M		60				20						
Cassin's Finch	<i>Carpodacus cassinii</i>	M		100 ^b	120	80		40	60			80	40	
Pine Grosbeak	<i>Pinicola enucleator</i>	R(?)			20 ^b	20 ^b		20	20			20	20	
Pine Siskin	<i>Carduelis pinus</i>	R		60	80	80		20	40			60	20	
Red Crossbill	<i>Loxia curvirostra</i>	R						40	40			40	20	
White-winged Crossbill	<i>L. leucoptera</i>	M							20					
Vesper Sparrow	<i>Pooecetes gramineus</i>	M	100				100					80		
Pink-sided Junco	<i>Junco hyemalis meurnsi</i>	M		200	160	100		140	80			150	100	
Chipping Sparrow	<i>Spizella passerina</i>	M		40	40	40		20	40			20	40	
Brewer's Sparrow	<i>S. breweri</i>	M	40				20					20		
White-crowned Sparrow	<i>Zonotrichia leucophrys</i>	M	40	60			20	40				20	40	
Total Breeding Density			180	1,110	1,148	926	140	520	672	764	120	720	1,098	818
Total Species Present			3	24	24	20	3	12	20	21	3	16	24	22

^a R = resident, M = migrant.^b Nonbreeding individuals.