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DENSITY, BIOMASS, AND ENERGETICS OF THE BIRD AND SMALL MAMMAL POPULATIONS OF AN ILLINOIS DECIDUOUS FOREST

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ABSTRACT

The population density, standing crop biomass, consuming biomass, diversity and standard metabolism of avian and mammalian communities were quantified over an annual cycle from studies of floodplain and upland forest plots in Hart Woods, Champaign County, Illinois. The floodplain bird and mammal populations each consistently had greater population density, standing crop biomass, consuming biomass and standard metabolism than their counterparts on the upland. Avian diversity was highest on the floodplain. Total annual minimal energy budgets are: floodplain mammals, 3,846 Mcal; floodplain birds, 3,371 Mcal; upland mammals, 2,684 Mcal; and upland birds, 2,214 Mcal.

INTRODUCTION

Surveys of mammals and birds present in deciduous forest are commonplace in biological literature. Population estimates of single species or censuses of total avian or mammalian populations are frequently encountered. There have been, however, few attempts to quantify simultaneously the populations of both groups at a single site through an entire annual cycle. The following study was made because it was felt that such an analysis might give new information about the relative importance of these two components of deciduous forest and further reveal how these communities interact.

The population data for this study were obtained in Hart Memorial Woods, a streamside forest on the east bank of the Sangamon River in Champaign County, Near Mahomet, Illinois. This area consists of 5.4 hectares (13.5 acres) of bottomland or floodplain and 9.6 hectares (24.0 acres) of upland forest and is part of a larger forested area. A description of the vegetation of this forest has been published elsewhere (Root, 1966; Blem and Blem, In press).

METHODS

Avian populations were assessed by means of transect counts along rows of stakes set at 50 M intervals throughout the forest. Obvious transients were excluded from the data. Three or more counts were made per month from February, 1966, through September, 1967. In addition, a singing male census was made by the spot-map method (Williams, 1936; Kendeigh, 1944) from March through August of both years.

Wooden live traps (Fitch, 1950) placed at 15 M intervals were used to capture small mammals on a 1.8 hectare grid on the upland and a 1.3 hectare grid on the floodplain. Mammals were collected from August, 1966, through August, 1967, on the floodplain. Censuses were made each month except December, 1966, January, 1967, and May, 1967, when weather conditions or flooding made trapping impossible. Ambient temperature was recorded by thermographs maintained on each plot throughout the study. Ten trapping periods each of eight consecutive days were completed in both areas. Population levels of the white-footed mouse, Peromyscus leucopus, were estimated by means of Jolly's (1965) stochastic model (Blem and Blem, In press). Absolute numbers were used as population estimates of small mammals other than Peromyscus, since capture-recapture data were insufficient for the stochastic model. The species involved are shorttail shrew, Blarina brevicauda, least shrew, Cryptotis parva, prairie vole, Microtus ochrogaster, pine vole, Microtus pinetorum, house mouse, Mus musculus, and Norway rat, Rattus norvegicus. Densities of fox squirrels, Sciurus niger, eastern cottontail, Sylvilagus floridanus, and woodchuck, Marmota monax, were determined from maps of repeated observations during transect counts. The occurrence of white-tailed deer, Odocoileus virginianus, red fox, Vulpes fulva, striped skunk, Mephitis mephitis, longtail weasel, Mustela frenata, muskrat, Ondatra zibethicus, raccoon, Procyon lotor, and opossum, Didelphis virginiana, was of a transitory nature, and these species are not included in the following analyses. Bats were observed but neither identified nor quantified and are also omitted from the total census. A crude estimate of the number of eastern moles, Scalopus aquaticus, was obtained by plotting substrate disturbances on the grids.

Diversity was calculated as $H'=1/N\ (N \log_{10} N - \Sigma n_i \log_{10} n_i)$, where N is the total population and n_i is the number of individuals of species i (Lloyd, Zar, and Karr, 1968). Standing crop biomass (SCB) was computed from published live weights of the appropriate species and our population estimates. Consuming biomass (CB) was obtained by summing weights adjusted to the exponent most closely related to metabolism in the group (Salt, 1957; Crowell, 1962). Metabolic rate of passerine and nonpasserine birds, when considered as separate groups, varies in proportion to body weight to the 0.72 power (Lasiewski and Dawson, 1967), while mammalian metabolism increases with weight to the 0.75 power (Kleiber, 1961). Standard metabolism is a minimal level of metabolism, usually measured while the animal is at rest in a postabsorptive condition, and, as defined by Kendeigh (1969), may include the energetic costs of thermoregulation. Metabolism of free-living animals is influenced by many factors including diet, activity, behavior, season, time of day and population density (Buckner, 1964). Since it was impossible to measure the effects of all of these factors, standard metabolic rates of total populations were calculated in order to compare the minimum energy requirements of the mammal and bird communities. Kilocalories per animal-day was obtained from the following equations:

Passerines (Kendeigh, 1969) 0°C $SM=4.77\ W^{0.417}$
30°C $SM=0.88\ W^{0.693}$

Nonpasserines (Kendeigh, 1969) 0°C $SM=3.34\ W^{0.526}$
30°C $SM=0.51\ W^{0.717}$

Rodents (computed from published values from many sources)
0°C $SM=2.62\ W^{0.579}$ (N=46)
30°C $SM=0.41\ W^{0.755}$ (N=32)

where SM is standard metabolism in Kcal/animal-day and W is weight in g.

Interpolations proportional to mean monthly temperatures were made between equations so as to predict minimal daily energy expenditures. The daily standard metabolism of mammals other than rodents was calculated from published values from many sources. Total standard metabolism (SM) is expressed in megacalories (Mcal) which equal 10^3 Kcal. Annual energy budgets were calculated by summing daily SM estimates multiplied by days in the month. Interpolated values were used for those months in which data were lacking. Paired t-tests were used to compare coincident monthly estimates of population density, SCB, CB, and SM. A 5% level of significance was used in all statistical tests.

RESULTS

Eighteen species of mammals were detected on both study plots (see Methods). The white-footed mouse and shorttail shrew were the most abundant of eleven resident species. Thirty-five species of birds were censused on both plots. The most abundant were Red-headed Woodpecker, *Melanerpes erythrocephalus*, Cardinal, *Cardinalis cardinalis*, and Tufted Titmouse, *Parus bicolor*. A complete list of the population density, diversity, standing crop biomass, consuming biomass and metabolism of all species recorded on both plots is available from the authors upon request.

Size and diversity of total avian populations are consistently greater on the floodplain. Number of species and individuals, diversity, SCB, CB and SM for the two study areas are statistically different. Maximum population density, SCB and CB occur during July and August at both sites. Diversity indices are highest and fairly stable from May through August. Average maximum floodplain SCB and CB is 2.1 X values for the upland. Peak SM occurs in July and August, and average floodplain values for these months are 1.4 X upland values. The annual avian energy budget for SM amounts to 3,371 Mcal/100 acres in the floodplain, or about 1.5 X the annual energy budget of 2,214 Mcal/100 acres calculated for the upland.

Although floodplain mammal populations are significantly larger than those of the upland, no difference in number of species or diversity was detected. Maximum population density during this study occurred in July and August on the upland and August through September on the floodplain. Upland SM is greatest in October and September in the upland and floodplain forests respectively. Plot differences in SCB, CB and SM are all statistically significant. Maximum floodplain SCB, CB and SM are 2.3, 1.9 and 1.8 X larger than corresponding upland values. The annual mammalian energy budget of the floodplain is 3,846 Mcal, and is 1.4 X greater than the upland estimate of 2,684 Mcal.

Table 1. Population densities per 100 acres (= 40 hectares). Number of species is in parentheses.

Time interval	Floodplain		Upland	
	Birds	Mammals	Birds	Mammals
Feb. 1966	237 (7)	--	227 (11)	--
March	274 (11)	--	237 (13)	--
April	366 (18)	--	273 (13)	--
May	813 (28)	--	439 (22)	--
June	919 (27)	--	510 (21)	--
July	1335 (27)	--	624 (21)	--
Aug.	1335 (27)	--	624 (21)	1159 (6)
Sept.	243 (13)	1608 (6)	198 (8)	946 (6)
Oct.	273 (11)	1610 (7)	189 (10)	754 (7)
Nov.	355 (12)	1339 (5)	206 (10)	342 (6)
Dec.	370 (12)	--	198 (10)	--
Jan. 1967	363 (12)	--	186 (10)	--
Feb.	370 (12)	582 (6)	188 (10)	321 (6)
March	267 (12)	360 (7)	165 (11)	287 (6)
April	302 (16)	369 (5)	170 (13)	196 (5)
May	867 (23)	--	440 (21)	--
June	1053 (26)	282 (5)	637 (21)	466 (6)
July	1513 (26)	1046 (6)	674 (21)	900 (7)
Aug.	1513 (26)	1395 (7)	674 (21)	880 (7)
Sept.	251 (13)	1250 (6)	209 (8)	--

Table 2. Standing crop biomass (B) and consuming biomass (CB) in Kg per 100 acres (= 40 hectares).

Time interval	Floodplain				Upland			
	Birds		Mammals		Birds		Mammals	
	B	CB	B	CB	B	CB	B	CB
Feb. 1966	8.6	2.8	-	-	12.5	3.5	-	-
March	10.3	3.3	-	-	13.5	3.8	-	-
April	19.5	5.5	-	-	17.0	4.7	-	-
May	37.9	11.1	-	-	24.0	6.6	-	-
June	41.9	12.4	-	-	26.8	7.5	-	-
July	63.9	18.6	-	-	32.3	9.1	-	-
Aug.	63.9	18.6	-	-	32.3	9.1	53.8	15.6
Sept.	14.5	4.0	124.2	30.0	12.1	3.3	50.7	14.0
Oct.	13.0	3.8	80.8	22.8	9.1	2.6	40.2	11.2
Nov.	17.2	4.9	42.2	15.6	8.5	2.5	27.4	3.9
Dec.	16.8	5.0	-	-	8.3	2.4	-	-
Jan. 1967	15.9	5.1	-	-	7.6	2.1	-	-
Feb.	19.7	5.4	26.8	7.3	6.4	2.0	34.2	7.8
March	9.6	3.0	58.7	10.7	6.8	2.1	29.6	6.9
April	16.8	4.7	83.7	14.5	11.3	3.1	28.0	6.0
May	40.1	11.9	-	-	22.0	6.1	-	-
June	46.3	13.8	94.7	16.2	32.3	9.1	34.5	8.9
July	70.8	20.8	107.4	23.4	33.2	9.4	53.0	14.9
Aug.	70.8	20.8	113.2	26.1	33.2	9.4	54.1	15.4
Sept.	14.5	4.0	111.2	25.2	12.0	3.3	-	-

Upland avian populations consistently have fewer total individuals of more species and greater diversity than their mammalian counterparts. Upland mammal populations have greater SCB and CB than avian populations, and except for June through August, use a greater amount of energy. Monthly differences between bird and mammal estimates are statistically significant in all of the above comparisons.

DISCUSSION

Although the number of species of breeding birds at both sites is not exceptionally large, population densities exceed previous estimates in similar habitats in Illinois (Fawver, 1947; Case, 1964; Karr, 1969). Modification of the communities by the death and decay of elms may be partly responsible for such large populations. For example, woodpeckers make up 25.6 and 27.4% of the total floodplain avifauna for 1966 and 1967 respectively; upland values are 14.6 and 20.0%. Karr (1969) censused undisturbed bottomland and upland forest with many dead elms in east-central Illinois in 1966; 19.2 and 25.2% of these species in these respective avian communities were woodpeckers. Population densities of Red-headed Woodpeckers at Hart Woods during the course of our study were the highest we have encountered.

Two avian population peaks (excluding transients) occur during the year in both habitats. The larger peak occurs at the end of July and beginning of August after nesting is completed. At the end of the nesting period and raising of young there is a rapid decrease in the size of the population. This decrease is similar to that demonstrated by Williams (1936), Twomey (1945) and Fawver (1947). By September, the population reaches an annual low. At this time nearly all summer residents have departed, and many of the winter residents have not yet arrived. The second peak occurs in winter from November to February when winter residents attain maximum population densities. Although individuals of permanent resident species remain throughout the year, population density fluctuates somewhat. For example, many Red-headed Woodpeckers winter in Hart Woods during some years, but the species may be absent during other winters, possibly because of scarcity of food. Avian diversity was greatest on both sites during summer (May-August), and was lowest in midwinter. Standing crop biomass, consuming biomass and standard metabolism all reach highest levels in July and August when population densities were greatest.

Peak mammalian population density, standing crop biomass, consuming biomass and standard metabolism were obtained in August-October, or roughly during the period in which the avian population is lowest. Spring populations (February-April) are more diverse, probably because of the increased equitability of numbers of individuals within a similar number of species. Large numbers of *Peromyscus leucopus* are responsible for much of the autumnal peak.

Differences between floodplain and upland populations do not completely coincide with predicted successional changes, possibly because of the increased spatial heterogeneity that accompanied the death of floodplain elms and the ensuing opening of the bottomland

Table 3. Diversity (H') and standard metabolism (SM) in Mcal/100 acres per day (100 acres = 40 hectares).

Time interval	Floodplain				Upland			
	Birds		Mammals		Birds		Mammals	
	H	SM	H	SM	H	SM	H	SM
Feb. 1966	1.82	5.1	-	-	1.92	5.8	-	-
March	2.11	5.1	-	-	2.08	5.4	-	-
April	2.47	7.4	-	-	1.98	6.0	-	-
May	3.14	13.9	-	-	2.87	7.9	-	-
June	3.14	15.1	-	-	2.73	9.5	-	-
July	3.04	14.3	-	-	2.79	9.8	-	-
Aug.	3.04	16.6	-	-	2.79	11.0	1.02	8.1
Sept.	2.32	4.7	0.72	17.7	1.82	3.7	1.06	9.6
Oct.	2.24	5.4	0.89	16.0	2.07	3.6	1.06	9.8
Nov.	2.21	7.1	0.71	15.6	2.10	3.9	1.04	6.3
Dec.	2.19	8.6	-	-	2.09	4.1	-	-
Jan. 1967	2.18	8.7	-	-	2.03	4.1	-	-
Feb.	2.17	9.6	1.39	7.8	2.03	4.0	1.25	8.2
March	2.28	4.8	1.47	4.0	2.16	4.2	1.42	6.3
April	2.66	5.9	1.09	3.8	2.38	3.7	1.28	4.3
May	2.91	11.2	-	-	2.86	6.2	-	-
June	3.19	12.5	1.21	6.0	2.81	9.0	1.29	5.4
July	3.21	14.5	1.12	11.1	2.80	11.4	1.29	9.3
Aug.	3.21	15.4	1.15	14.0	2.80	12.0	1.28	9.5
Sept.	2.45	4.8	1.07	15.1	1.64	3.8	-	-

canopy. Among expected successional trends (Margalef, 1958, 1963; Odum, 1969) are increased organismic size, increased biomass, decreased energy flow per unit biomass and decreased diversity in late seral stages. Over the entire year, average bird size is greater for upland forest (50.8 ± 1.8 g) than floodplain (47.3 ± 1.4 g), and is similar to average size of breeding birds, 50.5 and 47.4 g, respectively. Floodplain mammals average larger (120.3 ± 30.3 g) than those of the upland (78.0 ± 9.7 g) although there is considerable variation at both sites. Biomass of mammals and birds is consistently greater on the floodplain. Energy expenditure in terms of standard metabolism per unit biomass is similar for birds at both sites (0.377 ± 0.026 Kcal/Kg-day on floodplain, 0.382 ± 0.025 on upland) but is greater for mammals of the upland forest than on the floodplain (0.193 ± 0.011 Kcal/Kg-day and 0.154 ± 0.033, respectively). Diversity is lower in the upland avian community, but there is no significant difference between mammalian diversities.

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