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COMPARATIVE POPULATION BIOENERGETICS OF THREE INSECTIVOROUS PASSERINES IN A DECIDUOUS FOREST

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At all levels of organization from the individual to the ecosystem, energy resources play a diverse and profound role. The ways in which these resources are used by a species represent the results of natural selection and are expressed in the species' life history patterns and adaptations (King 1974). Therefore, analyses of energy budgets, especially among similar species occupying the same environment, provide a means for understanding the ecological and energetic consequences of different life history phenomena. In addition, determinations of energy utilization and budgeting within species populations are useful in quantifying certain aspects of bird community structure and dynamics (Wiens 1973, Holmes and Sturges 1975, Karr 1975).

Over the last two decades, energy budgets have been developed for several bird species occupying a variety of habitats (Orians 1961, Odum et al. 1962, Kale 1965, Brenner 1968, Pinowski 1968, Norton 1973, Custer 1974). No studies prior to ours (Black 1975; this paper), however, have been conducted on the population bionenergetics of insectivorous forest-dwelling passerines.

In this study, which is part of a larger investigation of bird community dynamics and energetics in the Hubbard Brook Experimental Forest, New Hampshire, we investigated the magnitude and seasonal patterns of time and energy use by three species of passerine birds: the Red-eyed Vireo (*Vireo olivaceus*), the Least Flycatcher (*Empidonax minimus*), and the Black-throated Blue Warbler (*Dendroica caerulescens*). These abundant and characteristic species of northern hardwoods forests differ in habits such as breeding schedules, densities, foraging modes and use of vertical strata. Thus, they offer an opportunity for analyzing differences in energetic demands among species with contrasting life histories within the same ecological system.

STUDY SITE

This study was conducted in the Hubbard Brook Experimental Forest in the White Mountains of north-central New Hampshire. The forest consists of uneven-aged hardwoods, dominated by sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), yellow birch (*Betula allegheniensis*), with occasional white birch (*B. papyrifera*) and white ash (*Fraxinus americana*). Some red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) occur along the ridges and upper north-facing slopes (Bormann et al. 1970). Herbaceous plants and shrubs are seedlings and saplings of the dominant tree species, one common fern (*Dryopteris spinulosa*), hobble bush (*Viburnum alnifolium*), and a variety of low-growing forbs (Siccama et al. 1970). The vegetation is relatively homogeneous and continuous throughout the Hubbard Brook basin. The mean canopy height is about 25–30 m.

METHODS

STANDING CROP DETERMINATIONS

Breeding populations of the three bird species were observed closely on two study areas: one, a 10-ha census plot described by Holmes and Sturges (1975) and the other, a 14.5-ha area studied by Black (1975). Both sites are at the same elevation (400 to 500 m) and are similar in vegetation, except that the latter has a slightly denser understory.

Although the birds have been under study since 1969, the data we report here were obtained mainly in 1971 and 1972 for the Red-eyed Vireo, and in 1972 for the Least Flycatcher and the Black-throated Blue Warbler. Densities were determined throughout the time when the birds were in the forest, approximately from early May through September, using the techniques for obtaining estimates of absolute abundance described by Holmes and Sturges (1975) and Black (1975). These consisted of modified spot-mapping of singing males, mark-recapture data from intensive mist-netting, location-mapping of color-marked individuals, locations of all or most nests, and the use of a song-playback technique for detecting the presence of the warblers late in the season (Black 1975). We measured densities weekly as numbers of birds of each sex and age category, and then converted them to biomass, using mean weights obtained from birds captured at Hubbard Brook, and to energy content, using a caloric density of 1.7 kcal/g live weight (Holmes 1976).

Nests of each species were located and their fate was followed through the season. Eggs and nestlings were not weighed during the study, either because the nests were not reachable (particularly flycatchers and vireos) or because of the disruption and increased likelihood of predation caused by this procedure (mainly for the warbler). Egg weights used to calculate standing crop and energy content of eggs were obtained from the literature (Table 1), and the average caloric content of unincubated passerine eggs (1.05 kcal/g net weight) was taken from Ricklefs (1974). No attempt was made to measure respiration of, or weight loss from, eggs during incubation. Nestling weights were estimated from growth curves of each species reported in the literature (Harding 1931, Southern 1958, Walkinshaw 1966).

The energy content of nestling tissue changes during growth because of changes in lipid and water content (Ricklefs 1967). Estimates of the energy content of nestlings were determined from the following equation, derived from an average of values for altricial passerines given by Ricklefs (1974: Table 24):

$$D = 0.67 + 1.13\ W,$$

where $D =$ density in kcal/g live weight, and $W =$ percent of adult weight.

Young after fledging were assumed to have weights (and respiration rates, see below) equal to those of adults in the post-breeding period. Survival of young was difficult to determine accurately after fledging, but census results and intensive field observations of family groups and of the young themselves were used to estimate post-fledging densities.

METABOLIC ENERGY EXPENDITURE

It is difficult to obtain realistic measures of the metabolic energy expended by free-ranging birds in their natural habitats. Yet, such measurements are important because 98% or more of the energy utilized by a terrestrial vertebrate population is used in respiration (Golley 1968). Two major methods have been employed previously: 1) determining the level of energy expenditure for caged birds (existence energy) and then extrapolating to field conditions (Kendeigh 1969); 2) determining time-activity budgets. These are combined with estimates of the energetic costs for each activity determined from a variety of studies in both the field and laboratory to form a composite energy budget (e.g., Pearson 1954, Orians 1961, Schartz and Zimmerman 1971, Collias et al. 1971, Custer 1974, Black 1975). The latter method has received support from studies by Utter (1971) and Utter and LeFebvre (1973) in which time budget determinations of metabolic energy expenditures were compared with those obtained by the $D_2{}^{18}O$ isotope method of measuring metabolic rates of free-living birds. The findings coincide within about 5–8%, a remarkable agreement considering the technical difficulties involved.

We used the time-activity budget/metabolic estimate method, modified from procedures outlined by Utter (1971). We measured the amount of the time spent by the birds of each species in basic physical activity categories, such as flying, sitting, hopping, and incubating. These data were recorded in the field on portable tape recorders. Two stopwatches were used, one to record the duration of each observation period and the other to measure the total length of time in flight. Individuals of each species were observed at all times of day, and through their period of residency in the forest. The amount of time spent in each activity was then expressed as a percent of daylight hours. Sampling periods coincided with nest cycle phases (territory establishment, nest building and egg-laying, incubation, nestling, post-fledging) which were synchronous for all individuals within the vireo and the flycatcher populations, but were staggered in the warbler population because of frequent nest failures and subsequent renestings. For the warbler, time budgets were determined and calculated for each pair in the study area on a weekly basis, from which a composite population budget was then formed.

The following equation was used to estimate daily energy expenditure (DEE) for males and females during each phase of the breeding cycle:

DEE = (hours of flight × metabolic cost of flight) + (hours of hopping × metabolic cost of hopping) + (hours of sitting × metabolic cost of sitting) + (hours of singing × metabolic cost of singing) + (hours of sleeping × metabolic cost of sleeping) + (hours of incubation × metabolic cost of incubation) + (estimated energy expenditure for specific dynamic action [SDA]). (SDA represents the rise in metabolism above basal level due to the process of digestion; Brody 1945.)

The metabolic cost of each activity was expressed as a multiple of the standard metabolic rate (SMR), which is defined as the metabolism of a bird resting without food, in a thermoneutral environment. The term SMR is used here rather than basal metabolic rate (BMR) because the rates for the vireo and the flycatcher were determined from birds during their active (daytime) period rather than at night (King 1974). SMRs were determined experimentally in our laboratory, using the apparatus and methods described by Holmes and Sawyer (1975). The metabolic rates were calculated using a respiratory quotient (RQ) of 0.7, where RQ equals the ratio between carbon dioxide liberated and oxygen taken up and varies with the type of food being metabolized. The caloric equivalent of 4.8 kcal/l of O_2 (Brody 1945) was used for converting oxygen consumption values into energy terms.

The estimates of costs of energy expended in each of the activity categories are the same as those used by Black (1975) in a study of time-and-energy budgeting in the Black-throated Blue Warbler. Since he compared and evaluated the various studies and metabolic estimates so obtained, we will only briefly discuss here the values we have used in this paper.

Flight (10 × SMR). A variety of techniques including the measurement of O_2 consumption of birds flying in wind tunnels (Tucker 1971), of CO_2 production by birds flying in large plastic tunnels (Teal 1969) and of body weight changes during periods of sustained migratory flight (e.g. Nisbet et al. 1963) have been used to measure the energetic costs of flight. The values obtained range from about 4–17 × SMR, averaging about 10–12 × SMR (King 1974, Black 1975). From an allometric equation relating flight energy to body weight given by Hart and Berger (1972), flight energy of the three species considered here should range between 8 and 10 × SMR.

From a review of these findings, we have chosen 10 × SMR as an average value to apply to flight energetics. This estimate is probably reasonable since the many short tortuous flights of these birds while foraging or moving through the forest canopies may be energetically more expensive than the longer sustained flights that have been measured in many studies.

Hopping (5 × SMR). Little is known about the energetics of terrestrial locomotion in birds (King 1974, Black 1975). The only information we know of on energetics of hopping comes from Pohl's (1970) study of a caged Chaffinch (*Fringilla coelebs*). Applying his regression to the species in our study and assuming that the average hop of these birds lasts 0.5 s, we estimate that hopping consumes energy at a rate of about 5 × SMR. This seems to be a relatively high figure, but we have no others for comparison. We therefore use it as the best, but only approximate, estimate.

Sitting (1.5 × SMR). Existence energy, that used during long-term low level activity by caged birds, ranges between 1.2 and 1.8 times basal levels (King 1974). We use a value of 1.5 × SMR as a good, although probably conservative, estimate of energy spent by alert birds sitting in their natural habitat during daylight hours. The same value has been used for equivalent behavior in other species by Custer (1974) and by Schartz and Zimmerman (1971).

Singing (2 × SMR). Since the Least Flycatcher does little hopping but instead often stays on one branch and sings for relatively long periods of time, we measured these periods and assigned them an energetic value of 2 × SMR. This was based on the assumption that singing and the associated shifting of position on the perch, etc. would be more costly energetically than sitting alertly but not as expensive as hopping. Orians (1961) used a similar value for blackbirds while displaying. This category was not distinguished in the physical activity time budgets of the vireo and warbler, who sang frequently while performing other activities which were being quantified.

Sleeping. Energy expenditure during night hours was assumed to be equivalent to SMR plus an additional metabolic increment necessary for thermoregulation when temperatures dropped below the species' zone of thermoneutrality. This increment was determined from the nightly forest temperatures experienced by the birds, as recorded under the forest canopy at Hubbard Brook, and from the temperature-metabolism curves developed for each species experimentally in the laboratory. Temperatures at two hour intervals (20:00 to 04:00) through each night during the residency period were combined by computer with the species' metabolism curves and the total energy required for existence by an individual of each species was calculated. The result was compared to the standard metabolic rate for an individual for the same number of hours and expressed as an average ratio for the season.

We did not consider thermoregulatory costs during the daylight hours to be important, because ambient temperatures then were usually high, often near or within the birds' thermoneutral zones, and because the birds were exercising which might compensate for any additional heat needs.

Incubation (1.3 × SMR). Recent studies of the energetics of incubation have been reviewed by Ricklefs (1974). Values from these studies range between 1.1 and 1.4 × SMR for small, altricial birds incubating a clutch of no more than 50% of adult body weight in an open nest. We have used 1.3 × SMR as the estimate of the energetic cost of incubation.

Egg production. The energetic cost of egg production was estimated directly for each species from the following formula (Black 1975):

Energetic cost/egg (kcal) = W × (1.05 kcal/g × 1.3), where W = live weight of a newly laid egg in grams, 1.05 kcal/g = caloric equivalent of passerine eggs (Ricklefs 1974), 1.3 = coefficient compensating for energy utilized in egg production not incorporated into the egg (Dol'nik 1971).

Since these birds lay one egg per day, the energetic cost calculated from the above formula was added to the DEE for each female during the egg-laying period. The values may overestimate energy costs during the late laying phase, and underestimate them in the early phase due to the start of follicular development prior to the laying of the first egg (Black 1975).

Specific dynamic action (0.3 × SMR). Another component of the energy metabolized by an animal is that used in the heat increment of feeding, or specific dynamic action (SDA). SDA varies with the kind and amount of food consumed, with the relative portions of carbohydrate, fat and protein in the food, and with environmental temperatures (Brody 1945, Owen 1970). Estimates of SDA in birds vary between 6 and 45% of basal rates (see review in Ricklefs 1974), and an average estimate for animals under natural conditions is difficult to determine (Calder and King 1974). From reviewing available information, we chose a value of 0.3 × SMR, which admittedly is only a crude estimate of a very complex process. Since the value is a constant in our equations, however, its effect on seasonal and comparative patterns of energy utilization is negligible.

These values for DEE were then combined with those on standing crop to yield energy budgets for each population throughout the breeding season.

Nestling respiration was calculated from Ricklefs' (1974) model, as modified by Black (1975). This model uses data on the standard metabolic rates (SMR) of adults (see below), species' growth curves obtained from the sources listed above, and the energy content of the tissues (Ricklefs 1974). Combined with field estimates on the numbers of young in nests through the breeding period, these provided estimates of nestling respiration for each population.

RESULTS

BREEDING SYSTEMS, PRODUCTIVITY AND PHENOLOGY

The species under study are small (9–17 g) passerines that nest in summer in deciduous woodlands in eastern North America. The Least Flycatcher and the Black-throated Blue Warbler occur primarily in the northern sector of the eastern deciduous forest, while the Red-eyed Vireo occurs in woodlands throughout eastern North America. At Hubbard Brook, the three species are syntopic.

All three species possess basically similar breeding systems (Table 1). They arrive in the breeding area in mid-May; males establish and defend territories; only females build nests and incubate; both sexes feed nestlings, with females doing the greater share (Southern 1958, Walkinshaw 1966, Black 1975); the lengths of incubation and nestling periods are approximately the same (Table 1).

The species differ in typical densities, heights of nesting, nesting success, foraging heights and techniques, and durations of stay in the breeding area (Table 1, Fig. 1). The flycatchers and vireos nest relatively high in the subcanopy or in lower portions of the canopy. They forage at these same heights; the flycatcher hawks for insects in the air and hovers for insects on leaves (Holmes et al., in press). The warbler, which is less abundant,

TABLE 1. Population parameters and characteristics, based on data from the Hubbard Brook Experimental Forest unless noted otherwise.

	Least Flycatcher (1972)	Red-eyed Vireo (1971, 1972)	Black-throated Blue Warbler (1972)
Adult weight in g ($\bar{x}$)	10.0	17.0	9.4
No. of breeding pairs/10 ha	26 (+3 ♂)[a]	14.5 (11)[b]	4.2
Clutch size ($\bar{x}$)	3.95[c]	3.3[d]	3.91
No. eggs laid/10 ha	95	48 (7)[b]	16.5
No. young fledged/10 ha	71	26 (0)[b]	5.5
Fledging success	74.7%	54.5% (0%)[b]	33%
Sex building nest	♀ only	♀ only	♀ only
Incubating adult	♀	♀	♀
Incubation period (days)	13–14[c]	12–13[d]	12–13
Male participation in feeding nestlings	50%	30%	50%
Nesting period (days)	12–16[c]	10–11[d]	11–12
$\bar{x}$ Nest height (m)	12.9 (n = 24)	11.1 (n = 26)	0.25 (n = 41)
Nest loss (relative)	Low	Low	High
Foraging strata	Subcanopy	Canopy	Subcanopy (♂) Shrub (♀)
Foraging mode	Hawk/Hover	Glean/Hover	Glean

[a] Unmated, territorially-active males.
[b] Data from 1972 in parentheses.
[c] Walkinshaw 1966.
[d] Lawrence 1953.

places its nest in low shrubs often less than 1 m above the ground, and feeds primarily by gleaning insects from foliage in the shrub (females) and lower canopy (males) strata (Black 1975, Holmes et al., in press).

The seasonal changes in standing crop of adults, eggs, nestlings, and fledglings for each of the three populations under study reflect differences in density and phenology (Fig. 1). Least Flycatchers and Red-eyed Vireos were represented on the study area in June by 26 and 11 breeding pairs/10 ha, respectively, but were nearly equal in population biomass and caloric density because of differences in their body weights. The flycatcher had high fledging success, producing 71 young on the 10-ha study plot from an estimated 95 eggs laid (Table 1), while the vireo had moderate breeding success in 1971 but failed to produce any surviving fledglings in 1972. The Black-throated Blue Warblers had a density of 4.2 pairs per 10 ha, considerably lower than that of the other two species, and consequently had a markedly lower population standing crop (Fig. 1). Their breeding success varied greatly from year to year but usually was less than 40% (Black 1975). The prime cause of breeding failure was predation, which was mainly on nests that were in low shrubs, and hence accessible to chipmunks (*Tamias striatus*) and other ground-active predators (Black 1975).

Least Flycatchers departed from the Hubbard Brook forest in mid- to late July, or about 10 to 15 days after the fledging of their young (Fig. 1). Most vireos and warblers stayed in the forest through the month of August, with their numbers decreasing by late August and September (Fig. 1).

STANDARD METABOLISM AND NOCTURNAL THERMOREGULATION

Standard metabolism rates determined in the laboratory for each species (Table 2) are within 10% of the values calculated from the appropriate equation of Aschoff and Pohl (1970). Metabolic responses to decreasing temperatures differed among the species (Table 2). The flycatcher, with a high, lower critical temperature (LCT) and a comparatively steep slope to the regression line of oxygen consumption on ambient temperature, must increase its metabolic rate sooner and faster in response to decreasing temperatures than either of the other two species. The warbler, with the lowest LCT, can tolerate cooler temperatures before increasing thermogenesis, but because of the steeper slope to its regression line (Table 2), it uses energy faster in response to decreasing temperatures than does the vireo. Combining these results with those on nocturnal temperatures in the Hubbard Brook forest in 1971 (for the vireos) and 1972 (for the flycatcher and warbler), we computed the energy expenditures necessary for thermoregulation by a sitting ("sleeping") bird of each species at night. The results show that flycatchers, vireos and warblers, expend an average of 2.8, 1.8 and 2.2 × SMR per hour, respectively, at night for thermoregulatory costs during their summer stay in the Hubbard Brook forest (Table 2). These values seem

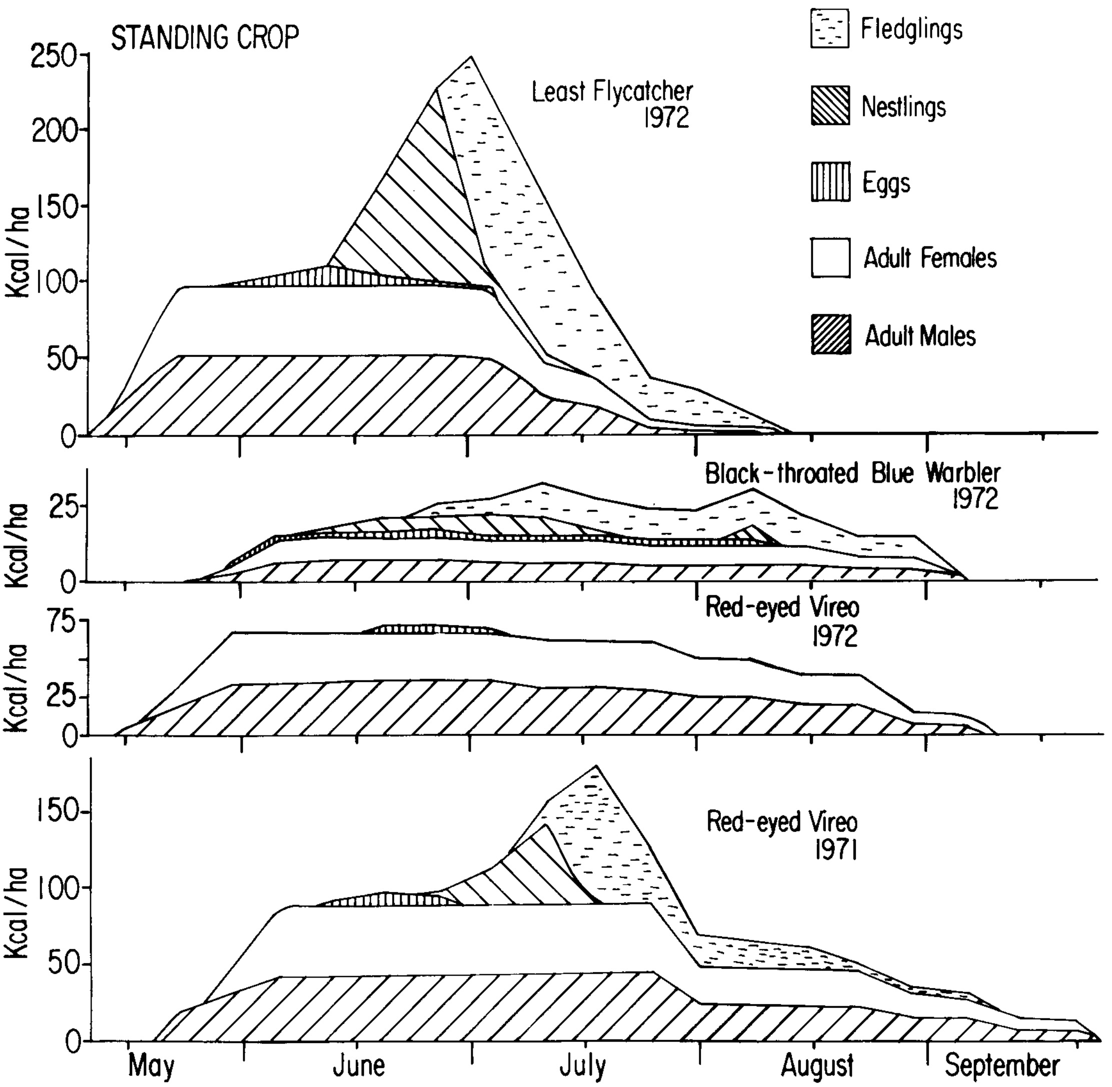

FIGURE 1. Seasonal patterns of standing crop biomass for breeding Least Flycatcher, Black-throated Blue Warbler and Red-eyed Vireo populations in the Hubbard Brook forest, 1971–1972. Note difference in scale (2×) for the warbler.

high but they indicate the importance that cool night temperatures can have on an individual's energy budget.

TIME BUDGETS AND DAILY ENERGY EXPENDITURES (DEE)

The time and energy budgets for each species during their stay in the Hubbard Brook forest are given in Tables 3, 4, and 5. The sample sizes indicated for the time budgets represent the accumulated times that individuals were in full sight. These differed among the species, depending on their ease of observation; because the vireo and flycatcher occurred higher in the forest canopy, they could be followed directly only for short periods of time (seconds to a few minutes at most) before going out of sight behind foliage. However, even when they were out of view, we usually knew their general whereabouts and activities, and we feel from the hundreds of hours spent collecting the data in the tables that the results represent accurately the proportion of time spent in each activity by individuals of each of the three species. The most significant and variable feature of these budgets is the amount of time and energy spent in flight. Because flight is both energetically expensive and an important component of the major activities of the breeding period, changes in its frequencies explain many changes in energy expended.

Overall DEE values were higher for the Least Flycatcher than the other two species,

TABLE 2. Weights, metabolic responses, and estimated night metabolism.

	Least Flycatcher	Red-eyed Vireo	Black-throated Blue Warbler
x̄ Adult weight (g)	10.0	17.0	9.4
Standard metabolic rate ± SD (cc O_2/g/h)	4.27 ± 0.13	3.38 ± 0.55	3.49 ± 0.15
Temperature-metabolism response (cc O_2/g/h)			
y intercept	11.29	7.32	7.87
slope	–0.209	–0.128	–0.184
regression correlation	0.98	0.85	0.92
lower critical temperature (°C)	32	30	24
x̄ Night metabolism (× standard metabolic rate)	2.76[a]	1.8[b]	2.2[a]

[a] Summer 1972.
[b] Summer 1971.

largely because it flew more while foraging. The warblers had an intermediate DEE level, while the vireo, with its larger body size and slower foraging mode involving comparatively less flight, had the lowest DEE.

Within each species, time and energy expenditures of males and females were approximately equal and parallel through the summer season, with some variation due to their different roles in breeding activities. Early in the nesting cycle, male flights were involved with territorial defense and feeding, while females flew to gather nest material and to feed. With the exception of male vireos during the nest-building phase (Table 4), males exhibited increasing frequencies of flight and energetic costs from the beginning of the nest cycle through incubation. Male vireos in fact had their maximum DEE during the incubation period, which corresponds to the most intense period of territorial defense (Holmes, unpubl. data). Similar patterns of increased territory size and/or intensity of defense by males during incubation have been reported by Root (1967), Yarrow (1970), Edington and Edington (1972) and others, suggesting that this phenomenon may be widespread among woodland passerines.

When dependent young were being fed, flight times and DEEs of male flycatchers increased sharply. Flight time accounted for slightly more than 20% of daylight hours and males sang very infrequently, reflecting reduced territorial activity (Table 3). Male warblers showed a moderate increase in flight-time and DEE with hatching of their young (Table 5), and some decline in singing frequency although not as great as that seen in the flycatcher (Black 1975). In contrast, male vireos showed a decrease in both flight time and DEE after their young hatched, corresponding to their lower rate of participation in the feeding of young (Table 1), to decreased territorial defense, and perhaps to an increase in available food at this time of the season (Holmes, unpubl. data).

Females of all three species expended the most energy when gathering nest materials,

TABLE 3. Physical time budget (percent daylight hours) and estimated daily energy expenditure (DEE in kcal/g/day) for Least Flycatchers, 1972.

	Prenesting: Percent time (DEE)	Building-laying: Percent time (DEE)	Incubating: Percent time (DEE)	Nestling: Percent time (DEE)	Post-fledging: Percent time (DEE)
MALES (n = 12,720 seconds)[a]					
Flight	5.8 (0.166)	5.8 (0.190)	6.5 (0.215)	15.5 (0.509)	19.5 (0.560)
Sing	7.0 (0.040)	7.0 (0.046)	7.0 (0.046)	– –	– –
Sit	87.2 (0.376)	87.2 (0.430)	86.5 (0.426)	84.5 (0.416)	80.5 (0.347)
Sleep	– (0.570)	– (0.456)	– (0.456)	– (0.456)	– (0.570)
SDA	– (0.147)	– (0.147)	– (0.147)	– (0.147)	– (0.147)
Total DEE	(1.299)	(1.269)	(1.290)	(1.528)	(1.624)
FEMALES (n = 13,560 seconds)[a]					
Flight	5.0 (0.144)	6.0 (0.197)	3.3 (0.133)	19.8 (0.648)	22.4 (0.644)
Sit	95.0 (0.410)	94.0 (0.463)	17.0 (0.103)	80.2 (0.395)	77.6 (0.334)
Sleep	– (0.570)	– (0.456)	– (0.456)	– (0.456)	– (0.570)
Incubate	– –	– –	79.2 (0.324)	– –	– –
Egg production	– –	– (0.183)	– –	– –	– –
SDA	– (0.147)	– (0.147)	– (0.147)	– (0.147)	– (0.147)
Total DEE	(1.271)	(1.446)	(1.163)	(1.646)	(1.695)

[a] Total accumulated observation time.

TABLE 4. Physical time budget (percent daylight hours) and estimated daily energy expenditure (DEE in kcal/g/day) for Red-eyed Vireos, 1971.

	Prenesting: Percent time (DEE)	Building-laying: Percent time (DEE)	Incubating: Percent time (DEE)	Nestling: Percent time (DEE)	Post-fledging: Percent time (DEE)
MALES (n = 23,340 seconds)[a]					
Flight	5.3 (0.122)	2.5 (0.066)	8.3 (0.219)	3.4 (0.090)	1.4 (0.032)
Hop	3.3 (0.038)	1.0 (0.013)	1.6 (0.021)	2.5 (0.033)	1.5 (0.017)
Sit	91.4 (0.317)	96.5 (0.383)	90.1 (0.358)	94.1 (0.373)	97.1 (0.337)
Sleep	– (0.300)	– (0.240)	– (0.240)	– (0.240)	– (0.300)
SDA	– (0.119)	– (0.119)	– (0.119)	– (0.119)	– (0.119)
Total DEE	(0.896)	(0.821)	(0.957)	(0.855)	(0.805)
FEMALES (n = 9,060 seconds)[a]					
Flight	4.9 (0.113)	7.1 (0.187)	0.99 (0.026)	8.2 (0.216)	2.6 (0.060)
Hop	5.6 (0.065)	2.4 (0.032)	0.56 (0.007)	3.8 (0.050)	2.5 (0.029)
Sit	89.5 (0.311)	90.5 (0.359)	21.57 (0.086)	88.0 (0.349)	94.5 (0.392)
Sleep	– (0.300)	– (0.240)	– (0.240)	– (0.240)	– (0.300)
Incubate	– –	– –	77.0 (0.265)	– –	– –
Egg production	– –	– (0.154)	– –	– –	– –
SDA	– (0.119)	– (0.119)	– (0.119)	– (0.119)	– (0.119)
Total DEE	(0.908)	(1.091)	(0.743)	(0.974)	(0.900)

[a] Total accumulated observation time.

and/or producing eggs and when feeding young (Tables 3, 4, and 5)—all times and activities involving frequent flights. DEEs were lowest for females during incubation when they were sitting on their nests for 75 to 80% of the daylight hours, even though energy was being used in the incubation process. The sudden and dramatic increase in flight time and DEE of female flycatchers with the hatching of young (Table 3), corresponding to the similar pattern in their males, suggests that foraging to feed young is a particularly demanding and costly activity for this species.

POPULATION ENERGETICS

Total population assimilation rates or energy flows for the three species during their stay in the Hubbard Brook forest were obtained by combining information on: (1) densities and biomass through the seasons (Fig. 1), (2) respiratory energy (DEE) expended by adults and fledged young as determined from time-budgets and metabolic estimates (Tables 3, 4, and 5), (3) the biomass and its caloric density of eggs and young produced, and (4) the respiratory energy utilized by nestlings. To calculate population energy flow

TABLE 5. Physical time budget (percent daylight hours) and estimated energy expenditure (DEE in kcal/g/day) for Black-throated Blue Warblers, 1972. (Adapted from Black 1975, unpubl. data.)

	Prenesting: Percent time (DEE)	Building: Percent time (DEE)	Laying: Percent time (DEE)	Incubating: Percent time (DEE)	Nestling: Percent time (DEE)	Fledging: Percent time (DEE)
MALES (n = 105,840 seconds)[a]						
Flight	5.2 (0.139)	5.1 (0.138)	6.9 (0.185)	7.1 (0.191)	7.2 (0.193)	7.2 (0.193)
Hop	3.4 (0.045)	3.7 (0.050)	3.8 (0.050)	4.2 (0.056)	6.5 (0.087)	6.7 (0.090)
Sit	91.4 (0.368)	91.2 (0.358)	89.0 (0.358)	88.7 (0.358)	87.6 (0.353)	88.2 (0.355)
Sleep	– (0.292)	– (0.292)	– (0.292)	– (0.292)	– (0.292)	– (0.292)
SDA	– (0.121)	– (0.121)	– (0.121)	– (0.121)	– (0.121)	– (0.121)
Total DEE	(0.965)	(0.959)	(1.006)	(1.018)	(1.046)	(1.051)
FEMALES (n = 94,980 seconds)[a]						
Flight	4.8 (0.128)	6.2 (0.166)	5.3 (0.143)	3.5 (0.094)	9.7 (0.260)	6.8 (0.183)
Hop	4.2 (0.056)	5.7 (0.076)	5.7 (0.076)	8.3 (0.112)	7.4 (0.099)	6.7 (0.090)
Sit	91.0 (0.368)	88.9 (0.358)	89.0 (0.358)	12.4 (0.047)	83.8 (0.338)	86.3 (0.348)
Sleep	– (0.292)	– (0.292)	– (0.292)	– (0.292)	– (0.292)	– (0.292)
Incubate	– –	– –	– –	75.5 (0.264)	– –	– –
Egg production	– –	– –	– (0.187)	– –	– –	– –
SDA	– (0.121)	– (0.121)	– (0.121)	– (0.121)	– (0.121)	– (0.121)
Total DEE	(0.965)	(1.013)	(1.177)	(0.981)	(1.110)	(1.034)

[a] Total accumulated observation time.

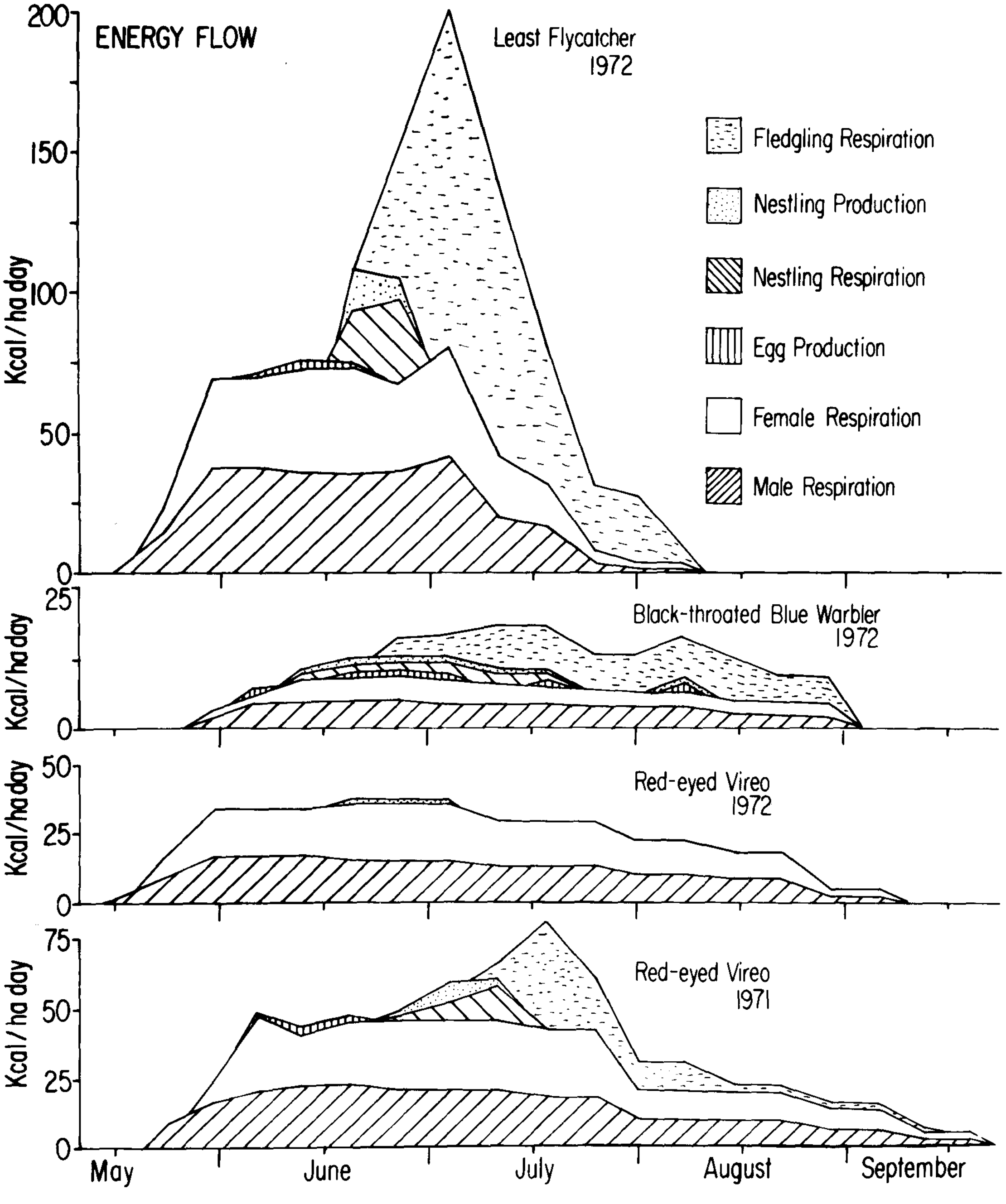

FIGURE 2. Seasonal patterns of energy utilization by breeding Least Flycatcher, Black-throated Blue Warbler and Red-eyed Vireo populations in the Hubbard Brook forest, 1971–1972. Note difference in scale (2×) for the warbler.

for Red-eyed Vireos in 1972, we used DEE values determined in 1971 in combination with the 1972 vireo density and reproductive data (Fig. 1, Table 1).

The total seasonal population energy budgets and especially the production of young were strikingly different among the three species (Fig. 2). The net production efficiency of the flycatcher was more than twice that for the warbler and 20% greater than that for the vireo in 1971. In 1972, the vireos failed to produce any young; nests were constructed and some eggs were laid, but incubation never commenced. Shortly after the nests were completed, certain pairs began building second nests, usually in different but nearby trees, often using materials from the first nest. In one case a pair was seen to build three successive nests, but the female never incubated. This aberrant behavior took place in the first season (1972) following the collapse of a defoliating caterpillar population which had been in outbreak phase during the preceding three summers (Holmes and Sturges 1975).

The timing of peak energy demand differed among the three species (Fig. 2), occurring in early July for the flycatcher, mid-July for the vireo, and at relatively low levels throughout the summer for the warbler. Total population energy flow in kcal/ha for the entire summer seasons were estimated to be as follows: 7,045 for the flycatcher (in 1972), 4,353 and 2,817 for the vireo (in 1971 and 1972, respectively), and 957 for the warbler (in 1972). Net production (energy content represented by all fledged young) equalled 126.5 kcal/ha for the flycatchers, 78.7 kcal/ha for the vireos, and 8.7 kcal/ha for the warblers; these represent 1.9, 1.6 and 0.9% of total energy assimilated by the populations during their stay in the breeding area. These net production values agree with previous estimates of production for the Hubbard Brook avian community as a whole (Holmes and Sturges 1975) and for terrestrial vertebrates in general (Golley 1968).

DISCUSSION

How realistic are the energy flow values obtained here, can they provide a basis for estimating energy utilization by larger segments of the avian community, and how can they be useful in considerations of life history patterns and community structure?

ENERGY BUDGET ESTIMATES

King (1974) reviewed studies of energy expenditure by free-living birds and found DEE/SMR ratios ranging from 1.7 to 6.1 and averaging 3.5. These were based on determinations of DEE from studies using a variety of techniques and included data from species at arctic latitudes, birds in winter, and short-term determinations of energy expended during specific activities such as egg-laying or feeding of nestlings. These are all circumstances that would be expected to yield relatively high DEE values.

To obtain DEE/SMR ratios for the species in this study, we compared the seasonal energy expenditures of each population with those for SMR by the same number of individuals of each species for the same time period which were calculated from Aschoff and Pohl's (1970) equation relating metabolism to body weight of passerines during the rest phase of their diurnal cycle. The ratios so obtained are 3.8, 2.2, and 1.8 × SMR for the flycatcher, vireo and warbler, respectively. These average 2.6 × SMR and include not only the energy involved in self-maintenance by all members of the population during their stay in the forest, but that channelled into the production of young as well. They do not include energy expenditure for fat deposition or for molt, both of which are insignificant in these species in summer at Hubbard Brook (Holmes 1976, unpubl. data).

The results presented here suggest that energy values ranging between 2.0 and 3.0 × SMR might be expected to give realistic but probably conservative estimates of population energy expenditure by insectivorous passerines during the breeding season in north temperate forests. Holmes and Sturges (1973, 1975), using a conversion factor of 2.5 × SMR (based in part on the results presented in this paper), estimated the energy flow for the entire avian community at Hubbard Brook and found general agreement with values predicted from energy transfer efficiencies. Therefore, despite the problems inherent in measuring time budgets of forest birds, in determining metabolic costs of the different activities and in combining these together, reasonable estimates of population energy budgets can be obtained. Such conversion factors when applied to a large number of species can provide a means for examining avian energetics at the community level when, for instance, the relative contributions of different species populations or guilds are being compared or when the overall magnitude of energy flow by various consumer groups is being considered.

ENERGETICS AND LIFE HISTORY ADAPTATIONS

The differences in population energy expenditures among Least Flycatchers, Red-eyed Vireos and Black-throated Blue Warblers in the Hubbard Brook forest can be accounted for largely by differences in their life histories.

The higher density and standing crop of the flycatcher population, and its greater metabolic requirements, made it the dominant energy user among the three species and indeed for the bird community as a whole (Holmes and Sturges 1975). The large DEE of the flycatcher resulted from its greater metabolic response to decreasing ambient temperatures, higher nesting success, and energetically more expensive methods of foraging, namely the high frequencies of flight involved in hawking and hovering for insects. The flycatchers foraged at mid-heights in the forest where foliage was most open and where they probably could perform aerial feeding maneuvers with least interference (Sherry 1975). Although the flycatchers used the most energy of the three species, they lived in the forest for the shortest length of time. Their mid-season departure may be related to a change in the abundance of a main food source (e.g. flying insects) or to lower night temperatures in late summer that would even further increase their metabolic expenditures.

Black-throated Blue Warblers used about one-sixth as much energy as the flycatchers even though they remained nearly twice as long in the forest. They had an intermediate rate of DEE and appeared to be more closely adapted to the cool understory of northern forests, as evidenced by their lower critical temperature and lower metabolic responses to decreasing temperatures. They occurred at low densities in the understory where their distribution was patchy, coinciding largely with areas of high density foliage where nesting and most feeding occur (Black 1975). Since nests were placed in dense foliage near the ground where they were susceptible to predation, productivity was low and the pairs tended to be asynchronous in their breeding effort so that no major peak in standing crop or energy utilization was evident during the summer season (Figs. 1 and 2). Their habit of foraging primarily by gleaning insects from foliage was energetically inexpensive compared to that of the flycatcher.

Red-eyed Vireos showed an intermediate pattern with respect to densities, productivities, metabolic responses to temperatures, and length of residency in the forest. They had the lowest DEE rate but because of their moderate numbers and larger body size, their total population energy flow was intermediate in level. Male vireos spent more time and energy in territorial defense, especially during the incubation period, than did males of the other species. During the two years of this study, they fed mainly by gleaning insects, primarily caterpillars, from the outer twigs and foliage of canopy trees. This foraging mode appears to be the most energetically economic when compared to those of the other two species, since it involves relatively fewer flights. This may be one reason why this species is so successful over wide areas of eastern deciduous forest. The production of young by vireos seems to be vulnerable to annual variations in certain types of prey, as indicated by the breeding failure in 1972.

Time-energy budgets, when combined with data on population and standing crop, can be used to assess quantitatively the energetic costs of different life history patterns. Further, and perhaps even more importantly, they provide information on the relative and seasonal energy demands of sympatric species that are necessary to understanding ecosystem trophic dynamics and bird community structure. The flycatcher, the vireo and the warbler represent three different ecological guilds ("flycatchers," the "canopy hoverers-gleaners," and the "shrub foliage gleaners," respectively). Because their adaptive habits, which represent different ways of exploiting the forest environment, require different levels of energy expenditure, analyses of the energetic demands of different populations and functional units within the community can provide critical information on patterns of resource utilization, interactions between species, and other aspects of community dynamics.

SUMMARY

Patterns of time and energy allocation were determined for breeding populations of Least Flycatchers, Red-eyed Vireos and Black-throated Blue Warblers in the Hubbard Brook Experimental Forest, New Hampshire. Daily energy expenditures ranged from 0.7 to 1.7 kcal/g/day, varying with the species and phase of nest-cycle.

Differences in population energy budgets relate to each species' life history characteristics, particularly its reproductive pattern, density, and foraging mode. Least Flycatchers, despite their relatively brief residency in the forest, were the dominant energy users because of their higher densities, greater productivity, higher metabolic responses to cool night temperatures, and more frequent flight associated with aerial foraging. Black-throated Blue Warblers used the least amount of energy for thermoregulation at night, required intermediate levels of energy expenditure for foraging, but had the lowest levels of production, largely because of high predation rates at nests. Red-eyed Vireos, although the largest of the three species, were intermediate in population energy flow and thermoregulatory responses. The foraging mode of vireos was the least expensive energetically, but their reproductive success appeared to be sensitive to the abundance of special prey items.

Total energy assimilated during their residence in the breeding area was 7,045, 4,353, and 975 kcal/ha for the flycatcher, vireo and warbler populations, respectively. These values represent 3.8, 2.2, and 1.8 × estimated seasonal standard metabolic rate (SMR) val-

ues and provide conversion factors for general use in studies of bird community structure and energetics.

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RECENT PUBLICATIONS

Migratory game bird hunters and hunting in Canada.—Edited by H. Boyd and G. H. Finney. 1978. Canadian Wildlife Service Report Series No. 43. 125 p. Paper cover. Canada $7.50, other countries $9.00. Available: Printing and Publishing, Supply and Services Canada, Ottawa, Canada K1A 0S9. Canada has perhaps the best surveys of migratory game bird hunters and hunting in the world. This report describes the genesis and development of those surveys and summarizes some of the principal results. Chapters by various authors present the survey system, profiles of the hunters, distribution of waterfowl kill, and a few specific studies. Boyd offers thoughtful conclusions on the role of harvest surveys in managing the exploitation of waterfowl in Canada. Administrators and managers of wildlife throughout North America will be interested in this book.

Birds Protected in Canada under the Migratory Birds Convention Act.—1978 edition. Canadian Wildlife Service Occasional Paper No. 1. 38 p. Paper cover. Available: as above. Cat. No. CW 69-1/1-1978. "This publication lists all species of migratory birds included in the Convention and found in Canada, the continental United States and adjacent waters to a distance of 320 kilometers from land or half the distance to a neighboring country, whichever is the least." The list is in taxonomic order and was largely prepared by W. E. Godfrey, former Curator of Ornithology, National Museum of Canada. Given for each species are its A.O.U. number, if any, its scientific, English, and French names, and its status.

Spatial changes in waterfowl habitat, 1964–74, on two land types, in the Manitoba Newdale Plain.—G. D. Adams and G. C. Gentle. 1978. Canadian Wildlife Service Occasional Paper No. 38. 27 p. Paper cover. Available: as above. Cat. No. CW 69-1/38. Newdale Plain, in southwestern Manitoba, is one of the finest waterfowl breeding regions in North America. With the aid of aerial photography, the effects of spatial changes in wetlands and vegetative cover were studied in sample areas over a ten-year span. The methods used and the findings will interest waterfowl biologists in the prairie provinces and neighboring U.S.