NUTRIENT AND ENERGETIC CHARACTERISTICS OF SWEEPNET-COLLECTED INVERTEBRATES

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Abstract.—As a result of the importance of food resources, primarily invertebrate biomass, to the understanding of reproductive strategies of grassland birds, the nutrient and energy characteristics of invertebrate biomass were investigated during late spring and early summer. Sweepnets were used to collect invertebrate biomass on two sites in eastern Kansas and the collections were separated into order or family groups. Nutrient and energy characteristics of those taxonomic groups with sufficient biomass at the family or order level were measured. Fat contents of families ranged from 8% (dry mass) for Acrididae to 32% for Miridae. Crude protein ranged from 54% for a composite sample of Hemiptera to 77% for Araneida. Crude fiber ranged from 5–8% for Araneida to 17–18% for Hemiptera. Calcium levels varied from 1292 ppm in Diptera to 2560 ppm in Lepidoptera, and phosphorous levels ranged from 5840 ppm in a composite Hemiptera sample to 9360 ppm in Pentatomidae. Gross energy contents ranged from 4906 cal/g for a sample of Acrididae to 6452 cal/g for Cydnidae. Pooled invertebrate biomass collections from the two sites differed in fat, crude fiber and energy content. Implications of these results on studies of the interactions of food resources, foraging behavior, habitat fragmentation and reproductive strategies of birds are discussed.

CARACTERÍSTICAS NUTRITIVAS Y ENERGÉTICAS DE INVERTEBRADOS COLECTADOS A TRAVÉS DE REDES

Sinopsis.—Dada la importancia de los recursos alimenticios, sobre todo la biomasa de invertebrados, con las estrategias reproductivas de aves en los pastizales, se investigó las características nutritivas y energéticas de la biomasa de invertebrados desde la primavera tardía hasta el verano temprano. Se usaron redes de barrido para colectar biomasa invertebrada que se dividió en órdenes y familias en dos lugares al este de Kansas. Se estudiaron las características nutricionales y energéticas de los grupos taxonómicos con suficiente biomasa al nivel de familia u orden. El contenido de grasa fluctuó entre 8% (masa seca) en Acrididae y 32% en Miridae. El contenido de proteína pura fluctuó entre 54% en una muestra compuesta de Hemíptera y 77% en Aranéida. El porcentaje de fibra cruda fluctuó entre 5–8% en Aranéida y 17–18% en Hemíptera. Los niveles de calcio fluctuaron entre 1292 ppm en dípteros y 2560 ppm en lepidópteros, mientras que los niveles de fósforo fluctuaron entre 5840 ppm en una muestra mixta de hemípteros y 6452 en pentatómidos. Los contenidos de energía bruta fluctuaron entre 4906 cal/g en una muestra de Acrididae y 6452 cal/g para Cydnidae. Las colecciones combinadas de biomasa invertebrada difirieron entre los dos lugares con respecto a su grasa, fibra bruta y contenido energético. Se discuten las implicaciones de estos resultados a estudios sobre las interacciones de recursos alimenticios, comportamiento de forrajeo, fragmentación de hábitat y estrategias reproductivas de las aves.

Avian demands for food resources are high during the breeding season. It is during this period that animal matter (primarily invertebrate biomass) provides an important source of nutrients and energy, often comprising over half of the dietary intake of grassland birds (Martin et al. 1951, Risser et al. 1981).

Limited food resources during the nesting period can adversely affect pre- and postfledging survival (Best 1978), and providing food needed by young during those stages is a significant component of the parental investment for altricial species (Weathers 1992). Avian territory size often is related to food abundance (Cody 1985), and nesting habitats with abundant food are thought to provide a selective advantage for birds over those where food is scarce (Blancher and Robertson 1987). Arcese and Smith (1988) found that clutch size, nestling mass and number of breeding attempts of Song Sparrows (*Melospiza melodia*) were affected by food supply, and Martin (1992) determined that adequate food resources near the nests of Song Sparrows could reduce predation and Brown-headed Cowbird (*Molothrus ater*) parasitism. Johnston (1993) demonstrated that diet quality effected nestling growth of an insectivorous passerine, the House Martin (*Delichon urbica*).

Although the nutritional and energetic requirements for growth of young birds are recognized, few specific data are available to evaluate qualitatively these characteristics of animal matter available to wild avian species. Golley (1961) found that a composite insect sample contained 5363 cal/g of energy, whereas 5050 and 5903 cal/g were reported by Robel et al. (1974 and 1979, respectively). Calvert et al. (1969) determined that Diptera samples contained 63% crude protein, and Landry et al. (1986) reported 49–58% for that in Lepidoptera. Calvert et al. (1969) found that Diptera pupae contained 16% fat, whereas Landry et al. (1986) reported that biomass of Lepidoptera contained 10–21% fat. Even though these class- and order-level data may be adequate for broad assessments of the nutritional characteristics and energy contents of invertebrate biomasses, we saw a need to characterize more precisely the qualitative aspects of invertebrate biomass available to unconfined avian species especially in light of nutrient content changes associated with diet, seasons and maturity of insects (Slansky and Scriber 1985).

Sweepnet collections obtained by Johnson (1993) and Henning (1993) in 1989 and 1990, respectively, provided material to assess some nutritional attributes of invertebrate biomasses in Kansas. Specifically, we determined (1) if taxonomic groups of invertebrates differed in nutrient or energy content and (2) if invertebrate biomasses from different sites differed in nutrient or energy content.

METHODS AND MATERIALS

Invertebrate samples used in this study were collected during the summers of 1989 and 1990 from three fields at two locations in the Flint Hills region of eastern Kansas. One field was on the Konza Prairie Research Natural Area (39°05′N, 96°35′W) near Manhattan, and two were on the

Fall River Wildlife Management Area (37°33'N, 95°58'W) just south of
Eureka. Annual precipitation in the area averages 76 cm, with 75% of it
falling as rain during the summer. The fields were on well drained low-
land soils not treated with insecticides or herbicides for at least 5 yr. Pre-
vious to this study, the field at Konza had been seeded to smooth brome
(*Bromus inermis*), whereas one of the Fall River fields had been used to
raise wheat (*Triticum astivum*) and the other to raise milo (*Sorghum bi-
color*). The fields were disked at various times beginning in 1988 and
allowed to revegetate naturally. The location of each field, its cropping
history, soil type and other characteristics are detailed in Henning (1993).

Invertebrate samples were collected by sweepnetting with standard can-
vas beating nets along three randomly located permanent transects in
each of the fields at 2-wk intervals; late June, early July, mid July, and late
July in both 1989 and 1990. Sampling was done between 1000 and 1500
hours on days when cloud cover was <50%, winds <24 km/h, and am-
bient temperature 25–40 C. Contents of sweepnets were placed in ethyl-
acetate kill jars until invertebrates were dead, then transferred to labeled
plastic bags, sealed and stored frozen.

The identity of the invertebrates was determined by separating the
thawed invertebrates from vegetative debris, allowing the invertebrates to
air dry, and sorting them to families or orders following procedures of
Elzinga (1987). The invertebrates in taxonomic groups were then dried
at 70 C for 48 h, and each group was weighed separately to 0.1 mg.
Voucher specimens of families and orders were deposited in the Ento-
mology Museum of Kansas State University (Voucher Collection No. 029),
Manhattan, Kansas.

After the invertebrates were identified and masses for sites and collec-
tion dates were determined, the 1989 samples were pooled by sampling
site and date (three sites and four sampling dates). The 1990 samples
were pooled by taxonomic group (family or order) by site (Fall River and
Konza). Pooled samples were placed in sealed glass vials and stored in
the dark at room temperature. These pooled samples were analyzed to
determine nutrient and energy characteristics of the invertebrate collec-
tions.

Analytical procedures.—For our invertebrate samples, we determined
ether extractable fat, crude protein, ash and crude fiber; calcium and
phosphorous levels (ppm); and gross energy content (cal/g). When bio-
masses of taxonomic groups were insufficient to determine all of the
above, we set priority in the following order; energy, crude protein, fat,
crude fiber, ash, and calcium and phosphorous. Each invertebrate sample
was ground into a homogeneous mixture prior to analysis. Duplicate anal-
yses were conducted for each, and the means reported or used in statis-
tical calculations. When the results of the duplicate analyses differed by
more than 9 or 2% for a nutrient or energy content, respectively, a third
analysis was conducted and the variant result discarded.

Gross energy contents of samples were quantified in a Parr series 1200
adiabatic oxygen bomb calorimeter under 27 atmospheres of pressure.

Proximate analysis (Crampton 1956) was used to separate nutrient contents of invertebrate samples as follows. Percent nitrogen levels determined using Kjeldahl digestion procedures were multiplied by 6.25 to estimate crude protein. Ether extractable fat content was determined in a Goldfisch extraction apparatus. Crude fiber percentages were determined using a Thermolyne crude fiber apparatus to digest samples, and percent ash was measured in a muffle furnace at 600 C. Calcium and phosphorous levels of ash were determined by atomic absorption; calcium using a Varian spectrophotometer at 422.7 nm, and phosphorous at 700 nm on a Gilford spectrophotometer. All measurements are expressed on a dry matter basis.

As invertebrate samples collected in 1990 were pooled by taxonomic groups and sampling site, those data did not have multiple samples and could not be analyzed statistically. The invertebrate samples collected in 1989 were pooled by collection dates (four) for each of three sites, and those multiple data points were analyzed using analysis of variance. The general linear models procedure of SAS (SAS Institute Inc. 1989) was used to measure differences between sites, and SAS linear regression models were used to measure changes with time. Nutrient or energy values were the dependent variables, and sites or dates of collection the independent variables. A probability level of $P = 0.05$ was considered significant, and where appropriate, means ($\bar{x}$) are presented $\pm$ standard errors (SE).

RESULTS

We collected 213 and 1049 g (dry mass) of invertebrate biomass from our experimental fields in 1989 and 1990, respectively. We identified 56 families (14 orders) of invertebrates in the 1989 sweepnet samples and 55 families (14 orders) in the 1990 samples. The 1990 collections contained sufficient biomass to conduct proximate analyses on samples of 12 families/orders, determine calcium and phosphorous levels for samples of 10 families/orders, and measure the energy content of samples of 17 families/orders. The taxonomic groups analyzed represented approximately 93% of the invertebrate biomass collected from the Fall River sites and 90% of that from the Konza site.

Acrididae (short-horned grasshoppers) constituted most of the invertebrate biomass collected in 1990 from the Fall River and Konza sites (Table 1). Of the other taxonomic groups collected, only Delphacidae (delphacid planthoppers), Lepidoptera (butterflies and moths) and Tettigoniidae (long-horned grasshoppers), contributed more than 6% to the total biomass of invertebrates collected from either site (Table 1). Details of biomasses of the various invertebrates collected are in Johnson (1993) and Henning (1993).

Fat contents of Acrididae from the Fall River and Konza sites were considerably lower than the fat contents of the other taxonomic groups (Table 1). The fat contents of Delphacidae, Miridae (plant bugs), Coccinellidae (ladybird beetles), and Hemiptera (true bugs except Miridae,

TABLE 1. Composition determined by proximate analysis of taxonomic groupings of invertebrate samples collected with sweepnets from the Fall River Wildlife Management Area (FR) and the Konza Prairie Research Natural Area (KO) during June and July 1990.

| Category | Site | Sample[a] | Dry mass composition (%) | | | |
			Fat	Crude protein	Ash	Crude fiber
Acrididae	FR	40.5	7.5	70.1	5.6	8.5
	KO	56.1	9.1	75.8	4.8	10.6
Delphacidae	FR	20.0	21.9	55.5	4.0	9.0
Lygaeidae	FR	4.2	17.6	55.9	4.4	13.4
Diptera	FR	4.0	11.4	65.8	4.0	10.9
Araneida	FR	4.9	19.6	70.2	4.2	5.4
	KO	5.1	15.7	77.1	5.5	7.6
Miridae	FR	5.8	31.7	54.9	3.5	7.8
Coccinellidae	FR	<2.5	24.5	62.4	3.0	13.1
Orthoptera[b]	FR	<2.5	17.2	67.0	4.6	6.5
Rhopalidae	FR	3.4	14.2	62.3	3.1	13.5
Hemiptera[c]	FR	<2.5	32.0	54.1	3.7	16.5
	KO	5.1	31.4	54.4	4.0	17.5
Lepidoptera	FR	<2.5	17.7	68.2	7.5	8.1
	KO	7.6	17.2	64.0	7.1	7.6
Tettigoniidae	KO	7.6	12.5	71.0	5.7	9.8

[a] Percent of total invertebrate biomass collected at each site.
[b] Comprises families in the order other than Acrididae and Tettigoniidae.
[c] Comprises families in the order other than Lygaeidae, Miridae and Rhopalidae.

Lygaeidae and Rhopalidae) exceeded 20%. The crude protein contents of the invertebrate groupings varied widely, ranging from 54 to 56% for Delphacidae, Lygaeidae (seed bugs), Miridae and Hemiptera to >70% for Acrididae, Araneida (araneae spiders), and Tettigoniidae (Table 1). The ash contents of the samples were generally <6%, except for Lepidoptera (7%). Crude fiber contents of the taxonomic groups ranged from lows of 5.4% (Araneida from Fall River) and 6.5% (Orthoptera) to highs of 16.5 and 17.5% for Hemiptera samples from Fall River and Konza, respectively (Table 1).

Calcium levels in the invertebrate samples ranged from 1292 ppm for Diptera (flies) from the Fall River site to 2560 ppm for Lepidoptera from the Konza site (Table 2). The concentration of calcium in Acrididae from Fall River appeared higher than that for Acrididae from Konza, whereas the calcium levels were almost identical for Araneida from Fall River and Konza. Phosphorous levels ranged from 5840 ppm for Hemiptera to 9360 ppm for Pentatomidae (stink bugs) from the Konza site (Table 2). The levels of phosphorous in Acrididae from Fall River and Konza were similar whereas the levels of phosphorous in Araneida from the two sites differed by approximately 350 ppm (Table 2).

Energy contents of the taxonomic groups ranged from 4906 to over 6000 cal/g (Table 3). The energy contents of Pentatomidae, Lepidoptera, Diptera and Acrididae were similar for those taxonomic groups collected

TABLE 2. Calcium and phosphorus contents (ppm) of taxonomic groupings of invertebrate samples collected with sweepnets from the Fall River Wildlife Management Area and the Konza Prairie Research natural Area during June and July 1990.

	Fall River		Konza Prairie	
Category	Calcium	Phosphorous	Calcium	Phosphorous
Acrididae	1779	7004	1376	6998
Delphacidae	1868	6730	—[a]	—
Diptera	1292	7539	—	—
Araneida	1458	8696	1489	9047
Miridae	1339	7184	—	—
Rhopalidae	1517	6042	—	—
Tettigoniidae	—	—	1674	7568
Hemiptera[b]	—	—	1629	5840
Lepidoptera	—	—	2560	7040
Pentatomidae	—	—	2442	9360

[a] Sample not large enough to conduct analysis.
[b] Comprises families in the order other than Pentatomidae, Miridae and Rhopalidae.

TABLE 3. Gross energy contents of taxonomic groupings of invertebrate samples collected with sweepnets from the Fall River Wildlife Management Area and the Konza Prairie Research Natural Area during June and July 1990.

	Energy content (cal/g dry mass)	
Category	Fall River	Konza Prairie
Acrididae	5043	4906
Delphacidae	5594	—[a]
Lygaeidae	5350	—
Diptera	5111	5186
Araneida	5616	5344
Miridae	6031	—
Tettigoniidae	5345	5010
Coccinellidae	5798	—
Orthoptera[b]	5221	—
Rhopalidae	5865	5518
Hemiptera[c]	6095	5691
Lepidoptera	5271	5248
Neuroptera	5482	—
Cicadellidae	5685	—
Pentatomidae	5459	5539
Coleoptera	5306	—
Cydnidae	6452	—

[a] Sample not large enough to conduct analysis.
[b] Comprises families in the order other than Acrididae and Tettigoniidae.
[c] Comprises families in the order other than Lygaeidae, Miridae, Pentatomidae, Cydnidae and Rhopalidae.

from the Fall River and Konza sites. Differences appeared to exist, however, in energy contents of some taxonomic groups between the Fall River and Konza sites, namely Araneida, Tettigoniidae, Rhopalidae (scentless plant bugs) and Hemiptera (Table 3). Overall, the mean energy content of the eight taxonomic groups common to both study sites was 5476 versus 5305 cal/g for the Fall River and Konza sites, respectively.

Nutritional characteristics of the 1989 pooled taxonomic group samples for each site did not differ greatly by collection periods from late June to July, but the mean fat content of the Konza samples (11.8 ± 1.6) was significantly lower than that of the samples from either the Fall River-wheat (26.6 ± 1.5) or the Fall River-milo (18.8 ± 0.4) sites, and the fat content of invertebrate samples from the Fall River-wheat site was significantly greater than that of samples from the Fall River-milo site. Mean crude protein levels in the invertebrate samples from Konza (68.2 ± 11.1) were not significantly different than those in the samples from the Fall River-wheat (57.7 ± 1.1) and Fall River-milo (63.3 ± 3.5) sites. Ash contents ranged from 3.3 to 4.6% for invertebrate samples from the three sites, and the means did not differ among sites. Crude fiber was significantly lower in invertebrate samples from the Konza site ($\bar{x}$ = 9.5 ± 0.5) than in samples from the Fall River-wheat ($\bar{x}$ = 12.8 ± 0.2) and Fall River-milo ($\bar{x}$ = 13.0 ± 0.2) sites, which did not differ from each other.

The energy content of the invertebrate samples collected on the Konza site averaged 5072 cal/g (SE = 128) over the four sampling periods and did not differ with time, but was significantly lower than that of samples collected on the Fall River sites. The mean energy content of the invertebrate samples from the Fall River-wheat site (5695 cal/g ± 155) was not significantly higher than that of the samples from the Fall River-milo site (5491 cal/g ± 67), and both declined significantly over the late June to late July sampling period.

DISCUSSION

We used sweepnets to collect our invertebrate samples because of the widespread acceptance of the technique. We do not contend that sweepnet samples represent an accurate picture of the invertebrate biomass available to foraging birds. They do, however, reflect the taxonomic heterogeneity of the invertebrate biomass present in the vegetative canopy of grassland areas (Evans et al. 1983).

We speculate that the differences we detected in nutrient and energy contents of invertebrate taxonomic groupings may have been due to different (1) genera or species within the samples, (2) proportions of adult and immature forms within the samples, (3) levels of nutrients in the food substrates of the invertebrates collected and/or (4) life history characteristics of genera or species within a taxonomic group (see Kerkut and Gilbert 1985). As the samples were ground for analysis and destroyed when analyzed, however, we could not reconstruct the taxonomic or life stage compositions of those samples to estimate their effect on the nutrient and energy contents determined. Knowing why differences exist in

nutrient and energy contents of taxonomic groupings of invertebrate bio-
mass could allow ecologists to predict year-to-year and/or site-to-site dif-
ferences in the characteristics of a particular avian food resource. Without
such knowledge, it will be difficult to probe the interactions of food re-
sources and behavioral strategies of avian species.

Ecological implications.—At one time, we were comfortable making
broad generalizations about nutritional and energy requirements of
breeding birds (Dunn 1980, Kendeigh et al. 1977, King 1973, Scott 1973).
Current efforts to understand interactions of food resources and repro-
ductive strategies and separating ecological adaptations, however, require
more precise data (Calder 1984, Weathers 1992), without which "specu-
lation concerning the evolution of avian reproductive patterns seems pre-
mature" (Weathers 1992:151). In recent years, the importance of food
limitations to avian reproductive strategies has been debated at length
(see Konishi et al. 1989, Martin 1987). The availability of food resources
has become a critical element in the theoretical modeling of nestling
growth rates, parental investment in young, foraging times, nest preda-
tion, and a host of other efforts to understand the fitness of avian species
in a changing environment (Martin 1992). Generally, theoretical and al-
lometric models use fixed, homogeneous, "food resource" inputs (Case
1978, O'Connor 1984, Reiss 1989, Ricklefs 1974).

Research on avian reproductive strategies has shown that experimental
supplementations of food resources reduced foraging time of Song Spar-
rows (Arcese and Smith 1988), increased nest guarding time and reduced
predation rates in Cactus Wrens (*Campylorhynchus brunneicappius*) (Sim-
mons and Martin 1990), and increased nesting success of Carrion Crows
(*Corvus corone*) (Yom-Tov 1974) and Black-billed Magpies (*Pica pica*)
(Hogstedt 1981). These are but a few of the many reports relating quan-
tities of food resources to nesting success and reproductive output. We
believe that differences in qualities of food resources will impact these
outcomes in a similar fashion.

Speculation on evolution of avian reproductive strategies has focused
primarily on energy requirements (Weathers 1992). The differences in
the energy and nutrient contents of the taxonomic categories of inver-
tebrate biomasses that we analyzed increases the complexity of the food
input variable by several magnitudes. Detailed field studies of the com-
position of dietary intake will be needed to refine existing energy models
into meaningful predictive equations for use or testing in the field.

Our results are applicable to resource management programs. For ex-
ample, Whitmore et al. (1986) attempted to evaluate Ring-necked Pheas-
ant (*Phasianus colchicus*) brood habitat by measuring the standing crop
of insect biomass. What those authors classed as excellent brood habitat
had an insect standing crop of 500 mg/m^2. Depending on the taxonomic
composition of that insect biomass, our data predict that the food re-
source on a square meter could contain 38–160 mg of fat, 272–379 mg
of crude protein, 27–88 mg of crude fiber, 1.3–2.6 µg of calcium, and
5.8–9.5 µg of phosphorous. Such a wide range in the availability of these

nutrients and the potential difference in energy content of the 500 mg/
m² biomass (2453–3226 cal) could result in a significant impact on the
suitability of the habitat for foraging chicks.

Recently, much attention has been devoted to determining the effects
of habitat fragmentation on floral and faunal communities (see review by
Saunders et al. 1991). Could patchy distributions of taxonomic groups of
low nutritional quality among invertebrate populations mimic fragement-
ed habitats? Might this patchiness of invertebrates of low or high nutri-
tional quality overlay traditionally defined landscape fragments and mask
or accentuate the impacts of that fragmentation? Until these questions
are addressed, conservation and landscape biologists may be confronted
by a myriad of confounding variables as they pursue the critical study of
habitat fragmentation.

LITERATURE CITED

ARCESE, P., AND J. N. M. SMITH. 1988. Effects of population density and supplemental food
    on reproduction in song sparrows. J. Anim. Ecol. 57:119–136.
BEST, L. B. 1978. Field Sparrow reproductive success and nesting ecology. Auk 95:9–22.
BLANCHER, P. J., AND R. J. ROBERTSON. 1987. Effect of food supply on the breeding biology
    of western kingbirds. Ecology 68:723–732.
CALDER, W. A., III. 1984. Size, function, and life history. Harvard Univ. Press, Cambridge,
    Massachusetts. 431 pp.
CALVERT, C. C., R. D. MARTIN, AND N. O. MORGAN. 1969. House fly pupae as food for poultry.
    J. Econ. Entomol. 62:938–939.
CASE, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in
    terrestrial vertebrates. Q. Rev. Biol. 55:243–282.
CODY, M. L. 1985. Habitat selection in birds. Academic Press, New York, New York. 558 pp.
CRAMPTON, E. W. 1956. Applied animal nutrition. W. H. Freeman and Co., San Francisco,
    California. 458 pp.
DUNN, E. H. 1980. On the variability in energy allocation of nestling birds. Auk 97:553–565.
ELZINGA, R. J. 1987. Fundamentals of entomology. 3rd ed. Prentice-Hall, Englewood Cliffs,
    New Jersey. 456 pp.
EVANS, E. W., R. A. ROGERS, AND D. J. OPFERMANN. 1983. Sampling grasshoppers (Orthop-
    tera:Acrididae) on burned and unburned tallgrass prairie: night trapping vs. sweeping.
    Environ. Entomol. 12:1449–1454.
GOLLEY, F. B. 1961. Energy values of ecological materials. Ecology 43:581–584.
HENNING, B. L. 1993. The response of plants, seed banks, and invertebrates to monthly soil
    disturbance by disking for wildlife. M.Sc. thesis. Kansas State Univ., Manhattan, Kansas.
    146 pp.
HOGSTEDT, G. 1981. Effect of additional food on reproductive success in the magpie (*Pica
    pica*). J. Anim. Ecol. 50:219–229.
JOHNSON, K. W. 1993. An evaluation of disking as a technique for creating wildlife food
    plots. M.Sc. thesis, Kansas State Univ., Manhattan, Kansas. 119 pp.
JOHNSTON, R. D. 1993. Effects of diet quality on the nestling growth of a wild insectivorous
    passerine, the house martin *Delichon urbica*. Funct. Ecol. 7:255–266.

KENDEIGH, S. C., V. R. DOL'NIK, AND V. M. GAVRILOV. 1977. Avian energetics. Pp. 127–204, *in* J. Pinowski and S. C. Kendeigh, eds. Granivorous birds in ecosystems. Cambridge Univ. Press, Cambridge, Massachusetts.

KERKUT, G. A., AND L. I. GILBERT. 1985. Comprehensive insect physiology, biochemistry, and pharmacology. Pergamon Press Inc., Elmsford, New York. 639 pp.

KING, J. R. 1973. Energetics of reproduction in birds. Pp. 78–105, *in* S. D. Farner, ed. Breeding biology of birds. National Acad. Sci., Washington, D.C.

KONISHI, M., S. T. EMLEN, R. E. RICKLEFS, AND J. C. WINGFIELD. 1989. Contributions of bird studies to biology. Science 246:465–472.

LANDRY, S. V., G. R. DEFOLIART, AND M. L. SUNDE. 1986. Larval protein quality of six species of Lepidoptera (Saturniidae, Sphingidae, Noctuidae). J. Econ. Entomol. 79:600–604.

MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. American wildlife and plants. McGraw-Hill Book Co., Inc., New York, New York. 500 pp.

MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Ann Rev. Ecol. Syst. 18:453–487.

———. 1992. Interaction of nest predation and food limitation in reproductive strategies. Curr. Ornithol. 9:163–197.

O'CONNOR, R. J. 1984. The growth and development of birds. Wiley and Sons, Chichester, 315 pp.

REISS, M. J. 1989. The allometry of growth and reproduction. Cambridge Univ. Press, Cambridge, Massachusetts. 182 pp.

RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 152–292, *in* R. A. Paynter, Jr., ed. Avian energetics. Publ. Nuttall Ornithol. Club, No. 15. Cambridge, Massachusetts.

RISSER, P. G., E. C. BIRNEY, H. D. BLOCKER, S. W. MAY, W. J. PARTON, AND J. A. WIENS. 1981. The true prairie ecosystem. US/IBP Synthesis Series No. 6, Hutchinson Ross Publ. Co., Stroudsburg, Pennsylvania. 577 pp.

ROBEL, R. J., A. R. BISSET, T. M. CLEMENT, JR., A. D. DAYTON, AND K. L. MORGAN. 1979. Metabolizable energy of important foods of bobwhites in Kansas. J. Wildl. Manage. 43: 982–987.

ROBEL, R. J., R. M. CASE, A. R. BISSET, AND T. M. CLEMENT, JR. 1974. Energetics of food plots in bobwhite management. J. Wildl. Manage. 38:653–664.

SAS INSTITUTE INC. 1989. SAS/SAT guide for personal computing. Version 6 Vol. 1. SAS Inst. Inc., Cary, North Carolina. 890 pp.

SAUNDERS, D. A., R. J. HOBBS, AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. Cons. Biol. 5:18–32.

SCOTT, M. L. 1973. Nutrition in reproduction—direct effects and predictive functions. Pp. 46–73, *in* D. S. Farner, ed. Breeding biology of birds. Natl. Acad. Sci., Washington, D.C.

SIMONS, L. S., AND T. E. MARTIN. 1988. Food limitation of avian reproduction: an experiment with the cactus wren. Ecology 71:869–876.

SLANSKY, F., AND J. M. SCRIBER. 1985. Food consumption and utilization. Pp. 87–163, *in* G. A. Kerkut and L. I. Gilbert, eds. Comprehensive insect physiology, biochemistry, and pharmacology. Pergamon Press Inc., Elmsford, New York.

WEATHERS, W. W. 1992. Scaling nestling energy requirements. Ibis 134:142–153.

WHITMORE, R. W., K. P. PRUESS, AND R. E. GOLD. 1986. Insect food selection by 2-week old ring-necked pheasant chicks. J. Wildl. Manage. 50:223–228.

YOM-TOV, Y. 1974. The effects of food and predation on breeding density and success, clutch size and laying date of the crow (*Corvus corone* L.). J. Anim. Ecol. 43:479–498.