FOOD AND OXYGEN CONSUMPTION IN THREE SPECIES OF OWLS (STRIGIDAE)

By RICHARD R. GRABER

There is a vast literature on the subject of food of owls based on pellet analysis, and an increasing number of papers on metabolism in birds. The important works of Kendeigh (1934, 1939, 1944, 1949), Pearson (1950), and Dawson (1958) show various approaches to the study of energy requirements of birds. In their excellent review King and Farner (1961) state that there is still a relative paucity of data on avian metabolism.

The present study, conducted in central Illinois, considers comparative energy requirements in three species of owls in winter based on analysis of over 2000 pellets and observations on food and oxygen consumption by captive specimens of Long-eared (*Asio otus*), Short-eared (*Asio flammeus*), and Saw-whet owls (*Aegolius acadicus*).

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METHODS

To acquire data on the kinds and relative amounts of prey consumed by owls in the natural state, I visited owl roosts in central Illinois (McDonough, Piatt, Champaign, and Vermilion counties) at least once a month in January, February, March, and April in 1957 and 1958. On each visit I attempted to determine the number of owls present at the roost and gathered all pellets.

Pellet collections from each roost were kept separate. In the laboratory all pellets were processed individually and obviously broken pellets were not used.

For each pellet, I recorded the number of skulls of each prey animal, and also, as an index to the quantity of food consumed, the number of humeri, ulnae, innominates, femurs, and tibiae. I depended on skull measurements given by Hoffmeister and Mohr (1957) to differentiate species of *Microtus* and species of *Peromyscus*. Sex determination of prey was based on the shape of the innominate bones found in the pellets (Guilday, 1951; Dunmire, 1955).

To calculate the quantity of food consumed by non-captive owls from the record of pellet contents, I used average weights for the prey species in each pellet, taking into consideration the sex of the prey. Weights for prey species were taken from freshly caught specimens collected in winter (January-March) near the owl roosts and from local winter specimens in the collections of the University of Illinois Museum of Natural History. The averages were based on the weights of 11 or more specimens. Weights in grams for the various prey species were: least shrew (*Cryptotis parva*),

both sexes, 5; short-tailed shrew (*Blarina brevicauda*), male, 19, female, 17; prairie deer mouse (*Peromyscus maniculatus*), male, 17, female, 15; woodland deer mouse (*Peromyscus leucopus*), male, 20, female, 19; bog lemming (*Synaptomys cooperi*), male, 34, female, 22; prairie vole (*Microtus ochrogaster*), male, 35, female, 36; pine vole (*Microtus pinetorum*), male, 25, female, 22; house mouse (*Mus musculus*), male, 13, female, 22. No quantitative calculations of food were made for pellets with rat (*Rattus*) or bird remains. Throughout this paper only the common names of birds are used but the nomenclature follows the A.O.U. Check-list of North American Birds, 5th Edition (1957).

The relative abundance of each prey species in a given sample of pellets was computed in two ways: per cent of total animals in the sample, and per cent frequency of occurrence of the prey species in all pellets of the sample. Scott (1941) found the latter measure to be more accurate, and per cent frequency is used in the tables of this paper.

Specimens of Long-eared (one male, one female, and two of unknown sex), Short-eared (one female, one of unknown sex), and Saw-whet owls (one male, one female) were captured with mist nests. These birds were held in captivity from December to early March in 1958, 1960, 1961, and 1962, for the purpose of determining food consumption and metabolic rates. Each experiment on food consumption and metabolism was repeated at least twice on every captive. The birds were kept indoors (temperature: 18° to 19°C.) in separate screened flight cages (3 x 7 x 7 feet) where they were exposed to natural daylight (10 to 11 hours of light). They were fed freshly killed laboratory mice (*Mus musculus*). Caloric determinations of these mice and of the natural prey species were made by the staff of the Department of Animal Science, University of Illinois, using a bomb calorimeter. Determinations were made for water content, dry substance, fat, and ash on one *Blarina brevicauda,* two *Peromyscus leucopus,* one *Peromyscus maniculatus* and five *Microtus ochrogaster*. Gross energy values for these specimens were: *Blarina,* 4340 gram-calories per gram; *Peromyscus maniculatus,* 4490; *P. leucopus,* 4321; and *Microtus,* 4193 to 4504 (average: 4348). Eleven specimens of house mice had an average gross energy value of 3945 gram-calories per gram. Calorimetric determinations were also made on pellets and fecal samples (24-hour accumulations) from two captive Long-eared Owls. These birds were fed specific quantities of *Mus* tissue to hold them at constant (day-to-day) weight. Pellets and excreta from these feedings were saved from each owl through two 24-hour cycles. The material was dried and weighed at the end of each day. Calorimetric determinations for the pellets varied from 2979 to 3340 (average: 3159) gram-calories per gram, and for the excreta samples from 2642 to 2832 (average: 2739) gram-calories per gram. Throughout this paper, the terms excretion and excreta refer to both nitrogen and fecal waste.

In calculating energy requirements of free-living owls from pellet data, I have had to assume that the birds maintained reasonably constant weight throughout the mid-winter period. I have also assumed that each pellet represented one (owl) day. This was certainly true of all captives, whether I force fed them or let them feed at will from an excess quantity of mice. At all the owl roosts, I found close to one whole pellet per owl per day. However, there were usually a few pellets in excess of this number, as well as some broken pellets which complicated the count. When studying a roost of Long-eared Owls in Michigan during April, Armstrong (1958) found from one to two pellets per owl per day with an average of 1.4. Austing (1958) studied roosts of Saw-whet Owls in Ohio during the winter. He found that the number of Saw-whet pellets at a roost indicated the number of days the roost had been used. This ratio, one pellet per

day, also appeared to hold for the roosts I checked in Illinois. Chitty (1938) indicated that each pellet from a Short-eared Owl represented a meal, that is, a forage, and that each pellet was disgorged before another meal was taken. He found that pellets were held an average of 5 to 7 hours before being ejected. In my experience with captives of all three species, the average time that pellets were held was close to 7 or 8 hours. I also found, especially when working with Long-eared Owls, that it was impossible to force feed a bird in the process of forming a pellet because birds in this state invariably regurgitated the food within minutes of the force feeding. For a nocturnal species, these conditions would tend to delimit the bird to one successful forage per night, and I believe the assumption that one pellet represents one (owl) day is reasonably accurate. Short-eared Owls are not strictly nocturnal although in winter in Illinois they appear to do little hunting in the daytime. During the daylight hours, I could count on finding Short-ears at their diurnal roosts where pellets accumulated at the rate of about one per owl per day.

The rate of oxygen consumption was determined with a closed circuit apparatus using Ascarite as a carbon dioxide absorbent. Oxygen was fed into the metabolism chamber from a pressure tank through a graduated 30 milliliter syringe to maintain constant pressure in the system.

During metabolism experiments, owls were kept in a dark, 2 x 2 x 1 foot chamber at a temperature of 18° to 19°C. Oxygen consumption was measured for 20 to 30 minutes every one to two hours during a 24-hour cycle for one Long-eared Owl (male), one Short-eared Owl (female), and two Saw-whet Owls (male and female). This 24-hour determination was conducted twice for each specimen; first, on the day after capture and then three to four days later. During the experiment, respiration rate and depth were recorded from fluctuations of the manometer meniscus. The birds were not fed during the 12 hours before the oxygen consumption measurements were started and they were not fed during the cycle. The measure of oxygen consumption was recorded only when the bird had been at rest with a constant minimal respiration rate for five minutes. Metabolism data, then, unless otherwise stated, represented as nearly as possible the standard (basal) condition. Oxygen consumption data were reduced to standard temperature and pressure (dry gas) and plotted on a time scale (fig. 1). The figure for the total daily (basal) consumption of oxygen given for each species was obtained by extrapolation of the 20 to 30 minute determinations. An average rate of oxygen consumption (mls./hr./bird) was calculated for each hour of the day from readings plotted on figure 1, and these rates were summed for the total. In cases where there was a two-hour interval between determinations (see fig. 1), the mean level between the two adjacent hours was used to represent the unknown hour. To calculate the food equivalent of the oxygen consumed, I used a factor (4.71 kilocalories/liter of oxygen) based on the relative fat-protein content of the natural food (mice) of the owls.

THE OWLS AND THEIR ROOSTS

Long-eared, Short-eared, and Saw-whet owls nest uncommonly in Illinois. Long-ears have been reported in about 10 per cent of the Illinois Christmas counts, Short-ears in 8 per cent, and Saw-whets in about 3 per cent (Graber and Golden, 1960).

Roosts of Long-eared and Saw-whet owls in Illinois were similar to those described by Randle and Austing (1952) and were located in planted groves of one or more species of pine (*Pinus virginiana, P. taeda, P. strobus*) and red cedar (*Juniperus virginiana*). Three of five such roosts were used by both Long-eared and Saw-whet owls, but certain differences were apparent in the roosting habits of these two species. Saw-

whets were solitary and usually roosted at the edge of the plantation, whereas Long-ears were gregarious (2 to 12 birds together) and sought the deeper, darker recesses of the roosting grove. All Saw-whet roosts were within 100 yards of extensive woodlands, whereas Long-ears were found roosting as far as two miles from forest. In contrast, Short-eared Owls roosted in open field habitats. Snyder and Hope (1938) reported Short-ears roosting in conifer plantings as well as in open fields in the Toronto region. Banfield (1947) explained that Short-eared Owls used tree roosts during periods of heavy snow cover. In Illinois, roosting sites of Short-ears were grassy-weedy fields or grass grown slopes of drainage ditches.

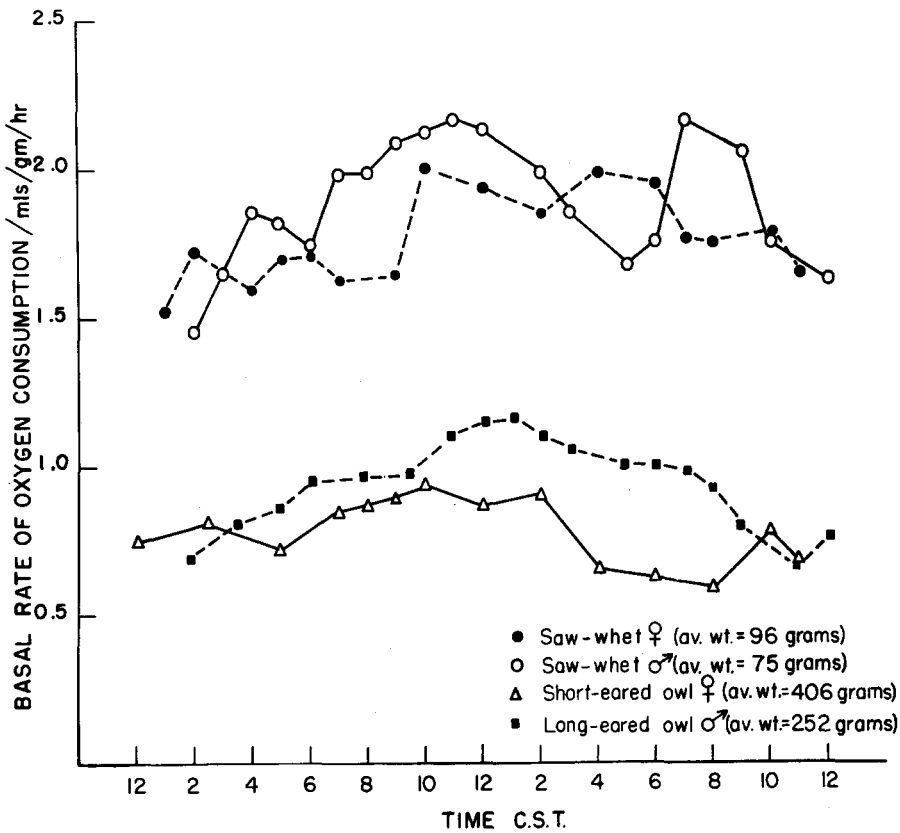

Fig. 1. Variation in standard (basal) rate of oxygen consumption, reduced to STP, in four owls (three species) during a 24-hour cycle (noon to noon).

VARIATION IN FOOD HABITS OF OWLS IN NATURE

Diet of owls varied seasonally, annually, according to locality, and perhaps between individual owls in the same time period at the same locality.

Long-eared Owl.—Data on the Long-eared Owl represent three localities, 22 owls, and about 1500 pellets collected in the period from November 1, 1956, to March 31, 1957, and from January 1 to March 31, 1958.

These pellets contained 29 species of prey, but species of *Microtus* (64 per cent of all animals taken), *Peromyscus* (18 per cent) and *Mus* (11 per cent) comprised the

essential sustenance for Long-ears. The detailed record of pellet contents (table 1) indicates that Long-ears usually consume voles and deer mice entirely, while house mice are more often only partly eaten.

TABLE 1

RELATIVE PERCENTAGE OF OCCURRENCE OF MAJOR BONES OF PREY ANIMALS IN PELLETS OF THREE SPECIES OF OWLS

Major bones	Long-eared Owl			Short-eared Owl			Saw-whet Owl		
	Microtus	*Peromyscus*	*Mus*	*Microtus*	*Peromyscus*	*Mus*	*Microtus*	*Peromyscus*	*Mus*
Skulls	99*	99	100	97	98	95	41	69	80
Humeri	92	78	69	100	94	85	71	82	80
Ulnae	87	80	66	91	86	85	65	80	100
Pelves	92	82	66	79	82	60	88	95	80
Tibiae	89	87	66	91	100	100	100	97	100
Femorae	94	99	81	100	94	95	100	100	80

* 99 per cent of pellets with *Microtus* remains.

Some idea of the individual variation in diet of Long-ears is indicated by data from adjacent roosts in Allerton Park, Piatt County. The two roosts, one in a grove of loblolly pines (roost 1) and one in Virginia pines (roost 2), were situated side by side only 10 feet apart. Four owls regularly spent the daylight hours in roost 1 and eight used roost 2. All of these birds probably hunted in the adjacent park and farm lands during January and early February, 1957, but there was marked difference in the prey taken by birds of the two roosts. There was nearly a twofold difference in frequency (34 versus 18 per cent) of deer mice taken by the two groups, and a threefold difference in frequency (9 and 3 per cent) of least shrews. Relative frequencies for house mice were 21 and 13 per cent and for birds 4 and 2 per cent (table 2). The relative amounts of certain prey species (*Peromyscus maniculatus,* for example) from the two roosts indicated that owls from roost 1 hunted more in "open field" habitat than owls from roost 2. The loblolly pine roost was deserted altogether by February 15, possibly in favor of the more dense Virginia pine roost.

Greater differences were apparent in the prey taken by Long-ears at more widely spaced roosts. Kickapoo and Allerton parks are located about 50 miles apart on the same latitude in east-central Illinois. The most striking difference in catch by Long-eared Owls at the two localities was that relating to avian prey. Frequencies of bird remains in pellets at the Kickapoo Park roost were 16 per cent (January) and 13 per cent (February to March), whereas at Allerton Park the frequency for bird remains never exceeded 4 per cent during this period (table 2).

With the passing of winter into spring, there was a marked increase in frequency of house mice and least shrews in pellets at both roosts. House mice may have become more available because of their vernal movement from human habitation. During this period, the frequency of bird remains in pellets increased at the Allerton Park roost. This increase probably reflects increased availability of birds with the influx of spring migrants.

From the standpoint of the nutrition of Long-ears, the most marked changes in diet associated with the passing of winter involved the principal prey species, voles and deer mice. Pellet samples at both roosts showed that the relative percentage of prairie voles decreased at the end of winter, as did the frequency of deer mice. However, the calculated weight of prey per forage did not fall below 48 to 50 gm. (table 3), because

TABLE 2

SPECIES OF PREY TAKEN IN 1957 BY LONG-EARED OWLS EXPRESSED AS PER CENT FREQUENCY OF OCCURRENCE IN PELLET SAMPLES

	Allerton Park Area				Kickapoo Park Area	
	Jan. 1-Feb. 15		Feb. 15-Mar. 1	Mar. 1-Apr. 1	Jan. 15-Feb. 1	Feb. 15-Apr. 1
Prey species	Roost 1 (4 owls)	Roost 2 (8 owls)	Roost 2 (7 owls)	Roost 2 (7 owls)	Roost 1 (7 owls)	Roost 1 (7 owls)
MAMMALS						
Cryptotis parva	9	3	1	3	5	13
Blarina brevicauda	+*	....	....	....	....	1
Peromyscus maniculatus	29	10	24	18	33	23
Peromyscus leucopus	5	8	11	5	6	6
Total *Peromyscus*	34	18	35	23	39	29
Synaptomys cooperi	+	....	....	1	1	6
Microtus ochrogaster	71	80	84	68	65	60
Microtus pinetorum	16	12	5	16	11	23
Total *Microtus*	87	92	89	84	76	83
Rattus norvegicus	....	....	....	....	....	+
Mus musculus	21	13	12	24	3	16
BIRDS						
Charadrius vociferus	....	+	....	....	....	....
Zenaidura macroura	....	+	....	....	....	....
Unidentified passerine	+	+	....	1	1	2
Thryothorus ludovicianus	....	....	....	....	1	....
Turdus migratorius	....	....	....	+	....	....
Passer domesticus	....	....	....	....	1	....
Unidentified meadowlark	....	....	....	....	....	1
Molothrus ater	+	....	....	....	....	....
Unidentified sparrow	....	....	....	+	1	1
Richmondena cardinalis	+	+	....	....	....	+
Hesperiphona vespertina	....	....	....	....	1	....
Junco hyemalis	2	+	+	....	6	3
Spizella arborea	....	....	....	....	3	1
Spizella pusilla	....	....	....	....	....	+
Zonotrichia albicollis	+	....	....	....	....	+
Passerella iliaca	....	....	....	+	....	....
Melospiza melodia	+	+	....	....	4	4
Total birds	4	2	+	4	16	13
Total number species found	13	10	8	12	14	19
Total number pellets	186	380	211	166	100	350

* + = less than 1 per cent.

of the relative increase in the catch of house mice, pine voles, bog lemmings, and shrews. In mid-winter, the average catch per forage was as high as 58 gm. Data on annual variation in winter prey taken by Long-eared Owls (table 4) show that the prey of Long-ears associated with a given locality maintain a certain constancy from year to year. For instance, at the Allerton Park roost in 1957 and 1958, voles occurred in pellets of Long-ears with a frequency of 89 per cent and 90 per cent, respectively. At Kickapoo Park the frequency of voles was 82 and 84 per cent, respectively, for the same two years. The frequencies of occurrence of deer mice, bog lemmings, and birds were consistently higher at Kickapoo than at Allerton, while the Allerton roost had consistently higher frequencies of house mice. These year to year consistencies may reflect a certain stability in the characteristics of the local prey population.

TABLE 3

PREY CONSUMPTION BY LONG-EARED OWLS IN CENTRAL ILLINOIS IN 1957

Number	Allerton Park Area			Kickapoo Park Area		
	Jan. 1-Feb. 15 Roost 1	Jan. 1-Feb. 15 Roost 2	Feb. 15-Mar. 1 Roost 2	Mar. 1-Apr. 1 Roost 2	Jan. 15-Feb. 1 Roost 1	Feb. 15-Apr. 1 Roost 1
Owls at roost	4	8	11	7	7	7
Pellets examined	186	380	211	166	100	350
Species of prey	13	10	8	12	14	19
Prey animals	414	844	429	329	209	769
Mean number of prey per pellet	2.2	2.2	2.0	2.0	2.1	2.2
Calculated weight of prey per pellet (gm.)	53	58	48	48	47	50

TABLE 4

ANNUAL VARIATION IN PREY TAKEN BY LONG-EARED OWLS AT TWO ROOSTS IN CENTRAL ILLINOIS IN WINTER, JANUARY TO MARCH

Prey species	Per Cent Frequency of Occurrence of Prey Animals in Pellet Samples			
	Allerton Park		Kickapoo Park	
MAMMALS	1957	1958	1957	1958
Cryptotis parva	4	14	11	5
Blarina brevicauda	+*	+	1	2
Peromyscus maniculatus	22	14	25	19
Peromyscus leucopus	7	5	6	9
Total *Peromyscus*	29	19	31	27
Synaptomys cooperi	+	....	5	11
Microtus ochrogaster	72	74	64	70
Microtus pinetorum	17	16	18	14
Total *Microtus*	89	90	82	84
Rattus norvegicus	....	....	+	....
Mus musculus	16	17	13	7
BIRDS	2	3	13	7
Number of owls	12	7	7	7
Number of pellets	943	253	450	255

* + = less than 1 per cent.

Short-eared Owl.—Data on this species, although limited, represent two localities, five owls, and 127 pellets (table 5). Again, the principal prey were voles (41 per cent of all animals found in pellets), deer mice (36 per cent), and house mice (20 per cent).

Pellets from two roosts about 10 miles apart in Champaign County differed markedly in relative per cent frequency of occurrence of prey species. Bird remains occurred in 12 per cent of pellets from one roost and in only 1 per cent of pellets from roost 2. At these two roosts, frequencies for least shrews were 12 and 2 per cent, for deer mice 35 and 50 per cent, for voles 71 and 68 per cent, and for house mice 12 and 25 per cent, respectively (table 5).

The calculated average weight of prey per forage was 41 gm. at roost 1 and 53 gm. at the second roost (table 5). The high frequencies of birds and shrews at roost 1 were possibly associated with a low catch of more favored prey species.

Saw-whet Owl.—A total of 386 pellets of this species was analyzed. These repre-

TABLE 5

PREY TAKEN IN WINTER (FEB.-MAR.), 1957, BY SHORT-EARED OWLS EXPRESSED AS PER CENT FREQUENCY OF OCCURRENCE IN PELLET SAMPLES

Prey species	Champaign County Roost 1 (1 owl)	Champaign County Roost 2 (4 owls)
MAMMALS		
Cryptotis parva	12	2
Peromyscus maniculatus	35	46
Peromyscus leucopus	....	4
Total *Peromyscus*	35	50
Microtus ochrogaster	71	54
Microtus pinetorum	....	14
Total *Microtus*	71	68
Mus musculus	12	25
BIRDS		
Unidentified passerines	12	1
Spizella arborea	6	....
Spizella pusilla	6	....
Total birds	24	1
Number of prey species	7	7
Number of pellets	17	110
Number of prey animals	33	268
Mean number of animals per pellet	1.9	2.4
Calculated weight of prey per pellet (gm.)	41	53

Saw-whet

sented four birds, one at each of four different localities in central Illinois for the period from January to February, 1957, and from November, 1957, to April 1, 1958.

Winter diet of the Saw-whet Owl is remarkably constant, a single prey species, the woodland deer mouse, comprising the essential sustenance (70 per cent of all prey animals taken). Frequencies of deer mice in different Saw-whet pellet samples from central Illinois varied from 67 to 91 per cent (table 6). A sample of 23 pellets from Richland County in southern Illinois showed 100 per cent frequency of deer mice; voles, 4 per cent, and house mice, 4 per cent, were the only other prey species represented. Randle and Austing (1952) also indicated that Saw-whets foraged principally in woodlands.

The constancy of the diet and similarity of the roosting sites indicates less individual variation in foraging habits in this species than is exhibited by the Long-eared and Short-eared owls. Such dietary variation as is shown can probably be attributed to seasonal changes which perhaps affect the prey population.

Annual variation in diet for February at one roost in McDonough County was virtually non-existent in two successive years (table 6).

One consistent change in diet which appeared to be related to the passing of winter into spring was an increase in frequency of birds as prey for Saw-whets. This increase may represent increased availability of birds because of the influx with spring migration.

Quantitatively, the estimated catch of prey by Saw-whets varied from 13.3 to 18.3 gm. per forage (table 7).

TABLE 6

PREY TAKEN BY SAW-WHET OWLS, EXPRESSED AS PER CENT FREQUENCY OF OCCURRENCE IN PELLET SAMPLES

	McDonough County			Piatt County			Vermilion County	
			Allerton Park		Lodge Park			Kickapoo Park
Prey species	Feb. 1957	Feb. 1958	Jan.-Feb. 1957	Mar.-Apr. 1957	Nov.-Dec. 1957	Jan.-Feb. 1958	Mar. 1958	Jan.-Mar. 1957
MAMMALS								
Cryptotis parva	....	....	2	....	....	2	....	1
Blarina brevicauda	....	....	2	2	....	2	....	....
Peromyscus maniculatus	....	....	10	27	22	19	22	6
Peromyscus leucopus	....	....	77	55	45	66	64	77
Total *Peromyscus*	91	89	87	82	67	85	86	83
Voles	9	10	7	0	....	11	8	18
Mus musculus	....	....	....	7	....	....	....	....
BIRDS								
Unidentified passerines	....	....	....	4	1	....	....	....
Unidentified swallows	....	....	....	2	....	....	....	....
Unidentified chickadees	....	....	....	2	....	....	....	....
Regulus calendula	....	....	....	2	....	....	....	....
Passer domesticus	....	....	....	....	....	1	....	....
Richmondena cardinalis	....	....	....	....	....	1	....	....
Unidentified junco	....	....	....	2	....	....	2	....
Spizella arborea	....	....	....	....	....	....	2	....
Spizella pusilla	....	....	....	....	1	....	....	....
Melospiza melodia	....	....	....	2	....	....	....	....
Total birds	....	....	....	14	2	2	4	....
Total number prey species	2–4	2–4	5–6	9	3	7–8	5–6	4–5
Number of pellets	22	19	40	45	61	61	37	76

TABLE 7

PREY CONSUMPTION BY SAW-WHET OWLS

	McDonough County			Piatt County			Vermilion County	
			Allerton Park		Lodge Park			Kickapoo Park
Number	Feb. 1957	Feb. 1958	Jan.-Feb. 1957	Mar.-Apr. 1957	Nov.-Dec. 1957	Jan.-Feb. 1958	Mar. 1958	Jan.-Mar. 1957
Owls at roost	1	1	1	1	1	1	1	1
Pellets examined	22	19	40	45	61	61	37	76
Species of prey	2–4	2–4	5–6	9	3	7–8	5–6	4–5
Prey animals	25	21	42	50	63	62	38	87
Mean number of prey per pellet	1.1	1.1	1.0	1.1	1.0	1.0	1.0	1.1
Calculated weight of prey per pellet (gm.)	18.3	13.6	15.2	15.6	13.7	13.4	13.3	18.2

ENERGY REQUIREMENTS OF OWLS AT STANDARD AND ACTIVE RATES

Weight changes related to availability of food for four captive owls are shown in figure 2. The owls, a male and female Long-ear, a female Short-ear, and a female Saw-whet, were kept in separate flight cages at a temperature of 18° to 19°C. and were exposed to natural daylight (10-hour photoperiod). They exercised by making short flights between the stick perches in the cage.

Conditions for the metabolism tests are described in the section on methods.

Long-eared Owl.—At the standard (basal) rate of metabolism in an environmental temperature of 18° to 19°C., a male Long-eared Owl (average weight during a 24–hour cycle: 252 gm., respiration rate: 24–28 per minute) consumed 5631 ml. of oxygen (corrected to STP) in 24 hours (fig. 1). This is the food equivalent of about 26 kilogram-calories per day or 105 kcal./kg. per day. The standard rate of metabolism was not constant throughout the 24–hour cycle for any of the species studied (fig. 1). For

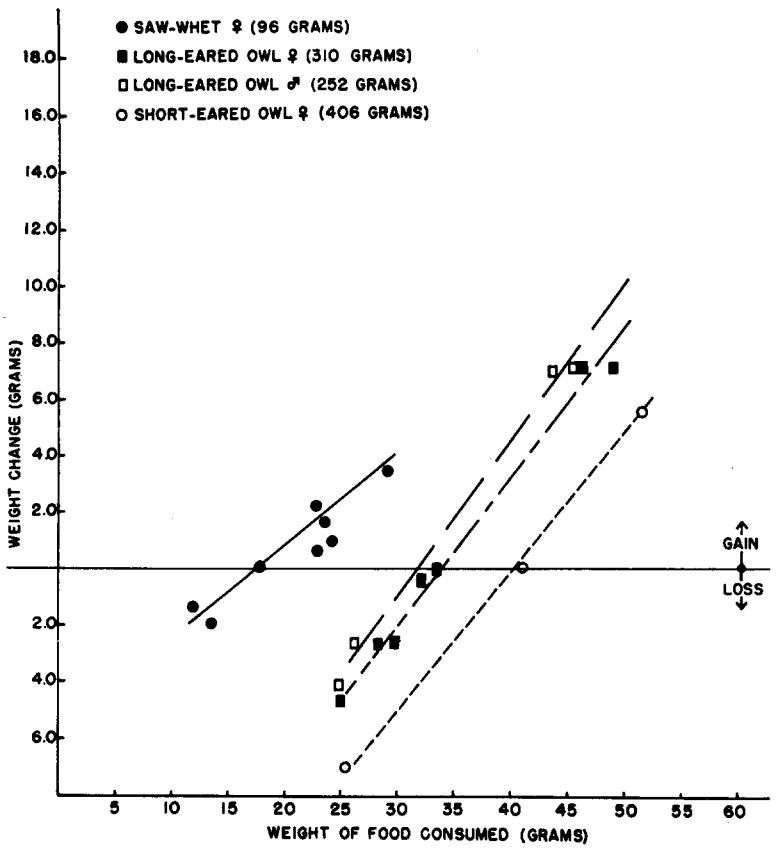

Fig. 2. Food consumption and weight change in four captive owls held in indoor flight cages at 18° to 19°C. with a 10- to 11-hour photoperiod.

the Long-eared Owl, the level of oxygen consumption fell at 2:00 p.m. CST to a low of 0.68 ml. per gm. of body weight per hour, the equivalent of only 77 kcal./kg. per day (fig. 1). The high extreme in oxygen consumption for the Long-ear, 1.16 ml./gm./hr. (equivalent to 131 kcal./kg. per day) occurred at 1:00 a.m. CST. The difference in extremes is about 41 per cent.

This graph (fig. 1) may be indicative of a peak in activity for the Long-ear around midnight. Similar fluctuations in standard metabolism have been shown for diurnal birds with the peaks in daytime and a nighttime low (King and Farner, 1961). These authors point out that the cycle is probably a result of variation in muscle tonus.

Under the aviary conditions specified above, the male Long-eared Owl (252 gm.)

required about 32 grams of tissue (laboratory mice) to sustain its weight through a 24–hour period, while a female Long-ear (310 gm.) required an average of 34 grams of food. The total caloric intake of these captive Long-eared Owls was 126 kcal. per 24 hours for the male and 134 for the female. Two other captive Long-ears of unknown sex, weighing 291 and 318 gm., required 31 and 32.5 gm. of *Mus,* respectively, for aviary existence without weight change. The average total caloric intake by all four Long-eared Owls for aviary life without weight change was 438 kcal./kg./day.

To determine what part of this total intake was actually metabolized, 24–hour accumulations of excreta and pellets were saved from two of the captives. Total caloric intake of the Long-ear weighing 291 gm. was 122 kcal. per day but 6.4 kcal. of this was ejected in the pellet (dry weight: 2.0 gm.) so that the actual gross intake was 116 kcal. Energy loss in excreta (dry weight: 3.9 gm.) was 9.6 kcal. so that the actual metabolized energy was 106 kcal. or 334 kcal./kg. of body weight. For the second owl, weighing 318 gm., the total daily caloric intake to maintain constant weight was 128 kcal., of which 5.6 kcal. were lost in the pellet (dry weight: 1.8 gm.), while the 24-hour excreta accumulation (dry weight: 3.5 gm.) represented 9.6 kcal. Metabolized energy for this bird was 113 kcal. or 355 kcal./kg. of body weight. Because no weight change occurred in these birds, metabolized energy equals existence energy for aviary life. During aviary existence (18° to 19°C. and 11 hours of daylight), daily caloric loss in excreta amounted to 8 per cent of the gross intake in both owls, whereas daily caloric loss from both excreta and pellets amounted to 12 and 13 per cent in the two birds.

In the natural situation, Long-eared Owls consumed a calculated weight of prey varying at different roosts from 47 to 58 gm., and averaging 51 gm. per forage (table 3). Voles, deer mice, and house mice comprised the bulk of this weight. Combining the caloric values for these prey species in proportion to the weight of each consumed by Long-eared Owls gives an estimate of the total caloric value of prey of 4160 gram-calories per gram. The caloric equivalent of prey per pellet, then, varied from 195 to 241 kcal. and averaged 210. As noted above, active captives were consuming only about 127 kcal. per day (average for four owls). This indicates either a much higher activity rate or weight increase for the wild birds. However, environmental conditions such as temperature must also be considered. The captives were kept at 18° to 19°C. In January and early February, Long-ears at two roosts in Allerton Park were consuming 220 to 240 kcal. (total intake) per day when the mean temperature of the environment was —1°C. (average for Decatur station). The same birds were taking only 200 kcal. in late February when the mean temperature was 1°C., but intake continued at 200 kcal. even in March when the temperature was 6°C. Birds in the wild had to search for and catch their own food and this activity could account for much of the difference noted.

The preceding paragraph presented data on total food intake by wild owls but not all of this food is metabolized. Average dry weight of pellets from wild (non-captive) Long-ears was 4 gm. and the average caloric value of this material was 3051 gram-calories per gram. Thus, about 12 kcal. are lost in the pellet by wild birds, leaving an average gross intake of about 198 kcal. per bird. I have no data on caloric loss in the excreta from wild birds, but Seibert (1949) showed that certain passerines lost increasing numbers of calories through excretion as the environmental temperature decreased and food intake increased. He found that caloric loss via excretion was minimal in four species of passerine birds at 22°C. (10–hour photoperiod), comprising about 8 per cent of the gross daily intake, as it did in the Long-ears under comparable

conditions. At —13°C. (10-hour photoperiod) the passerines studied by Seibert lost from 16 to 23 per cent of their daily intake through excretion. At a comparable loss-rate, wild Long-eared Owls in east-central Illinois would have metabolized between 153 and 166 kcal. per bird per day (winter average for all birds) in January or February, or 532 kcal./kg./day based on an average food consumption (all pellet data) and the average weight (299 gm.) of one male (271 gm.) and one female (327 gm.) Long-ear, both freshly killed, non-captives.

Short-eared Owl.—The standard metabolic rate of a female Short-eared Owl (average weight: 406 gm., respiration rate: 24–28 per minute) in terms of oxygen consumption was 7521 ml. (corrected to STP) per day (fig. 1) at an environmental temperature of 18° to 19°C. This is the food equivalent of about 35 kcal. per bird per day, or 87 kcal./kg. per day. The temporal pattern in standard metabolism shown by the Short-eared Owl was similar to that of the Long-ear with peak oxygen consumption occurring between 10:00 p.m. and 2:00 a.m., but with a low at 8:00 a.m. There were also marked depressions at 4:00 a.m. and 5:00 p.m.

In the aviary, this Short-ear required about 41 gm. of nutrient (*Mus*) to maintain its weight for 24 hours, the equivalent of 162 kcal. per day (fig. 2). If caloric loss via excretion and pellets is comparable in this species to that in the captive Long-ears, the actual metabolized (existence) energy for the Short-ear in the aviary would be 87 to 99 per cent of the total caloric intake or about 142 kcal. per day (350 kcal./kg. per day).

Calculated weights of prey for Short-eared Owls in nature varied from 41 to 53 gm. per pellet (table 5). The lower figure (41 gm.) represents only one owl, and the higher figure, which represents four birds, is more likely to be representative of the species. The essential prey species for Short-ears were voles, deer mice, and house mice. The caloric equivalents of these prey species combined in proportion to the weight of each that was eaten by Short-eared Owls gives a figure of 4330 gram-calories per gram. Expressing this weight of prey per forage in terms of calories, Short-eared Owls consumed 229 kcal. per day in the wild. Of this total intake, an average of about 13 kcal. are lost in the pellet, leaving a gross energy intake of 216 kcal. Mean environmental temperatures near (Urbana station) the Short-eared Owl roosts were 2° and 6°C., respectively, in February and March, 1957, when the fresh pellets were collected. At 10°C., passerine birds lost about 13 per cent of their total intake via excreation (Kendeigh, 1949; Seibert, 1949). At a comparable rate, metabolized energy of wild Short-eared Owls would amount to 188 kcal. per bird per day in February and March, or, based on winter weights given by Esten (1931), 522 kcal./kg. per day.

Saw-whet Owl.—At a standard rate of metabolism (fig. 1), a female Saw-whet Owl (average weight: 96 gm., respiration rate: 34 per minute) consumed 4070 ml. of oxygen (corrected to STP) in 24 hours at an environmental temperature of 18° to 19°C. The nutrient equivalent is 19 kcal. per day or 200 kcal./kg. per day. Under the same conditions, a male Saw-whet Owl (average weight: 75 gm., respiration rate: 35 per minute) consumed 3395 ml. of oxygen in 24 hours or 16 kcal. (213 kcal./kg. per day). As in the other owls, the oxygen consumption rate for Saw-whets was not constant through the 24-hour cycle but fell at about 1:00 to 2:00 p.m. to a low of 1.44 ml./gm. body weight/hr. (163 kcal./kg. per day) for the male and 1.52 ml./gm./hr. (172 kcal./kg. per day) for the female (fig. 1). The peak in the cycle came between about 10:00 p.m. and midnight which was similar to that of other owls, but the female showed a second peak at 4:00 a.m. when oxygen consumption by the male was falling, and the male showed a second peak at 7:00 a.m. The high extreme for the male at 11:00 p.m. and 7:00 a.m. was about 2.2 ml.0_2/gm./hr. (249 kcal./kg./day) and for the female at 10:00

p.m. and 4:00 a.m. 2.0 ml. O_2/gm./hr. (226 kcal./kg. per day). The difference in extremes was 35 per cent in the male and 24 per cent in the female. There is probably a great deal of individual variation in the rate of oxygen consumption, and present data should be considered only as estimates of the true basal energy requirements. There was a tendency for the metabolic rate to increase in this species with increase in fasting time (fig. 1).

The female Saw-whet Owl required 17.5 gm. of fresh tissue or the equivalent of about 69 kcal. to maintain its weight during 24 hours of aviary existence (fig. 2). About 3.5 kcal. of this total intake were lost in the pellet so that actual gross energy intake by the Saw-whet for aviary life was about 65 kcal. (677 kcal./kg.). Lacking data on caloric loss in excretion for this species, I again based estimates of metabolized energy on data from the Long-eared Owl and from passerine birds discussed by Kendeigh (1949) and Seibert (1949). In the aviary (temperature 18° to 19°C., 10 hours of daylight) about 8 per cent of the Saw-whet's gross energy intake (65 kcal.) would have been lost in excretion, leaving a metabolized (aviary existence) energy of 60 kcal. per bird per day (635 kcal./kg.).

For Saw-whets under natural conditions, the quantity of food consumed in winter varied from 13.3 to 18.3 gm. per forage (table 7). There was only one Saw-whet at each roost, and the extreme variation in food consumption may represent differences between individual owls and/or between sexes. The catch per forage (gm. of prey) was consistently lower in 1958 than in 1957. This is surprising because the winter months, from January to March, of 1958 were much colder than the winter of 1957. The reduced catch in 1958 may have reflected availability of prey, however. The 1957 (February to March) data on catch per forage by Saw-whets appear to be separable into two classes (table 7). Two of the Saw-whets (McDonough County and Vermilion County roosts) took about 18 gm. of prey per forage (table 7), whereas owls at two other roosts (Allerton Park and Lodge Park roosts) consumed about 15 gm. of prey per forage. This may represent a sexual difference, as female Saw-whet Owls are larger than males, and a captive female required about 17.5 gm. of *Mus* daily to maintain constant weight in the aviary. The principal winter food of Saw-whet Owls was *Peromyscus leucopus*; the caloric value of this prey species was determined to be 4321 gram-calories per gram. The total daily caloric intake of Saw-whet Owls from Allerton and Lodge parks was about 66 kcal., whereas the birds at McDonough County and Vermilion County consumed about 79 kcal. per bird per day. In this species, loss of calories with the pellet (average dry weight, 1.5 gm.) accounted for about 5 kcal., leaving a gross energy intake of 61 and 74 kcal. per day for the two groups of Saw-whets. These values are surprisingly close to the number of calories consumed by the captive female Saw-whet in my aviary where the environmental temperature was 18° to 19°C. In February, 1957, temperatures at the Saw-whet roosts averaged about 4°C., and, therefore, I would have expected the wild birds to require more food than the captive. One possible explanation for the similarity in caloric intake by captive and wild birds is that the captive may actually have been more active than the wild birds. Assuming a caloric loss via excretion of 13 per cent of the gross intake for wild Saw-whets in their natural winter environment, metabolized (natural existence) energy would have been 53 (males ?) and 64 (females ?) kcal. per bird for the two groups of Saw-whets. Based on average figures for food consumption (pellet data) and an average weight for one male (78 gm.) and one female (103 gm.) Saw-whet Owl, both freshly killed non-captives, the estimate of existence energy under natural conditions for the Saw-whet is 644 kcal./kg. per day.

SUMMARY

Estimates of the gross energy requirements for Long-eared, Short-eared, and Saw-whet owls based on pellet analysis and indirect calorimetry were made in central Illinois for three levels of activity: standard (basal) aviary existence (18° to 19°C. and 10– to 11–hour photoperiod), and natural existence (winter, with 10– to 11–hour photoperiod and temperatures around 0°±10°C.).

In terms of metabolized (existence) energy, expressed as kcal. per bird per day and kcal./kg. per day (in parentheses), average metabolic rates for each of the three species were: LONG-EARED OWL—standard (basal) rate: 26 kcal./bird/day (105 kcal./kg./day), aviary existence: 109 kcal./bird/day (357 kcal./kg./day), natural existence: 159 kcal./bird/day (532 kcal./kg./day); SHORT-EARED OWL—standard (basal) rate: 35 kcal./bird/day (87 kcal./kg./day), aviary existence: 142 kcal./bird/day (350 kcal./kg./day), natural existence: 188 kcal./bird/day (522 kcal./kg./day); SAW-WHET OWL—standard (basal) rate: 17.5 kcal./bird/day (206 kcal./kg./day), aviary existence: 60 kcal./bird/day (625 kcal./kg./day), natural existence: 59 kcal./bird/day (644 kcal./kg./day).

The standard rates for these owls are about comparable to determinations on birds of similar weights given by other authors (Brody, 1945; King and Farner, 1961). The rates for these owls appear to vary with the 0.70 to 0.73 power of body weight (see Brody, 1945:371; King and Farner, 1961:229). The Saw-whets are best represented by the low factor (0.70) and the Long-eared and Short-eared owls approach the high extreme (0.73). Even considering the differences in size, Saw-whets have relatively higher metabolic rates than Long-eared and Short-eared owls.

Standard rates of oxygen consumption varied in all three species with peaks occurring between 10:00 p.m. and midnight in the Saw-whet Owls, and between 10:00 p.m. and 2:00 a.m. in the Long-eared and Short-eared owls. There was a tendency for a secondary high to occur between 4:00 and 8:00 a.m.; this was most marked in Saw-whet Owls. Low points in the cycle occurred between noon and 2:00 p.m. for all species. The male Saw-whet and female Short-ear also showed marked depressions between 2:00 and 4:00 a.m.

Food habits were similar in the Long-eared and Short-eared owls, although Short-ears utilized relatively more *Peromyscus* and fewer *Microtus* than Long-eared Owls. Saw-whet Owls were most specialized in diet and depended primarily on a single prey species, *Peromyscus leucopus*. Saw-whets roosted near forests and apparently hunted in or near woods or brushy areas.

Pellets of both Saw-whet and Long-eared owls indicated greater variation in diet between birds at different roosts in the same year than was shown at one roost in different years.

There was a tendency for the diet to change with the passing of winter. As spring approached, relatively more birds and house mice were consumed, probably reflecting increased availability of these prey species.

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