CHARNOV, E. L. AND J. R. KREBS. 1974. On clutch size and fitness. Ibis 116:217–219.
COULTER, M. C. 1973. Breeding biology of the Western Gull, *Larus occidentalis*. M.S. thesis, Oxford Univ., England.
CROSSNER, K. A. 1977. Natural selection and clutch size in the European Starling. Ecology 58:885–892.
HAARTMAN, L. v. 1971. Population dynamics. Pp. 392–461 *in* Avian biology. Vol. 1 (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York.
HARRIS, M. P. AND W. J. PLUMB. 1965. Experiments on the ability of Herring Gulls *Larus argentatus* and Lesser Black-backed Gulls *Larus fuscus* to raise larger than normal broods. Ibis 107:256–257.
HAYMES, G. T. AND R. D. MORRIS. 1977. Brood size manipulations in Herring Gulls. Can. J. Zool. 55:1762–1766.
HÖGSTEDT, G. 1980. Evolution of clutch size in birds: adaptive variation in relation to territory quality. Science 210:1148–1150.
KLOMP, H. 1970. The determination of clutch-size in birds, a review. Ardea 58:1–124.
LACK, D. 1947. The significance of clutch-size. Parts I and II. Ibis 89:302–352.
———. 1948. The significance of clutch-size. Part III. Ibis 90:25–45.
———. 1966. Population studies of birds. Clarendon Press, Oxford, England.
NUR, N. 1984. The consequences of brood size for breeding Blue Tits I. Adult survival, weight change and the cost of reproduction. J. Anim. Ecol. 53:479–496.
REID, W. V. 1987. Constraints on clutch size in the Glaucous-winged Gull. Studies in Avian Biology 10:8–25.
RICKLEFS, R. E. 1983. Comparative avian demography. Current Ornith. 1:1–32.
SCHIFFERLI, L. 1978. Experimental modification of brood size among House Sparrows *Passer domesticus*. Ibis 120:365–369.
VERMEER, K. 1963. The breeding ecology of the Glaucous-winged Gull (*Larus glaucescens*) on Mandarte Island, B.C. Occas. Pap. B.C. Prov. Mus. 13:1–104.
WARD, J. G. 1973. Reproductive success, food supply and the evolution of clutch size in the Glaucous-winged Gull. Ph.D. diss., Univ. of British Columbia, Vancouver, British Columbia, Canada.

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Fall migration of Ruby-throated Hummingbirds in the northeastern United States.—The Ruby-throated Hummingbird (*Archilochus colubris*) migrates long distances between its breeding range in eastern North America and its winter range in the southern United States and Middle America (Bertin 1982, A.O.U. 1983). Most references to the overland migration of Ruby-throated Hummingbirds concern their regional status or report large numbers of fall migrants, while behavioral, ecological, and energetic aspects of their migration have received little attention. The ridges of the Appalachian Mountains are major routes for southbound migrants, and in this study we describe the seasonal and daily timing of migrating Ruby-throated Hummingbirds and the influence of wind direction and velocity at one such Appalachian lookout, Hawk Mountain Sanctuary, Pennsylvania. We also present data from

TABLE 1

SUMMARY OF RUBY-THROATED HUMMINGBIRD COUNTS IN NORTHEASTERN UNITED STATES: 1985 DATA ONLY

	Site[a]						
	A Quaker Ridge, CT	B Lighthouse Point, CT	C Mt. Peter, NY	D Montclair, NJ	E Hawk Mountain, PA	F Waggoner's Gap, PA	G Tuscarora Summit, PA
Count period (mo/day)	9/7–9/30	8/29–9/30	9/1–9/29	8/31–9/29	8/1–9/30	8/17–9/30	9/1–9/30
Days	20	32	27	29	46	24	27
Season summary:							
Hours	243.00	213.50	178.00	191.50	304.50	94.25	165.25
Total birds	21	113	9	20	120	10	18
Birds per hour	0.13	0.58	0.05	0.11	0.39	0.10	0.10
Peak flight:							
Date (mo/day)	9/14	9/12	9/2	9/1	8/28[b]	8/23	9/7
Single-day total	9	17	3	6	20	9	6
Birds per hour	0.95	2.13	0.42	0.10	3.16	1.80	1.50
Date (mo/day) on which last migrant seen	9/20	9/23	9/23	9/21	9/25	9/21	9/20

[a] Sites are ordered from northeast to southwest; coordinates (°N and °W) for each site: A = 41°05′ 73°35′; B = 41°10′ 72°50′; C = 41°10′ 74°10′; D = 40°45′ 74°10′; E = 40°35′ 75°55′; F = 40°20′ 77°25′; G = 39°40′ 77°50′.

[b] Excluding August data, there were two peak flights at Hawk Mountain: 1.53 birds/h on 6 September and 1.40 birds/h on 11 September.

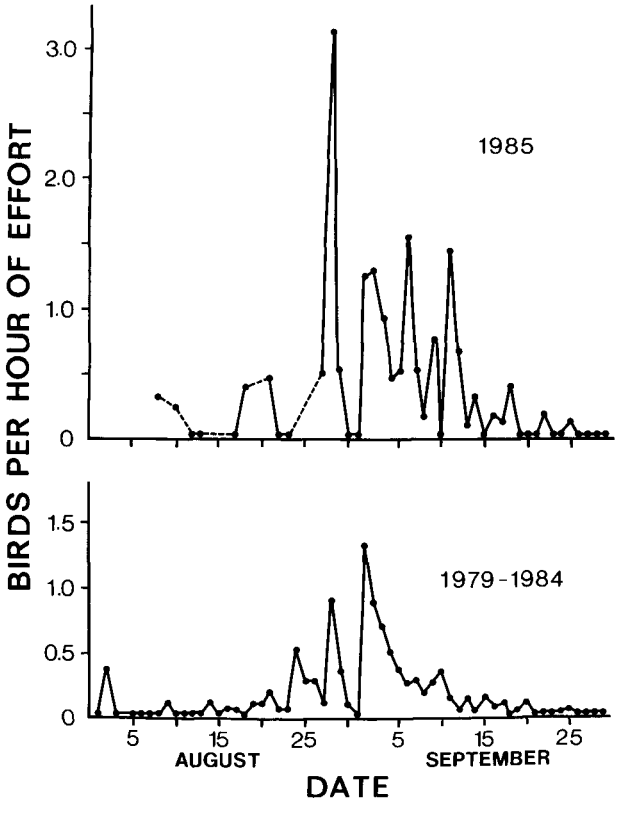

FIG. 1. Number of Ruby-throated Hummingbirds per hour migrating past the North Lookout, Hawk Mountain Sanctuary, by day in August–September. Data points for the years 1979–1984 are birds per hour for all years combined. A dashed line connects data points when coverage was not daily.

other sites in the northeastern U.S. and consider evidence for differences in the seasonal timing of different age-sex classes.

Study area and methods.—Hummingbirds were counted on 44 days from 1 August–29 September 1985 at the North Lookout (elevation = 463.6 m), Hawk Mountain Sanctuary (HMS), on the Kittatinny Ridge on the Schuylkill-Berks county line in southeastern Pennsylvania. Broun (1939) describes the physical setting with respect to the migration of raptors and other birds. Observations were made on 29 of 30 days in September, but only on 15 of 31 days in August. Because northwest winds are conducive to good flights of migrants, all days in August with such winds were covered. Observations were typically made between 8:00–18:00 h, Eastern Standard Time, for a total of 304.45 h. Observations were made by a single person from a central location overlooking the ridge to the northeast and the broad valleys to the north and the southeast. It was not possible to record the age and sex of individual migrants. Number of hummingbirds, air temperature, wind speed and direction and cloud cover were recorded hourly.

TABLE 2

DAILY TIMING OF MIGRATING HUMMINGBIRDS AT HAWK MOUNTAIN SANCTUARY AND TWO SITES (COMBINED) IN CONNECTICUT

Time period (EST)	Hawk Mountain[a]				Connecticut[b]			
	Total coverage (h)	Total number of birds	% Total birds	Birds per hour	Total coverage (h)	Total number of birds	% Total birds	Birds per hour
06:00–09:59	57.0	12	11	0.21	62.0	32	31	0.52
10:00–13:59	73.0	77	71	1.06	64.0	61	59	0.95
14:00–17:59	39.0	20	18	0.51	15.5	10	10	0.65
Total	169.0	109	100		141.5	103	100	

[a] Distribution of birds/h significantly different from uniform: $G = 65.197$, $df = 2$, $P < 0.001$.
[b] Distribution of birds/h significantly different from uniform: $G = 13.455$, $df = 2$, $P < 0.005$.

Daily counts of migrant hummingbirds at Hawk Mountain from 1979–1984 were summarized by adding all hummingbirds recorded for a given date over the 5-year period and dividing by the total hours of effort. Other observations are available from the journals of the first HMS curator, the late Maurice Broun (years 1942 and 1946–1960, archived at the Dept. of Biology, Muhlenberg College, Allentown, Pennsylvania).

Data gathered in 1985 at six other northeastern U.S. sites were used to supplement observations from HMS. Four of the sites are north of HMS; two are south (Table 1). Unlike HMS, counts of hummingbirds at these sites were incidental to counts of migrating raptors.

We examined specimens of Ruby-throated Hummingbirds at the Academy of Natural Sciences of Philadelphia and the American Museum of Natural History in New York to explore whether there are differences in the seasonal timing of migrants from different age and sex classes. Immature birds were distinguished from adult birds by the presence of serrations on the bills of the immatures (Ortiz-Crespo 1972). We did not distinguish the sexes of immature hummingbirds.

Seasonal timing.—The migration of Ruby-throated Hummingbirds at HMS in 1985 spanned 8 August through 25 September; we counted a total of 120 hummingbirds. The migration peaked from 26–30 August (highest count was 20 = 3.16 birds/h on 28 August) and remained high from 31 August–12 September (Fig. 1). More than 90% of all hummingbirds had been counted through 14 September. During 1979–1984, most hummingbirds at HMS were counted from 21 August–15 September (Fig. 1). The average date on which at least 90% of

TABLE 3

NUMBERS OF MIGRATING HUMMINGBIRDS AT DIFFERENT WIND SPEEDS[a]

Wind speed (km/h)	Birds observed	Birds per hour[b]	% Total birds
1–5	9	0.23	16
6–11	21	0.72	38
12–19	26	0.83	46

[a] Only days with NW or W winds and >6 h coverage.
[b] Distribution significantly different from uniform: $G = 39.99$, $df = 2$, $P < 0.001$.

all migrants had been recorded was 11 September (SE = ± 2.2 days, range = 1–17 September). The highest single-day count of migrating hummingbirds at HMS, 45, was on 3 September 1975. The earliest migrant was on 2 August 1983; the latest were recorded by Broun on 29 September in 1953 and again in 1956.

At the supplementary sites in the northeast in 1985, based primarily on September coverage, single-day peak flights ranged from 3–17 hummingbirds on 1–14 September (Table 1). The last date on which hummingbirds were recorded in 1985, including those at HMS, ranged from 20–25 September (Table 1).

Daily timing.—At HMS and a combination of the Lighthouse Point and Quaker Ridge, Connecticut sites, 109 and 103 hummingbirds, respectively, were recorded on days with >7 h coverage. We pooled these data within 4-h periods and found that the distributions of hummingbirds among the 4-h time periods were significantly different from being uniform both at HMS and in Connecticut (Goodness of Fit test, Sokal and Rohlf 1981; Table 2). The greatest proportion of hummingbirds and the highest number of birds/h at HMS and in Connecticut were during mid-day hours, 10:00–14:00 h.

Wind direction and velocity.—In 1985, the days with the highest counts of hummingbirds at HMS (28 August and 11 September) coincided with the arrival of strong cold fronts and northwest winds. More hummingbirds were recorded with northerly winds (0.55 birds/h) than with southerly winds (0.39 birds/h), but this difference was not statistically significant ($G = 2.74$, $df = 1$, $P > 0.05$). Our counting periods were biased toward days with northwest or west winds; more data need to be collected on winds from other directions. The relation between wind velocity and numbers of hummingbirds was clearer. For days with >6 h coverage and with northwest or west winds, the number of hummingbirds counted increased significantly with wind speed (Table 3).

Differences between age and sex classes.—We examined 102 museum specimens of Ruby-throated Hummingbirds, including 16 adult males, 35 adult females, and 51 immatures. No adult males had been collected in the U.S. after 30 August. Adult females or immatures collected in the U.S. were taken before 24 September. We could not detect a difference in the schedules of adult females and immatures of either sex. Broun's journals indicate that at HMS locally breeding male hummingbirds depart before the females. For example, in 1955 he noted that the males had departed by 27 August, but that females were at his feeders until 11 September. Similarly, in 1957 he noted that females were present until 16 September, long after the departure of local males.

Seasonality and differential migration.—Differences in the migrations of sex- and age-classes have been noted in several species of hummingbirds in the western U.S. (e.g., Phillips 1975). Bent (1958) and others (e.g., Sprunt and Chamberlain 1949, Johnsgard 1983) reported that adult male Ruby-throated Hummingbirds precede adult females and immatures during fall migration. Of 32 hummingbirds captured or collected in Aiken County, South Carolina, 6–24 September 1955 (Norris et al. 1957), all but two were immature.

The fact that there are age- and sex-specific differences in the migration schedules of Ruby-throated Hummingbirds is a confounding variable when considering data recorded or reported without regard to age and sex classes. Nonetheless, our results, especially the closely grouped dates for "last migrants" (Table 1), and reports in the literature suggest that the migration of Ruby-throated Hummingbirds is temporally compressed compared to that of such western species as the Allen's Hummingbird (*Selasphorus sasin*) and the Rufous Hummingbird (*S. rufus*) (Phillips 1975). For example, average departure dates reported by Oberholser (1924) and others (e.g., Poole 1964) for all age-sex classes of hummingbirds from Maine to North Carolina and west to Indiana and Michigan occur within a single month—September. North to south—from Maine to Louisiana—the period covering all average departure dates spans less than two months: 3 September–25 October (Oberholser 1924).

Various investigators have suggested that the phenology and availability of food resources along migration paths or at stopovers influence the timing of bird migrations (e.g., Schneider and Harrington 1981), and dependency on ephemeral food supplies could result in contracted migrations. Grant and Grant (1967) link movements of various hummingbird species to the flowering phenology of hummingbird-pollinated plants. Bertin (1982) specifically hypothesizes that the peak fall migration of Ruby-throated Hummingbirds is nearly synchronous with peak flowering of a major food source, jewelweed (*Impatiens biflora*). The timing and progression of their migration in the northeast are consistent with Bertin's (1982) hypothesis, although he apparently does not consider the differences in the timing of migrations of the age-sex classes or the timing of the flowering of other plant species.

Daily timing.—Hummingbirds are diurnal, and they fast through the night (Calder 1974). The onset of morning activity is correlated with the intensity of light needed for successful foraging, and their time budget should allow maximum use of daylight feeding. We do not know whether Ruby-throated Hummingbirds fly at night during their overland migration. Even if they do not, the first hours of daylight must be used to replenish their energy reserves after a night's fast. At the end of the day, they must refuel before fasting for the night. The mid-day hours, in effect, may be the only time available for protracted migration flights, and it is during these hours that we counted the most migrants (Table 2). Migrant hummingbirds on the Allegheny Front in West Virginia are usually seen in mid-day or afternoon, in contrast to nocturnal-migrant songbirds which are mostly recorded early in the day (Hall and Bell 1981).

Wind direction and velocity.—In the northeastern U.S., the passage of a cold front typically brings strong northwest winds and large flights of raptors and songbirds (Broun 1939, Hall and Bell 1981) and hummingbirds (e.g., Heintzelman and MacClay 1972). Hummingbirds may benefit energetically from the lift provided by higher wind velocities or other phenomena associated with the passage of low-pressure systems. We saw more hummingbirds at higher wind velocities (Table 3), but it is not known whether more hummingbirds are actually flying under such conditions or whether they are simply more visible from mountain lookouts.

Ruby-throated Hummingbirds concentrated in autumn at a site in South Carolina defended "vague territories," and, near the time of their departure, had sufficient reserves to allow nonstop flights from South Carolina across the Gulf of Mexico (Norris et al. 1957). However, the basic pattern of Ruby-throated Hummingbird migration over land has not been established. Mid-day flights in the context of a temporally compressed migration suggest a strategy that is based on daily "short-hop" flights southward, rather than extended stops during a prolonged migration that is typical of such western species as the Rufous Hummingbird and Allen's Hummingbird (Phillips 1975). More than likely, some combination of both is employed, depending on such variables as weather and food supply.

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LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. 6th ed. Amer. Ornith. Union, Washington, D.C.

BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and their allies. U.S. Nat. Mus. Bull. No. 211.

BERTIN, R. I. 1982. The Ruby-throated Hummingbird and its major food plants, ranges, flowering phenology and migration. Can. J. Zool. 60:210–219.

BROUN, M. 1939. Fall migration of hawks at Hawk Mountain, Pennsylvania 1934–1938. Auk 58:429–441.

CALDER, W. A., III. 1974. Consequences of body size for avian energetics. Pp. 86–151 *in* Avian energetics (R. A. Paynter, Jr., ed.). Publ. Nuttal Ornith. Club No. 15.

GRANT, K. A. AND V. GRANT. 1967. Effects of hummingbird migration on plant speciation in the California flora. Evolution 21:457–465.

HALL, G. A. AND R. K. BELL. 1981. The diurnal migration of passerines along an Appalachian ridge. Am. Birds 35:135–138.

HEINTZELMAN, D. S. AND R. MACCLAY. 1972. An exceptional Ruby-throated Hummingbird migration. Cassinia No. 53, p. 45.

JOHNSGARD, P. 1983. The hummingbirds of North America. Smithsonian Institution Press, Washington, D.C.

NORRIS, R. A., C. E. CONNELL, AND D. W. JOHNSTON. 1957. Notes on fall plumages, weights, and fat condition in the Ruby-throated Hummingbird. Wilson Bull. 69:155–163.

OBERHOLSER, H. C. 1924. The migration of North American birds: XXIV. Ruby-throated, Black-chinned, and Calliope hummingbirds. Bird Lore Mar–Apr:108–111.

ORTIZ-CRESPO, F. I. 1972. A new method to separate immature and adult hummingbirds. Auk 89:851–857.

PHILLIPS, A. R. 1975. The migrations of Allen's and other hummingbirds. Condor 77: 196–205.

POOLE, E. L. 1964. Pennsylvania birds, an annotated list. Livingston Publishing Company, Narbeth, Pennsylvania.

SCHNEIDER, D. AND B. HARRINGTON. 1981. Timing of shorebird migration in relation to prey depletion. Auk 98:801–811.

SOKAL, R. AND J. ROHLF. 1981. Biometry. Freeman, New York, New York.

SPRUNT, A., JR. AND E. B. CHAMBERLAIN. 1949. South Carolina Bird Life. Univ. South Carolina Press, Columbia, South Carolina.

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Fulvous Whistling-Duck abundance and habitat use in southwestern Louisiana.—The Fulvous Whistling-Duck (*Dendrocygna bicolor*) is a locally common breeding bird of the rice (*Oryza sativa*) belt of southwestern Louisiana, which had nesting densities of 13–20 pairs within a 12.95-km^2 area in the mid-1950s (Meanley and Meanley 1959). This species declined rapidly in the 1960s, apparently from exposure to pesticides applied to rice (Flickinger and King 1972). The population increased in the 1970s with the discontinued use of aldrin-treated rice seed and the conversion from aerial seeding to drill planting, and by late