Timing of Hummingbird Migration in Southeastern Arizona: Implications for Conservation[1]

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Abstract

We examined the distribution and abundance of hummingbirds at three study sites in southeastern Arizona, where over 8,000 individuals of twelve species were banded. Banding occurred at two sites in the early 1990s and is currently active at the third. Anna's (*Calype anna*), Black-chinned (*Archilochus alexandri*), and Rufous (*Selasphorus rufus*) Hummingbirds were the most abundant species. A massive southbound fall migration occurred at the study sites with fewer hummingbirds moving northward in spring. The large numbers of migrants were spaced over time within seasons, and the timing of peak migration for a species varied among years. Fall-migrant Black-chinned peaked earliest, followed by Rufous (predominantly juveniles), then Anna's. Of these species, Rufous used the sites during migration only while the other species bred at one or more sites. Because the timing of migration differed among species, the resources critical for migration of each species likely differed as well. The implications for hummingbird conservation are discussed.

Key words: Anna's Hummingbird, Black-chinned Hummingbird, conservation, hummingbird, migration, Rufous Hummingbird, southeastern Arizona.

Introduction

Migration patterns are poorly known for hummingbirds. Most of the more than 300 hummingbird species do not migrate and those that do migrate breed farthest north or south of the tropics (Schuchmann 1999). Our knowledge about the routes and timing of migration is based mainly on a few North American species that include Rufous (*Selasphorus rufus*), Allen's (*Selasphorus sasin*) and Calliope (*Stellula calliope*) hummingbirds (Phillips 1975, Calder 1993, Calder and Calder 1994). These species breed in the higher latitudes of North America and traditionally migrate in an elliptical route. In late summer and early fall, they fly south following the Rocky Mountains and in late winter and early spring, their northbound migration usually occurs farther west and at a lower elevation (Phillips 1975, Calder 1993, Calder and Calder 1994).

The timing of southbound migration varies among these species with the age and sex of individuals. Typically, adult males migrate before adult females, which in turn precede the juveniles (Stiles 1972, Phillips 1975, Calder 1987). This pattern has also been documented for Ruby-throated Hummingbirds (*Archilochus colubris*) (Mulvihill and Leberman 1987). A slight variation of the pattern has been documented for other species such as Black-chinned Hummingbird (*Archilochus alexandri*) and Costa's Hummingbird (*Calypte costae*), in which males precede females and young of the year, the latter two groups migrating at similar times. It has been documented for both north- and south-bound migrations in Black-chinned, but only in late summer movement patterns for Costa's (Baltosser and Scott 1996, Baltosser and Russell 2000, Wethington and Russell 2003).

In this paper we compare temporal migration patterns for three common hummingbird species: Black-chinned, Anna's (*Calypte anna*), and Rufous at three sites in southeastern Arizona. The general shapes of these patterns was previously described for two sites, where banding occurred in the early 1990s (Wethington and Russell 2003). Ten years later, we compare these temporal patterns from those sites to another site, which is to the east and at a higher elevation. The consistency of these temporal patterns may suggest factors important for the conservation of North American hummingbirds.

Study Areas and Methods

The Sonoita study site (31°038'51"N, 110°039'18"W, elevation 1530 m, 2 km south of Sonoita, Arizona) lies in an intermontane valley between the Santa Rita and Huachuca mountains in oak (*Quercus emoryi* and *Q. arizonica*) woodland at the southern end of open grasslands. Bock and Bock (1986, 1988) have described the

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area's vegetation. Flowers used by hummingbirds are scarce during all seasons. After a pilot study in 1987, we banded approximately every week while birds were present, from the first part of April to the end of October for five years (1988-1992).

In 1991, we established a second site along Harshaw Creek (31°030'00"N, 110°040'50"W, elevation 1370 m) approximately 16 km south of the Sonoita site, and operated it concurrently in 1991 and 1992. Banding continued there in 1993. This study site lies within a riparian zone bounded by oak and mesquite woodlands. Desert willow (*Chilopsis linearis*), Arizona sycamore (*Platanus racemosa*), Fremont cottonwood (*Populus fremontii*), Arizona walnut (*Juglans major*), willows (*Salix* spp.), and seep willow (*Baccharis salicifolia*) grow within the riparian zone. Surface water flows intermittently at the site.

In 2000, a third banding site was established at Miller Canyon in the Huachuca Mountains (31°030'N, 110° 015'W, elevation 1780 m) on the border of a 4 ha apple orchard. The neighboring woods are dominated by several species of oak and Manzanita (*Arctostaphylos pungens*) with Arizona sycamore along the creek. Banding occurred once every two weeks from late March to mid-October.

Commercial hummingbird feeders were maintained at all sites, providing an unlimited food supply and may have increased the number of hummingbirds in the area. We used a sugar solution of 1 part sugar to 4 parts water. At the Sonoita and Miller Canyon sites, feeders had been maintained for many years. We introduced feeders at the Harshaw Creek site in 1991 where other feeders were more than 2 km away.

At Sonoita and Harshaw Creek, we captured hummingbirds using a trap (Russell and Russell 2001) made from a 6-m long mist net with a 24-mm mesh, arranged as an open-ended box and baited with one or two feeders on poles inside. Another mist net covered the top. At Miller Canyon, two Hall traps were used (Russell and Russell 2001). At all sites, we trapped hummingbirds during the morning hours. At Sonoita and Harshaw Creek, we began approximately 30 min before sunrise and usually continued until the first of three ending conditions occurred: we had captured 100 birds; an hour had passed with no new birds captured; or the hour of 1100 was reached. At Miller Canyon, trapping began approximately 30 min after sunrise and continued for at least 5 hrs.

We banded all hummingbirds with U.S. Fish and Wildlife Service bands and aged and sexed individuals using plumage and flight feather characters (Stiles 1972, Baltosser 1987) and bill corrugations (Ortiz-Crespo 1972). We also weighed each individual to 0.1g.

For site comparisons, we standardized the data by matching 15 dates from each site. The matched dates typically occurred within 5 days of each other. Seven days was the maximum number of days separating paired banding days.

To determine if the abundance for each age-sex class per species differed among sites, we used the Friedman rank sum test. In these analyses, the grouping factor was the site, the blocking factor was the banding day, and the response variable was the number of birds captured. For Sonoita and Harshaw Creek, we averaged each banding day's capture across years of the study and used the average in the analyses. Sonoita's average contained five years of data, Harshaw Creek three. Miller Canyon had one. If a significant difference in abundance was detected, we then used the Wilcoxon rank-sum test to determine which pairs of sites differed. Because the number of birds captured each banding day fluctuated, we used Friedman's super smoothing algorithm (Friedman 1984) to show a smoothed pattern to the abundance data.

We used a standard $P < 0.05$ to indicate statistical significance. Values presented are means ± SD. All analyses were done with AXUM 6.0 (Mathsoft Inc. 1999). Because the number of birds captured each banding day varied, we used Friedman's super smoothing algorithm (Friedman 1984) to display a smoothed pattern to the abundance data.

Results

During the study at Sonoita and Harshaw Creek, peak numbers of the three species during fall migration occurred at different times, Black-chinned in late August to early September, followed by Rufous and then Anna's (*fig. 1*). For these species, migration times also varied among years. We identified the date for the median hummingbird captured from July through October for each year at each study site (*table 1*). In some age-sex classes, these dates varied by over four weeks. Ten years later, the same temporal patterns for these species is documented at Miller Canyon ($Z < 0.8$, $P > 0.44$ for three pair-wise comparisons; *fig. 2*, *table 1*).

Black-Chinned Hummingbird

Black-chinned Hummingbird was the most abundant species (*fig. 3*). Males arrived between late March and early April. By mid-April, adults of both sexes were present. Juveniles first appeared at the feeders in mid-June. The abundance of juvenile females differed significantly among sites (Friedman $\chi^2_2 = 14.5$, $P < 0.01$) and the difference in abundance was almost significant for adult males (Friedman $\chi^2_2 = 5.9$, $P < 0.06$). During the time in which juveniles were present, the average number of juvenile females per banding day at Miller Canyon was 1.3 ± 2.5, at Sonoita 3.6 ± 3.5, and at Harshaw Creek 6.4 ± 6.4. The abundance at Miller Canyon differed significantly between Sonoita ($Z = 2.2$, $P < 0.03$) and between Harshaw Creek ($Z = 2.4$, $P < 0.02$).

The abundance of adult males differed significantly between Sonoita and Harshaw Creek ($Z = 2.4$, $P < 0.02$) only. The ratio of adult males to adult females differed significantly between these sites ($\chi^2_1 = 80.5$, $P < 0.01$). Males averaged 72 ± 5 percent of the adult population in Sonoita but only 37 ± 2 percent in Harshaw Creek. These percentages remained consistent throughout the season. Males averaged 62 percent at Miller Canyon.

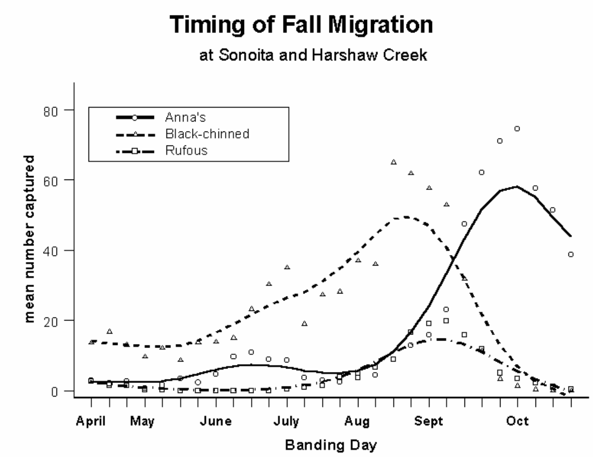

Figure 1— The smoothed seasonal distribution of the three most commonly captured hummingbird species. Point values are average number of hummingbirds per species per banding day from Sonoita and Harshaw Creek.

Anna's Hummingbird

Anna's Hummingbird was the most abundant species during September and October (*fig. 4*). The abundance for both age-sex classes of females differed significantly among sites (Friedman $\chi^2_2 > 7.1$, $P < 0.03$). At Harshaw Creek, adult females occurred throughout the banding season. At Sonoita, adult females did not consistently occur until August and then they stayed later in October than at Harshaw Creek. This pattern likely explains the significant difference for adult females between these two sites ($Z = -2.1$, $P < 0.04$).

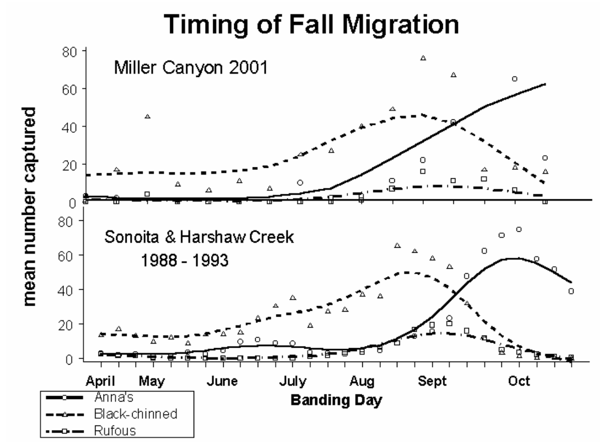

Figure 2— Comparison of one year of data from Miller Canyon with the smoothed seasonal distribution of the three most commonly captured hummingbird species from Sonoita and Harshaw Creek. Although the number of Anna's had declined at the end of banding at Miller Canyon, the smoothing algorithm does not show it.

Table 1— *Dates for capture of the median hummingbird for each age-sex class during migration (July-October).*

Species	Sonoita					Harshaw Creek			Miller Canyon
Age/sex classes	1988	1989	1990	1991	1992	1991	1992	1993	2001
Anna's Hummingbird									
Juvenile male	29 Sept	14 Sept	29 Sept	3 Oct	25 Sept	28 Sept	20 Sept	12 Sept	18 Sept
Juvenile female	12 Oct	25 Sept	24 Sept	26 Sept	25 Sept	5 Oct	27 Sept	25 Sept	2 Oct
Adult male	29 Sept	25 Sept	29 Sept	3 Oct	25 Sept	28 Sept	20 Sept	19 Sept	18 Sept
Adult female	29 Sept	7 Oct	29 Sept	3 Oct	3 Oct	28 Sept	20 Sept	25 Sept	18 Sept
Black-chinned Hummingbird									
Juvenile male	31 Aug	18 Aug	27 Aug	19 Aug	31 Aug	1 Sept	15 Aug	15 Aug	21 Aug
Juvenile female	9 Sept	27 Aug	12 Sept	10 Aug	19 Aug	1 Sept	15 Aug	15 Aug	6 Sept
Adult male	22 Aug	25 July	17 Aug	10 Aug	19 Aug	24 Aug	15 Aug	8 Aug	9 Aug
Adult female	26 Aug	27 Aug	17 Aug	25 Aug	27 Aug	24 Aug	23 Aug	15 Aug	21 Aug
Rufous Hummingbird									
Juvenile male	9 Sept	31 Aug	12 Sept	10 Sept	31 Aug	8 Sept	4 Sept	5 Sept	6 Sept
Juvenile female	9 Sept	10 Sept	12 Sept	10 Sept	10 Sept	15 Sept	4 Sept	29 Aug	21 Aug
Adult male									
Adult female									

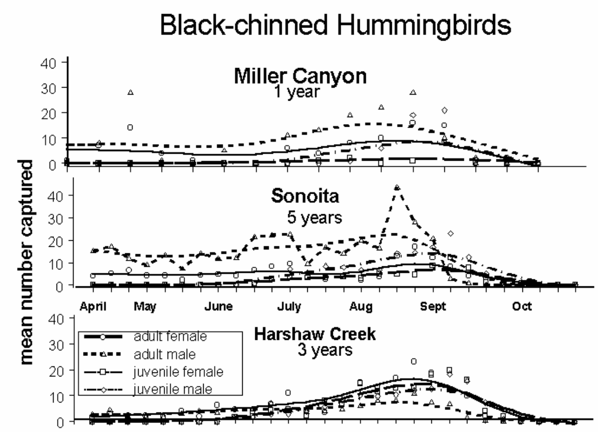

Figure 3— The smoothed seasonal distribution of Black-chinned Hummingbird (Archilochus alexandri) captured at each study site. Values are averaged across years with five years of data from Sonoita, three years of data from Harshaw Creek, and one year of data from Miller Canyon. The unsmoothed line on the Sonoita graph indicates, on average, a significant increase in adult males occurs in the third week of August. The data from Miller Canyon shows a similar pattern.

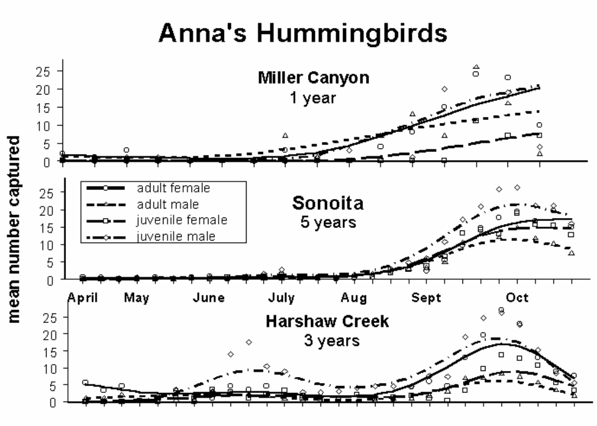

Figure 4— The smoothed seasonal distribution of Anna's Hummingbirds (*Calypte anna*) captured at each study site. Values are averaged across years with five years of data from Sonoita, three years of data from Harshaw Creek, and one year of data from Miller Canyon.

The abundance of juvenile females differed significantly between Miller Canyon and Sonoita (Z = -2.3, P < 0.02) and between Miller Canyon and Harshaw Creek (Z = -2.3, P < 0.03). At Miller Canyon, juvenile females were not captured until the middle of September. At both Sonoita and Harshaw Creek, juvenile females occurred in small numbers from May through August.

Rufous Hummingbird

Rufous Hummingbird, which does not breed in the Southwest, was most numerous during fall migration

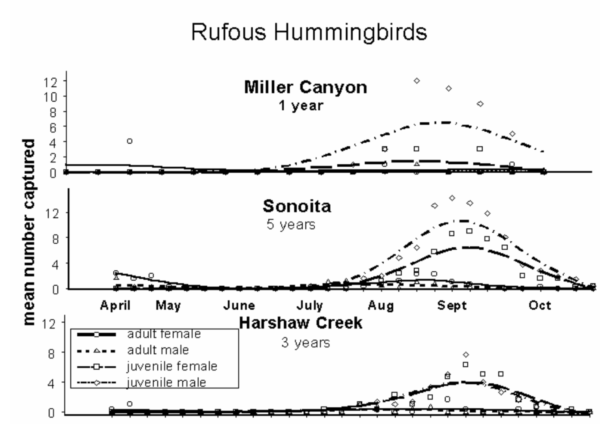

Figure 5— The smoothed seasonal distribution of Rufous Hummingbird (*Selasphorus rufus*) captured at each study site. Values are averaged across years with five years of data from Sonoita, three years of data from Harshaw Creek, and one year of data from Miller Canyon.

(*fig. 5*). Approximately 90 percent of the migrating Rufous was juveniles. Because adults occur in low numbers during spring and fall, we compared only the juveniles' abundance. No significant differences occurred between site comparisons for either sex class (*Z* < 0.88, *P* > 0.38 for males, three pair-wise comparisons, *Z* < 0.8, *P* > 0.13 for females, three pair-wise comparisons).

Discussion

A massive southbound migration of hummingbirds has been documented at two study sites in southeastern Arizona (Wethington and Russell 2003) and now, confirmed at a third site. Migration begins in July and lasts through October. Black-chinned Hummingbird migration peaks earliest followed by Rufous Hummingbird (predominantly juveniles), and then Anna's Hummingbird. Factors affecting the timing of migration probably vary for each species. These factors are unknown but likely include geographical locations of breeding sites and conditions affecting food resources along the migration routes (Russell et al. 1993).

The lack of migrating adult Rufous Hummingbirds at these mid-elevation sites is puzzling. The difference in timing of migration for different age groups could cause such a pattern. With the later migration times of juveniles, it is possible that southeastern Arizona provides more food resources than the expected adult route through the Rocky Mountains. Another possible factor is elevation. Rufous Hummingbirds have been documented migrating through sites at much higher elevations than our study sites (Kodric-Brown and Brown 1978, Calder 1993). If adult Rufous migrate through Arizona at higher elevations, our study would miss this migration. Alternatively, juveniles may be forced to use suboptimal habitats because they are less successful at maintaining territories along their migration routes than adults (Gass 1978). Whether our study sites represent sub-optimal habitats for migrating Rufous or a better food source at the later migration time of juveniles is unknown.

Black-chinned Hummingbird migration patterns at our study sites are confounded because the influx of southbound migrants begins when individuals in the breeding populations are still at our sites. Consequently, the pattern of adult males arriving first at a site, then adult females and juveniles, is not easily detected. We determined the date when we captured the median bird in each age-sex group as an alternative to first occurrence (*table 1*). In five of the nine years, the median adult male occurred at the same time as the median of another age-sex group and in the remaining four years, the median adult male occurred earlier. Southern Arizona is at the southern end of the breeding range for Black-chinned and their range is large. Migrants are joining the southward movement over a large geographic area, at different times because of the differences in breeding seasons at different latitudes. We think the pattern exists, but it is not always detected here.

Another confounding factor in Black-chinned migration patterns is the consistent differences in sex ratios among the sites. The sex ratios varied significantly between Harshaw Creek and Sonoita but remained consistent at each site throughout the breeding season and migration. The causes of the sex ratio difference are unknown. One hypothesis suggests the quality of habitat for breeding could be reflected in sex ratios but this does not suggest a reason for the pattern to continue through migration.

The migration route of Anna's Hummingbirds is fundamentally different from the previous two species. Anna's follow an east-west migration route instead of the more typical north-south route (Russell 1996). Of the species discussed here, it is likely that the number of migrating individuals in each age-sex class peaks at about the same time (*fig. 3, table 1*).

The identification of factors that improve hummingbird survivorship along their migration routes is critical for effective conservation of hummingbirds. The extended length of time in which migration occurs in southeastern Arizona suggests that hummingbirds here do not migrate in synchrony with peak flowering of any particular plant species. This lack of synchrony has been documented for Ruby-throated Hummingbird migration (Bertin 1982). Consequently, an area that provides a continuous supply of nectar throughout the migration period is likely an important area for improving survivorship along the migration route.

Southeastern Arizona, the Sky Island region in the state, supports a large diversity of vegetation types that occur in the isolated mountain ranges and in the desert valleys. Consequently, migrating hummingbirds have a choice of habitats in which to stopover. Our mid-elevation sites document the importance of these habitats to migrating hummingbirds but the importance of other elevations is virtually unknown here. Earlier, we hypothesized that elevation could be important for determining migration routes for adult Rufous Hummingbirds. If so, it becomes important for hummingbird conservation to identify these routes. It is also unknown if hummingbirds use any physiographic features such as corridors within elevational ranges or river drainages to guide their migration. Some evidence suggests that hummingbird migration does not occur at all locations in southeastern Arizona but that some river drainages could be important routes (Wethington and Russell 2002).

Southeastern Arizona supports the greatest diversity (Johnsgaard 1997) and likely the highest density of migrating hummingbirds in the United States and Canada. Here, the isolated mountain ranges provide a natural experimental arena for testing effects of elevation and vegetation type on hummingbird migration. In addition, the methodologies of our studies provide a framework on which to build a protocol that would monitor hummingbird migration, productivity, and survivorship. This is an area of concern. While the productivity and survivorship of other landbirds have nationwide attention, the methodology used by programs such as MAPS does not include hummingbirds. Their mist nets rarely catch hummingbirds and when caught, few bird banders have the permission or the ability to band them. We use the same methodology for studying hummingbird migration as we do for studying their productivity and survivorship. Without a separate methodology, specifically focused on hummingbirds, the productivity and survivorship of species in the avian family, *Trochilidae*, remain unstudied in the United States. We are encouraging hummingbird banders to adopt a standardized protocol that would allow us to gather the information needed to identify factors important for hummingbird conservation.

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Literature Cited

Baltosser, W. H. 1987. **Age, species, and sex determination of four North American hummingbirds.** North American Bird Bander 12: 151-166.

Baltosser, W. H., and S. M. Russell. 2000. **Black-chinned Hummingbird (*Archilochus alexandri*).** In: A. Poole and F. Gill, editors. The Birds of North America, No. 495. Philadelphia, PA: The Birds of North America, Inc.

Baltosser, W. H., and P. E. Scott. 1996. **Costa's Hummingbird (*Calypte costae*).** In: A. Poole, and F. Gill, editors. The Birds of North America, No. 251. Philadelphia, PA: The Birds of North America, Inc.

Bertin, R. I. 1982. **The Ruby-throated Hummingbird and its major food plants: ranges, flowering phenology, and migration.** Canadian Journal of Zoology 60: 210-219.

Bock, C. E., and J. H. Bock. 1988. **Grassland birds in southeastern Arizona: Impacts of fire, grazing, and alien vegetation.** In: P. Gorivp, editor. Ecology and Conservation of Grassland Birds. Cambridge, England: International Council for Bird Preservation; 43-58.

Bock, J. H., and C. E. Bock. 1986. **Habitat relationships of some native perennial grasses in southeastern Arizona.** Desert Plants 8: 3-14.

Calder, W. A. 1987. **Southbound through Colorado: Migration of Rufous Hummingbirds.** National Geographic Research 3: 40-51.

Calder, W. A. 1993**. Rufous Hummingbird (*Selasphorus rufus*).** In: A. Poole and F. Gill, editors. The Birds of North America, No. 53. Philadelphia, PA The Birds of North America, Inc.

Calder, W. A. and L. L. Calder. 1994. **Calliope Hummingbird (*Stellula calliope*).** In: A. Poole and F. Gill, editors. The Birds of North America, No. 135. Philadelphia, PA: The Birds of North America, Inc.

Friedman, J. H. 1984. **A variable span smoother.** Tech. Rep. No. 5. Palo Alto, CA: Department of Statistics, Stanford University.

Gass, C. L. 1978. **Territory regulation, tenure, and migration in Rufous Hummingbirds.** Canadian Journal of Zoology 57: 914-923.

Johnsgard, P. A. 1997. **The Hummingbirds of North America.** Washington, DC: Smithsonian Institution Press.

Kodric-Brown, A., and J. H. Brown. 1978. **Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds.** Ecology 59: 285–296.

Mathsoft, Inc. 1999. **AXUM 6.0 user's guide.** Seattle, WA: Data Analysis Products Division, Mathsoft, Inc.

Mulvihill, R. S., and R. C. Leberman. 1987. **Bird banding at Powdermill, 1985—with a summary of Ruby-throated Hummingbrid banding data.** Powdermill Nature Reserve research report. No. 46. Pittsburgh, PA: Carnegie Museum of Natural History.

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: 25-32.

Russell, R. W., F. L. Carpenter, M. A. Hixon, and D. C. Paton. 1993. **The impact of variation in stopover habitat quality on migrant Rufous Hummingbirds.** Conservation Biology 8: 483-490.

Russell, S. M. 1996. **Anna's Hummingbird (*Calypte anna*).** In: A. Poole and F. Gill, editors. The Birds of North America. Philadelphia, PA: The Birds of North America, Inc.

Russell, S. M., and R. O. Russell. 2001. **The North American Bander's Manual for Hummingbirds.** Point Reyes Station, CA: North American Banding Council. Available online at http://nabanding.net/nabanding/pubs.html.

Schuchmann, K. S. 1999. **Order Apodiformes. Family Trochilidae (Hummingbirds).** In: J. D. Hoyo., A. Elliott, and J. Sargatal, editors. Handbook of the Birds of the World: Volume 5. Barn-owls to Hummingbirds. Barcelona, Spain: Linx Edicions; 468 535.

Stiles, F. G. 1972. **Age and sex determination in Rufous and Allen's hummingbirds.** Condor 74: 25-32.

Wethington, S. M., and S. M. Russell. 2002. **A snapshot of hummingbird migration in southeastern Arizona.** North American Bird Bander 26: 157-160.

Wethington, S. M., and S. M. Russell. 2003. **The seasonal distribution and abundance of hummingbirds in oak woodland and riparian communities in southeastern Arizona.** Condor 105(3): 484-495.