



Wintering hummingbirds in Alabama and Florida: species diversity, sex and age ratios, and site fidelity

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ABSTRACT. Over the past several decades, there have been numerous reports of hummingbirds wintering in the southeastern United States. However, little is known about the species present and their relative abundance. From November 1998 to March 2008, we examined the species diversity, sex and age ratios, and site fidelity of hummingbirds wintering in southern Alabama and northern Florida. We captured and banded 1598 individuals representing 10 species, and the most frequently captured species were Rufous Hummingbirds (*Selasphorus rufus*; 51.6%), Ruby-throated Hummingbirds (*Archilochus colubris*; 23.5%), and Black-chinned Hummingbirds (*Archilochus alexandri*; 16.9%). Other species captured included Buff-bellied Hummingbirds (*Amazilia yucatanensis*), Calliope Hummingbirds (*Stellula calliope*), Allen's Hummingbirds (*Selasphorus sasin*), Broad-tailed Hummingbirds (*Selasphorus platycercus*), Broad-billed Hummingbirds (*Cynanthus latirostris*), Anna's Hummingbirds (*Calypte anna*), and Costa's Hummingbirds (*Calypte costae*). Most hummingbirds (71.8%) were captured in December and January. For most species, sex ratios were male-biased for juveniles and female-biased for adults, indicating possible differential mortality. Of 1598 hummingbirds captured, 144 representing five species returned to the same wintering location at least once. Female Rufous Hummingbirds (20.4% of individuals captured) exhibited the greatest site fidelity. Recaptures of banded Rufous Hummingbirds in autumn and early winter revealed that some individuals moved south into Alabama or Florida from Tennessee, northern Georgia, and northern Louisiana. Same-season recaptures of banded Rufous Hummingbirds suggest that their spring migration route is west along the Gulf Coast. Our results suggest that Alabama and Florida are viable overwintering areas for several species of hummingbirds, with numbers of species and individuals higher than previously recognized. However, more study is needed to confirm migration routes and to determine if Ruby-throated Hummingbirds wintering in our study area are year-round residents or migrants.

SINOPSIS. Estadía invernal de Colibríes en Alabama y Florida: Diversidad de especies, sexo y rangos de edad, y fidelidad de lugares

A lo largo de las últimas décadas, han ocurrido numerosos reportes de Colibríes pasando el invierno en el sureste de los Estados Unidos. Sin embargo, poco se conoce sobre la presencia de las especies y su abundancia relativa. Desde Noviembre 1998 hasta Marzo 2008, nosotros examinamos la diversidad especies, el sexo y los rangos de edades y la fidelidad de lugares de Colibríes pasando el invierno en el sur de Alabama y el norte de la Florida. Nosotros capturamos y anillamos 1598 individuos pertenecientes a 10 especies, las especies capturadas con mayor frecuencia fueron *Selasphorus rufus* (51.6%), *Archilochus colubris* (23.5%) y *Archilochus alexandri* (16.9%). Entre las otras especies capturadas se incluyeron a *Amazilia yucatanensis*, *Stellula calliope*, *Selasphorus sasin*, *Selasphorus platycercus*, *Cynanthus latirostris*, *Calypte anna*, *Calypte costae*. La mayoría de los colibríes (71.8%) fueron anillados en Diciembre y Enero. Para la mayoría de las especies, los radios de los sexos estuvieron sesgados hacia los machos para los juveniles y hacia las hembras en individuos adultos, lo cual posiblemente indica una mortalidad diferencial. De los 1598 Colibríes capturados, 144 representaron cinco especies que retornaron por lo menos una vez a la misma localización invernal. Las hembras de *Selasphorus rufus* (20.4% de los individuos capturados) exhibieron la mas alta fidelidad espacial. Recapturas de individuos anillados de *Selasphorus rufus* en el otoño y temprano en el invierno revelaron que algunos individuos se movieron hacia el sur a Alabama o la Florida desde Tennessee, norte de Georgia y el norte de Louisiana. Recapturas durante una misma temporada de *Selasphorus rufus* sugieren que las rutas de migración durante la primavera se ubican al oeste d la costa del golfo. Nuestros resultados sugieren que Alabama y la Florida son áreas viables para pasar el invierno para varias especies de colibríes, con un número mayor de especies e individuos que los reportados previamente. Sin embargo, mas estudios son requeridos para confirmar las rutas de migración y para determinar si *Archilochus colubris* que pasa el invierno en nuestra área de estudio es un residente permanente durante todo el año o migra.

Key words: *Archilochus*, hummingbirds, migration, overwintering, *Selasphorus*, sex ratios, site fidelity

The first record of a hummingbird wintering in the southeastern United States dates from a

specimen of a Rufous Hummingbird (*Selasphorus rufus*) taken in Charleston, South Carolina, on 18 December 1909 (Conway and Drennan 1979). Until the 1970s, most overwintering

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hummingbirds in the southeast were assumed to be Ruby-throated Hummingbirds (*Archilochus colubris*) that failed to migrate after the breeding season. However, in the late 1970s, Newfield (1983, 1984) examined the diversity of wintering hummingbirds in Louisiana and documented the presence of Rufous Hummingbirds, Allen's Hummingbirds (*Selasphorus sasin*), and Calliope Hummingbirds (*Stellula calliope*). In the 1980s and 1990s, Black-chinned Hummingbirds (*Archilochus alexandri*), Buff-bellied Hummingbirds (*Amazilia yucatanensis*), Broad-tailed Hummingbirds (*Selasphorus platycercus*), and Rufous, Allen's, and Calliope hummingbirds were captured and banded in several other southeastern states (Foy 1990, 1995, Sargent 1990, Sargent and Sargent 1993a, 1993b, 1995, 1996). Hill et al. (1998) reported an expansion of the winter distribution of Rufous Hummingbirds in Florida, Georgia, Alabama, Mississippi, and Tennessee from 1988 to 1995.

With one exception (Newfield 1992), no long-term studies of wintering hummingbirds in the southeastern United States have been published, and few data are available concerning the species present, their abundance, or their sex and age ratios. In addition, philopatry by hummingbirds to nonbreeding sites has been little studied (Robinson et al. 1996, Healy and Calder 2006), and the migration routes of hummingbirds from breeding areas in the western United States to the southeast are largely unknown.

Over a 10-yr period, we studied hummingbirds wintering in southern Alabama and northern Florida. Our objectives were to document species diversity and abundance, determine age and sex ratios, and examine site fidelity and migration routes.

METHODS

From 1998 to 2008, we located wintering hummingbirds by developing a network of volunteers who maintained sugar-water feeders at their homes throughout the fall and winter. News releases, flyers, posters, presentations to garden and birding clubs, and interviews with local media were some of the methods used to generate the publicity necessary to establish and maintain this network. We stayed in contact with participants through periodic reports sent by email. Volunteers notified us by phone or

email when they observed a hummingbird at their home. No attempt was made to standardize response or trapping times, but we attempted to band all reported hummingbirds as quickly as possible.

Our study area covered southern Alabama and the panhandle and northern peninsula of Florida (Fig 1). During our study, we banded hummingbirds at 258 homes in Alabama and 253 homes in Florida. Because we visited homes only when a hummingbird was present, the number of homes visited varied among years (Table 1). Some homes were visited once during the 10-yr period, whereas others were visited several times during a single season when multiple hummingbirds were reported.

We captured hummingbirds using round traps made of galvanized cage wire. The traps were 51 cm high and 51 cm in diameter, and stood on 36-cm-high legs. We hung a sugar-water feeder that was already being used by the bird inside the cage, and the 25 cm × 25 cm vertical sliding door was held open with a monofilament line. Either one or two traps were used, depending on the number of feeders present. Any additional feeders were taken down during trapping.

After capture and banding, each hummingbird was aged and sexed based on plumage (Stiles 1972, Baltosser 1987, Pyle 1997) and bill corrugations (Ortiz-Crespo 1972). We weighed each bird using a digital scale (± 0.1 g), recorded fat deposits and molt sequence, and measured the wing chord, tail, and culmen. In most cases, two rectrices were removed and retained for identification purposes and future DNA research.

Ruby-throated Hummingbirds, the only hummingbird species known to breed in eastern North America, are common Neotropical migrants in our study area until 15 November and after 1 March. Therefore, they were counted as overwintering birds only when captured between 15 November and 1 March. Other species were documented and banded whenever encountered.

RESULTS

We banded 10 species of hummingbirds ($N = 1598$ individuals) from November 1998 to March 2008, including 824 Rufous Hummingbirds (51.6%), 375 Ruby-throated



Fig. 1. Map of the southeastern United States showing main banding and recapture locations.

Hummingbirds (23.5%), 270 Black-chinned Hummingbirds (16.9%), 49 Buff-bellied Hummingbirds (3.1%), 36 Calliope Hummingbirds (2.2%), and 22 Allen's Hummingbirds (1.4%). The other four species comprised less than 1% each of the total, including 12 Broad-tailed Hummingbirds, 6 Broad-billed Hummingbirds (*Cynanthus latirostris*), 3 Anna's Hummingbirds (*Calypte anna*), and 1 Costa's Hummingbird (*Calypte costae*). On average, we banded seven species per season (Table 1).

Table 1. The number of homes visited and the number of hummingbirds and species banded in Alabama and Florida from 1998 to 2008.

Winter	Homes	Birds banded	Number of species
1998/1999	30	44	5
1999/2000	30	45	7
2000/2001	114	185	7
2001/2002	98	154	8
2002/2003	145	253	7
2003/2004	101	175	8
2004/2005	121	216	7
2005/2006	92	174	8
2006/2007	113	197	7
2007/2008	104	155	9
Total	511	1598	10

Most hummingbirds (71.8%) were captured and banded in December and January (Table 2). The earliest and latest banding dates for the five most common species of western hummingbirds were 2 August and 29 March for Rufous Hummingbirds, 31 October and 4 April for Black-chinned Hummingbirds, 25 August and 2 March for Buff-bellied Hummingbirds, 31 October and 28 February for Calliope Hummingbirds, and 14 August and 6 March for Allen's Hummingbirds.

The mean mass of captured hummingbirds ranged from 5.0 g for male Buff-bellied Hummingbirds to 2.8 g for both male and female Calliope Hummingbirds (Table 3). Fewer than 2% of the hummingbirds had any fat deposits.

The mean number of birds banded per year varied among age and sex classes for Rufous, Ruby-throated, Black-chinned, Buff-bellied, Calliope, and Allen's hummingbirds (Table 4). Age ratios were juvenile-biased for Rufous Hummingbirds (1.2 juveniles:1 adult), Ruby-throated Hummingbirds (3.5:1), and Black-chinned Hummingbirds (2.2:1), but adult-biased for Buff-bellied Hummingbirds (2 adults:1 juvenile). Adult sex ratios were female-biased for Rufous Hummingbirds (8.6 females:1 male), Ruby-throated Hummingbirds (2.2:1), and Black-chinned Hummingbirds (3.5:1), but

Table 2. The mean number (± 1 SD) of Rufous (RUHU), Ruby-throated (RTHU), Black-chinned (BCHU), and Buff-bellied (BUFH) hummingbirds banded during each month in Alabama and Florida from 1998 to 2008.

Month	RUHU	RTHU	BCHU	BUFH
August	0.6 \pm 1.0	0	0	0.1 \pm 0.3
September	0.5 \pm 0.9	0	0	0
October	1.5 \pm 2.0	0	0.2 \pm 0.4	0.2 \pm 0.4
November	7.4 \pm 4.6	4.6 \pm 3.3	2.7 \pm 2.0	0.4 \pm 0.7
December	26.7 \pm 16.7	9.9 \pm 7.1	9.6 \pm 6.8	2.3 \pm 2.0
January	31.7 \pm 16.3	16.1 \pm 12.0	10.5 \pm 7.1	1 \pm 1.1
February	11.0 \pm 4.6	3.9 \pm 3.5	2.8 \pm 3.3	0.7 \pm 0.8
March	2.9 \pm 3.4	0	0.8 \pm 0.9	0.2 \pm 0.4

male-biased for Buff-bellied Hummingbirds (2.7 males:1 female). Sex ratios for juveniles were male-biased for Rufous Hummingbirds (1.4:1), Ruby-throated Hummingbirds (2.4:1), and Black-chinned Hummingbirds (4.1:1). We captured equal number of juvenile Buff-bellied Hummingbirds (Table 4).

Site fidelity. A total of 144 hummingbirds of five species returned at least once to the same 10-min block of latitude and longitude in a different season (the U.S. Bird Banding Laboratory's definition of a banding return). In our study area, a 10-min block is approximately 16 km \times 18.5 km. Birds banded during 2007–2008 were not included in this analysis.

Among species, return rates ranged from 3.3% (8 of 246 banded individuals; 3.0% for males and 3.5% for females) for Black-chinned Hummingbirds to 17.1% (7 of 41) for Buff-bellied Hummingbirds. Return rates were 14.4% for Rufous Hummingbirds (109 of 757; 8.4% for males and 20.4% for females), 5.2% for Ruby-throated Hummingbirds (17 of 327;

3.6% for males and 7.4% for females), and 8.6% for Calliope Hummingbirds (3 of 35).

Thirty-seven individuals of four species, Rufous Hummingbird ($N = 26$), Ruby-throated Hummingbird ($N = 3$), Black-chinned Hummingbird ($N = 7$), and Buff-bellied Hummingbird ($N = 1$), returned to the same home during three or more winters. One exceptional male Rufous Hummingbird was banded on 16 November 2001 in Pensacola, Florida, and was subsequently recaptured during six consecutive winters at the same location. This male also demonstrated fidelity to a migration stopover site, being recaptured in Thibodaux, Louisiana (346 km west of its wintering site) on 14 March 2005 and again on 2 February 2006 (N. Newfield, pers. comm.).

One Allen's Hummingbird was captured during three successive winters at three different locations. This bird was banded in Montgomery, Alabama, on 7 November 1999, and returned the next winter to a site in Montgomery located 4 km from the first location. This same

Table 3. Body mass of six species of hummingbirds wintering in Alabama and Florida from 1998 to 2008. Data shown as means ± 1 SD (range).

Species ^a	Males		Females	
	N	Mass (g)	N	Mass (g)
RUHU	302	3.5 \pm 0.3 (2.8–5.0)	522	3.5 \pm 0.3 (2.9–5.2)
RTHU	214	3.2 \pm 0.3 (2.5–4.4)	161	3.4 \pm 0.4 (2.7–5.2)
BCHU	144	3.4 \pm 0.3 (2.7–4.3)	126	3.5 \pm 0.3 (2.8–4.7)
BUFH	32	5.0 \pm 0.4 (4.3–5.8)	17	4.6 \pm 0.3 (4.2–5.0)
CAHU	22	2.8 \pm 0.2 (2.5–3.1)	14	2.8 \pm 0.3 (2.5–3.3)
ALHU	15	3.6 \pm 0.3 (3.0–4.0)	7	3.3 \pm 0.2 (2.9–3.5)

^aRUHU = Rufous Hummingbird; RTHU = Ruby-throated Hummingbird; BCHU = Black-chinned Hummingbird; BUFH = Buff-bellied Hummingbird; CAHU = Calliope Hummingbird; and ALHU = Allen's Hummingbird.

Table 4. Mean number (± 1 SD) of individuals of six species of hummingbirds captured per year by age and sex class in Alabama and Florida, 1998–2008.

Species ^a	Adult males	Adult females	Juvenile males	Juvenile females
RUHU	3.9 \pm 3.3	33.5 \pm 13.7	26.3 \pm 17.6	18.7 \pm 12.2
RTHU	4.1 \pm 2.6	8.9 \pm 5.4	17.3 \pm 10.6	7.2 \pm 8.3
BCHU	2.6 \pm 1.6	9.7 \pm 6.8	11.8 \pm 7.9	2.9 \pm 2.6
BUFH	2.4 \pm 1.4	0.9 \pm 0.5	0.8 \pm 1.0	0.8 \pm 0.9
CAHU	0.2 \pm 0.4	1.0 \pm 1.6	2.0 \pm 1.5	0.4 \pm 0.7
ALHU	0.3 \pm 0.5	0.6 \pm 0.8	1.2 \pm 0.6	0.1 \pm 0.3

^aRUHU = Rufous Hummingbird; RTHU = Ruby-throated Hummingbird; BCHU = Black-chinned Hummingbird; BUHF = Buff-bellied Hummingbird; CAHU = Calliope Hummingbird; and ALHU = Allen's Hummingbird.

hummingbird was recaptured the next winter in Pensacola, Florida, 231 km south of Montgomery. No Broad-tailed, Broad-billed, Anna's, or Costa's hummingbirds were recaptured in subsequent winters.

Movements and migration. During our study, 51 banded hummingbirds representing six species were either recaptured or recovered. We captured 23 hummingbirds originally banded in Texas, Georgia, Tennessee, Louisiana, North Carolina, or northern Alabama. In addition, 22 hummingbirds we banded were either recaptured or recovered in northern Alabama, Virginia, Mississippi, Louisiana, or Tennessee. Six hummingbirds we banded were recaptured at a different location in our study area.

For Rufous Hummingbirds ($N = 37$), distances between banding and recapture locations ranged from 53 to 1437 km and the elapsed time from 1 to 40 mo. For Ruby-throated Hummingbirds ($N = 5$), distances ranged from 20 to 384 km and the elapsed time from 1 to 12 mo. For Black-chinned Hummingbirds ($N = 6$), distances ranged from 96 to 279 km and the elapsed time from 2 weeks to 15 mo. For three species, Calliope, Buff-bellied, and Allen's hummingbirds, just one banded individual was

recaptured and distances (and elapsed times) between locations were 231 km (11 mo), 902 km (8 mo), and 231 km (25 mo), respectively.

Fifteen hummingbirds were recaptured during the same season in the southeastern United States (Table 5). Some multiple recaptures linked migration and wintering sites. A male Rufous Hummingbird banded in Niceville, Florida, on 8 December 1998 was recaptured 615 km to the northwest in Memphis, Tennessee (C. Sloan, pers. comm.), on 21 October 1999. This bird then returned to the site where it was originally banded in Niceville, Florida, and was recaptured on 20 December 1999. We banded a female Rufous Hummingbird in Montrose, Alabama, on 16 January 2002, that was recaptured in Shreveport, Louisiana (P. Dickson, pers. comm.), on 3 December 2002, 596 km to the northwest. We recaptured this bird again on 27 January 2003 in Fairhope, Alabama, 8 km from the original banding location.

DISCUSSION

Rufous Hummingbirds. These hummingbirds breed from Washington, Oregon, Idaho, and western Montana, north to Alaska,

Table 5. Movements of hummingbirds ($N = 15$) recaptured during the same migration period in the southeastern United States.

Species	Season	Direction	Number of birds
Rufous Hummingbird	Fall	East	1
Rufous Hummingbird	Fall/Winter	Southeast	2
Rufous Hummingbird	Fall/Winter	South	3
Rufous Hummingbird	Spring	West	5
Ruby-throated Hummingbird	Winter	North	2
Black-chinned Hummingbird	Spring	West	1
Buff-bellied Hummingbird	Fall	East	1

with most individuals wintering in Mexico (Healy and Calder 2006). There were only sporadic records of Rufous Hummingbirds in the southeastern United States before 1970, but increasing numbers were reported during the 1970s (Conway and Drennan 1979). Hill et al. (1998) documented an increase in the number of overwintering Rufous Hummingbirds in the southeastern United States through the 1980s and 1990s. Rufous Hummingbirds were the most abundant species of hummingbird in our study area.

Recaptures of banded wintering Rufous Hummingbirds in Mexico suggested winter site fidelity and seasonal residence, rather than continual wandering throughout the winter range (Healy and Calder 2006). In our study, Rufous Hummingbirds exhibited the greatest site fidelity, with a return rate of 20.4% for females and 8.4% for males. On their breeding grounds in British Columbia, site fidelity rates were 18.2% for females and 6.6% for males (Finlay 2007).

Hill et al. (1998) suggested that the Gulf Coast served as a migration corridor for Rufous Hummingbirds moving from western breeding areas to wintering areas in the southeastern United States. However, we did not find this to be the case. Our recapture data suggest that Rufous Hummingbirds move south or southeast in the fall and early winter from Tennessee, northern Georgia, or northwestern Louisiana into Alabama or Florida. For example, we recaptured a Rufous Hummingbird originally banded in Atlanta, Georgia, on 15 October 2000 (F. Moore, pers. comm.) in Alligator Point, Florida (430 km south of Atlanta) on 7 January 2001.

Hill et al. (1998) also reported that the spring migration routes of Rufous Hummingbirds were unknown. Our recapture data suggest that Rufous Hummingbirds wintering in Florida and Alabama move west along the Gulf Coast during spring migration. For example, a female banded in Mobile, Alabama, on 27 January 2008 was recaptured less than a month later on 21 February 2008 (L. Beall, pers. comm.) in Covington, Louisiana, about 199 km west of the original banding location. In addition, a male Rufous Hummingbird banded in Fairhope, Alabama, near Mobile Bay, on 2 December 2006 was recaptured 313 km to the west on 5 March 2007 in Baton Rouge, Louisiana (N. Newfield, pers. comm.).

When migrating from their breeding grounds to wintering locations in Mexico, most Rufous Hummingbirds follow an elliptical southeast–west–northward annual routing (Calder and Jones 1989, Healy and Calder 2006). Our results suggest that Rufous Hummingbirds may also follow an elliptical migration to and from wintering areas in the southern United States.

Ruby-throated Hummingbirds. Although Ruby-throated Hummingbirds were the second most common wintering species of hummingbird in our study and other investigators have reported these hummingbirds wintering from Alabama and Florida to coastal North Carolina (Robinson et al. 1996, R. Sargent, pers. comm.), most winter from Mexico to northern Panama (Robinson et al. 1996). Little is known about winter site fidelity of Ruby-throated Hummingbirds. Of eight wintering birds banded in Palo Verde, Costa Rica, Robinson et al. (1996) reported a 25% return rate. Of six wintering birds banded in Valle Central, Costa Rica, none returned (Robinson et al. 1996). During our study, the overall return rate was 5.2%. However, Ruby-throated Hummingbirds may not always defend feeding areas. At least some individuals appear to trapline and follow a foraging route from yard to yard, making it more difficult to recapture birds because they may only visit a yard for brief periods during a day (R. Sargent, pers. observ.).

We had no evidence of wintering Ruby-throated Hummingbirds remaining in our study area during the breeding season. Similarly, no Ruby-throated Hummingbirds banded during the breeding season in Alabama or Florida have been recaptured in our study area during the winter. However, additional study is needed to determine if wintering Ruby-throated Hummingbirds in our study area are migrants or year-round residents.

Black-chinned Hummingbirds. This species breeds throughout the western United States and most winter in Mexico. However, Black-chinned Hummingbirds occur regularly along the U.S. Gulf Coast during the winter (Baltosser and Russell 2000). In southern Louisiana, 184 Black-chinned Hummingbirds were banded from 1979 to 1999 (Baltosser and Russell 2000). During the early years of the study, five Black-chinned Hummingbirds were banded for every Ruby-throated Hummingbird, but the ratio changed over the years and, during

the winter of 1998–1999, nearly equal numbers of the two species were banded. During our study, with the exception of 1 yr (2004–2005), when we banded 69 Black-chinned Hummingbirds, we banded more Ruby-throated Hummingbirds than Black-chinned Hummingbirds.

Site fidelity by Black-chinned Hummingbirds seems to be low and they appear to trapline (pers. obs.), a behavior that may reduce trapping success. Arizmendi and Ornelas (1990) reported that wintering Black-chinned Hummingbirds in Jalisco, Mexico, were trapliners, feeding in a somewhat predictable pattern from flower patches that were not defended by resident hummingbirds.

Buff-bellied Hummingbirds. This species breeds in eastern Mexico and southern Texas, and is the only North American species of hummingbird known to migrate north and east into the Gulf Coast states after breeding (Chavez-Ramirez and Moreno-Valdez 1999). One immature male, banded in Victoria, Texas, on 12 May 2007 (B. Ortego, pers. comm.) was recaptured 902 km to the east in Fairhope, Alabama, on 4 January 2008. No published information is available on winter site fidelity in this species. Although our sample size was small ($N = 49$), Buff-bellied Hummingbirds seem to exhibit a strong fidelity to winter territories, actively defending territories and chasing smaller species of hummingbirds (pers. obs.).

Calliope, Allen's, and Broad-tailed hummingbirds. Relatively few Calliope, Allen's, and Broad-tailed hummingbirds appeared to winter in our study area. Calliope Hummingbirds breed in the mountains from British Columbia south into northern California and Nevada (Calder and Calder 1999). Most Calliope Hummingbirds winter in central Mexico, but they have been reported wintering in Louisiana since 1984 (Newfield 1984).

Allen's Hummingbirds breed along the Pacific Coast of North America, where one subspecies is nonmigratory and a second subspecies winters in central Mexico (Phillips 1975). Broad-tailed Hummingbirds breed primarily in the Rocky Mountains and winter in Mexico (Calder and Calder 1992). We saw no evidence of site fidelity by either Allen's or Broad-tailed hummingbirds. However, three male Calliope Hummingbirds returned to the same wintering site in subsequent years.

Other species. Few Broad-billed, Anna's, and Costa's hummingbirds appeared to winter in our study area. Broad-billed Hummingbirds breed from the southwestern United States to southern Mexico (Powers and Wethington 1999), whereas Anna's Hummingbirds commonly breed from Arizona to California and north to British Columbia (Russell 1996). Costa's Hummingbirds breed in the southwestern United States and northwestern Mexico. These three hummingbird species are generally short- to medium-distance migrants and may not have the capability of flying ≥ 4000 km from the western United States to Alabama or Florida.

Species diversity. During our 10-yr study, 51.6% of the hummingbirds we banded were Rufous Hummingbirds. These hummingbirds are pugnacious, usually dominating other species of hummingbirds of equal or smaller size at feeders and flowers, and it is possible that they chased away other less aggressive species. However, Buff-bellied Hummingbirds also actively defend feeders (pers. obs.) and their numbers in our study area were low (3.1%). The southeast–west–north elliptical migration of Rufous Hummingbirds may orient some individuals toward the southeastern United States. However, Broad-tailed, Allen's, and Calliope hummingbirds have a similar elliptical migration (Calder and Calder 1992, 1999, Mitchell 2000) and few individuals of these three species were encountered in our study area. In addition, Rufous Hummingbirds breed as far north as southeastern Alaska and may be especially cold hardy. However, Calliope and Broad-tailed hummingbirds breed at high elevations in western mountains (Calder and Calder 1992, 1999) and experience summer temperatures similar to those encountered by Rufous Hummingbirds.

Abundance. We banded most hummingbirds (71.8%) during December and January, but we do not know if numbers were actually higher during those 2 mo. By mid-December, the onset of cold weather likely curtails the availability of insects and natural nectar sources. As a result, hummingbirds visit sugar-water feeders more frequently and, therefore, are more frequently observed and captured.

Body mass. The mean body mass of wintering hummingbirds in our study area was higher than those reported for hummingbirds wintering in Mexico and Central America,

perhaps because hummingbirds in our study had access to sugar-water feeders. For example, Healy and Calder (2006) reported the mean weights of 3.27 g for male and 3.35 g for female Rufous Hummingbirds wintering in Jalisco, Mexico. The mean weights of Rufous Hummingbirds in our study were 3.5 g for both males and females.

The mean weights for wintering Ruby-throated Hummingbirds ($N = 36$) in Costa Rica (Robinson et al 1996) were 3.08 g for males and 3.17 for females. In our larger sample size ($N = 375$), the mean body mass was 3.2 g for males and 3.4 g for females. Nine wintering Calliope Hummingbirds (both sexes) captured in the mountains of Jalisco, Mexico, averaged 2.68 g (Calder and Calder 1999). In our study, the mean weights for Calliope Hummingbirds were 2.8 g for both males and females. No weights have been reported in the literature for wintering Buff-bellied, Allen's, or Black-chinned hummingbirds. Fewer than 2% of the hummingbirds in our study had noticeable fat; normally, only migrating hummingbirds have noticeable stores of fat (Johnsgard 1983, Healy and Calder 2006).

Sex ratios. We found male-biased sex ratios for juvenile Ruby-throated, Black-chinned, and Rufous hummingbirds. For adults, sex ratios in our study were female-biased for Ruby-throated, Black-chinned, and Rufous hummingbirds, and male-biased for Buff-bellied Hummingbirds. Changes from male-biased sex ratios for juveniles to female-biased sex ratios for adults of most species of hummingbirds in our study suggest possible differential mortality.

Few comparative data are available concerning sex ratios of hummingbirds. In central California, adult Rufous and Allen's hummingbirds in the spring exhibited identical 2.3:1 female-biased ratios (Howell and Gardali 2003). Mulvihill and Leberman (1992) reported that sex ratios of Ruby-throated Hummingbirds in Pennsylvania were female-biased for juveniles (1.1 females:1 male) in late summer and fall as well as for adults in the spring (1.4:1), summer (3.1:1), and fall (4.1:1). These authors suggested a possible relationship between reversed sexual size dimorphism and reduced male survivorship, with higher male mortality possibly caused by low mid-summer weights and increased metabolic demands during the breeding season. Male Black-chinned and Rufous hummingbirds also exhibit sexual size dimorphism (Baltosser

and Russell 2000, Healy and Calder 2006), but Buff-bellied Hummingbirds do not.

The number of adult females captured in our study may also be artificially high because of the difficulty of separating adult females and juvenile females during late winter. Hummingbirds are aged primarily by corrugations on the bill (Ortiz-Crespo 1972). These striations begin to disappear 5–9 mo after hatching. Plumage differences between adult and juvenile female hummingbirds are not pronounced and, once the corrugations are gone, all females are aged as after-hatching year (adult) birds. In males, however, gorget feathers are the last to molt and provide a reliable method for aging them as second-year (immature) birds even after the striations have disappeared. Thus, some females aged as after-hatching year (adult) birds in late January or February in our study were likely second-year birds without corrugations.

Conclusions. Our results suggest that Alabama and Florida are viable overwintering areas for several species of hummingbirds, with numbers of species and individuals higher than previously recognized. However, more study is needed to confirm migration routes and to determine if Ruby-throated Hummingbirds wintering in our study area are year-round residents or migrants. With the exception of one Buff-bellied Hummingbird and one Rufous Hummingbird banded in Texas and recaptured in Alabama and Florida, respectively, we have not encountered any birds banded in the western United States. In addition, no hummingbirds banded in our study area have been recaptured or recovered in the western states. Thus, the breeding areas of hummingbirds wintering in Alabama and Florida remain unknown.

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