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## Recent Change in the Winter Distribution of Rufous Hummingbirds

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Rufous Hummingbirds (*Selasphorus rufus*) breed in northwestern North America (Idaho and Oregon north to Alaska) and winter primarily in northwestern and central Mexico (Calder 1993). The species was first recorded east of the Mississippi River during winter in Charleston, South Carolina on 18 December 1909 (Conway and Drennan 1979). After this initial detection, records of Rufous Hummingbirds east of the Mississippi River remained sporadic until the 1970s, when steadily increasing numbers were reported in the fall and winter along the Gulf Coast (Conway and Drennan 1979). This increase has continued to the present, and Rufous Hummingbirds are now considered regular along the Gulf Coast in winter from Texas to Florida (Newfield 1992, Calder 1993). Here, we document the rate and extent of increase in Rufous Hummingbirds wintering in the southeastern United States and discuss hypotheses that might explain this recent increase in numbers.

*Documenting the increase.*—Conway and Drennan (1979) summarized sight records of Rufous Hummingbirds east of the Mississippi River through the 1970s. We used their summary to plot the number of Rufous Hummingbirds reported in winter east of the Mississippi River by decade and found a relatively steady increase through the first seven decades of this century (Fig. 1).

Beginning in the fall of 1988, RRS and MBS began studying wintering hummingbirds in Alabama, Georgia, Florida, Mississippi, and Tennessee. They compiled reports of wintering hummingbirds in these states and, when possible, captured and banded the birds. This work has been conducted with relatively constant effort over an eight-year period, during which the number of Rufous Hummingbirds banded and sighted has increased rapidly (Fig. 2). When these recently compiled sight records are compared with sight records compiled by Conway and Drennan (1979), the magnitude of the increase in wintering Rufous Hummingbirds in the Southeast is easy to discern. In the 70 years between 1909 and 1979, 68 Rufous Hummingbirds were sighted east of the Mississippi (Fig. 1). In the six winters from 1990–91 to 1995–96 in just the five-state region covered by the wintering hummingbird study, 1,643 *Selasphorus* hummingbirds were reported (Fig. 2). Between 7

September 1988 and 13 January 1996, 358 Rufous Hummingbirds were banded in the five-state region, including 125 females and 120 males in their first winter after hatching (using terminology of the Bird Banding Laboratory, "HY" before 1 January and "SY" after 1 January), and 86 females and 27 males in at least their second winter after hatching. Based on the banding data, about 95% of *Selasphorus* hummingbirds sighted in the region were Rufous Hummingbirds.

The banding and sight reports compiled by RRS and MBS have documented not only a large and rapidly increasing number of Rufous Hummingbirds wintering in the southeastern United States, but also an interesting distribution of wintering birds. Most treatments of the winter range of the Rufous Hummingbird that consider its presence in the Southeast state that it occurs only on the Gulf Coast (e.g. Peterson 1980, National Geographic Society 1987). At the time these field guides were published, that may well have been the case. Now, however, relatively large numbers (dozens) of Rufous Hummingbirds winter each year in areas such as Huntsville, Alabama and Atlanta, Georgia, which lie on the Appalachian Plateau about 400 km inland from the Gulf Coast.

Rufous Hummingbirds are not evenly distributed throughout their current winter range in the Southeast. Rather, they appear to be clumped in particular neighborhoods, and the clumps include both returning, previously banded birds as well as unbanded hatching-year or second-year birds. The spotty distribution of wintering Rufous Hummingbirds throughout the Southeast suggests the establishment of traditional wintering areas. With the limited information available, however, there is no way to rule out alternative explanations for the clumped distribution of Rufous Hummingbirds, such as clumped distribution of resources or preferred habitats, or the clustering of hummingbird enthusiasts who tend to attract hummingbirds and report them.

The coastal areas of Mississippi, Alabama, and northwestern Florida have concentrations of not only wintering but also of what apparently are transient Rufous Hummingbirds. The first adult male Rufous Hummingbirds are reported in late July and early August each year in these coastal areas, followed by immatures of both sexes and then adult females. Arrival dates are similar to those for Rufous Hum-

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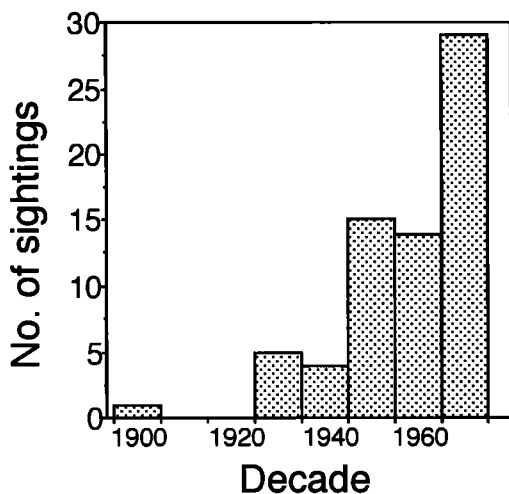


FIG. 1. Temporal distribution of sight records of Rufous Hummingbirds east of the Mississippi grouped by decade. Data are from reports in *American Birds* and *Audubon Field Notes* compiled by Conway and Drennan (1979).

mingbirds migrating through the southern Rocky Mountains en route to Mexico after completion of their breeding season in the Pacific Northwest (Calder 1993). Most sightings in July and August in this coastal area are limited to one or two days. These observations suggest that the Gulf Coast serves not only as a wintering area, but also as a migration corridor for birds moving from their western breeding areas to their eastern wintering areas. No equivalent movement of birds has been detected in late winter and early spring in the Gulf Coast region, and the routes that Rufous Hummingbirds use for their westward journey at the end of the winter are unknown. In contrast to what occurs in the coastal corridor, most Rufous Hummingbirds that become winter residents in the Southeast are first detected in November or December, six weeks or more after Rufous Hummingbirds have departed from the western United States.

*Possible observer bias.*—Although the number of Rufous Hummingbirds reported in the southeastern United States has increased in recent years, so too has observer effort. Especially since the 1970s, the number of people capable of identifying a Rufous Hummingbird has increased substantially. In addition, since 1988 RRS and MBS have run seminars and circulated literature throughout the Southeast in an effort to increase the number of hummingbird feeders that are maintained in winter and to increase the number of sites being monitored for wintering hummingbirds. The result is an increase of unknown magnitude in the number of hummingbird feeders that are maintained in winter and in the probability

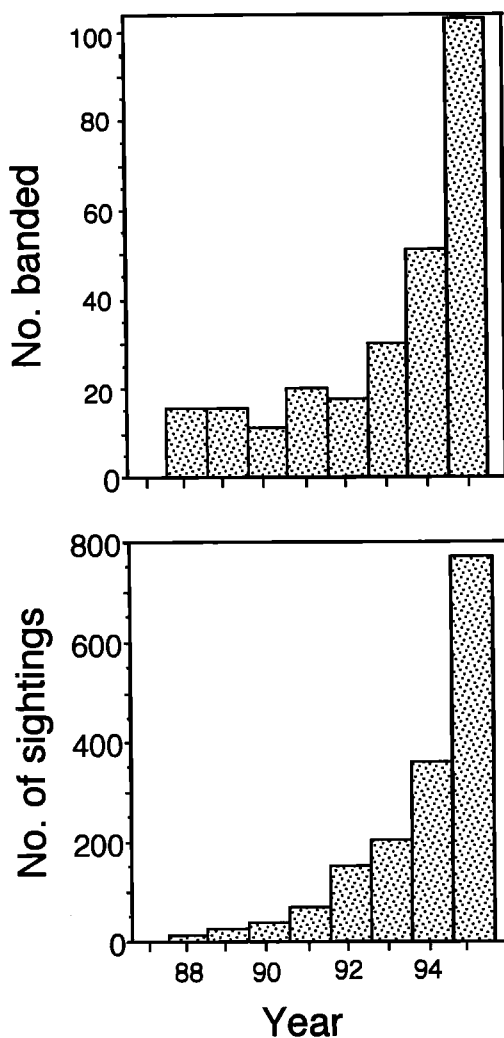


FIG. 2. Temporal distribution of Rufous Hummingbirds banded (upper) and *Selasphorus* hummingbirds sighted (lower) in Alabama, Georgia, Florida, Mississippi, and Tennessee between fall 1988 and spring 1995. Banding records indicate that 95% of *Selasphorus* hummingbirds wintering in the southeastern United States are Rufous Hummingbirds.

that a wintering hummingbird is detected. Therefore, it is possible that the same number of wintering Rufous Hummingbirds has always been present in the Southeast and only the ability to detect them has changed.

We doubt that this explanation accounts for the dramatic increase in Rufous Hummingbirds wintering in the Southeast. First, the increase seems too dramatic to be attributed completely to increases in detection. Many species of birds that breed in west-

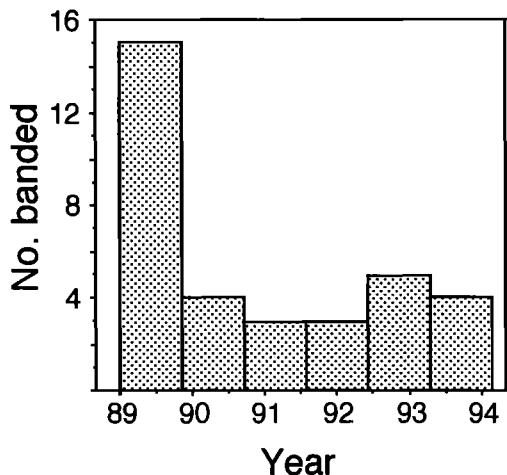


FIG. 3. Temporal distribution of Black-chinned Hummingbirds banded in Alabama, Georgia, Florida, Mississippi, and Tennessee between fall 1988 and spring 1995.

ern North America have been known as vagrants in the Southeast since the early part of this century. Interest in these "rarities" has increased in proportion to the increased interest in birding in the region, just as interest in Rufous Hummingbirds has increased. Nevertheless, no other western species has shown an increase in occurrence comparable to that of the Rufous Hummingbird.

Among the species of birds that occur as winter vagrants in the Southeast, other species of hummingbirds that breed in western North America and historically have wintered south of the United States provide the most relevant comparisons with Rufous Hummingbirds. Over the same five-year period that produced more than 1,500 Rufous Hummingbirds, only two Anna's (*Calypte anna*), four Calliope (*Stellula calliope*), four Buff-bellied (*Amazilia yucatanensis*), and eight Allen's (*Selasphorus sasin*) hummingbirds were banded in the five-state area monitored by RRS and MBS. Increased observer effort did not turn up rapidly increasing numbers of these species. Only 34 of the next most abundant hummingbird wintering in the Southeast, the Black-chinned Hummingbird (*Archilochus alexandri*), were reported between 1988 and 1995, and there was no increase in the number of Black-chinneds reported over this period (Fig. 3). We are aware of no reason why observer bias would have disproportionately affected detections of Rufous Hummingbirds versus these other species.

*Discussion.*—Clearly, many more Rufous Hummingbirds are wintering in the southeastern United States now than a few decades ago, and their numbers seem to be increasing rapidly. These observations beg the question of why Rufous Hummingbirds are expanding their winter distribution. We propose

three hypotheses for the change in behavior that is being observed: cultural transmission, rapid evolution of novel migratory behavior, and independent exploration and settlement.

The change in winter distribution of Rufous Hummingbirds might represent a learned behavioral pattern that is spreading through the population through cultural transmission. This hypothesis requires that in the early part of this century, one or a small number of Rufous Hummingbirds migrated to the southeastern United States instead of western Mexico, returned to their breeding area the next spring, and subsequently were followed back to the Southeast by more hummingbirds, perhaps their offspring, the next fall. Because the suburban gardens of the Southeast provided good food resources, birds moving southeast in the fall tended to survive and return to the breeding area. This process was then repeated with more hummingbirds being recruited into the new wintering area each year.

Several problems exist with this hypothesis. First, most small birds, including the hummingbird species that have been studied, are nocturnal migrants (Berthold 1993). Assuming that Rufous Hummingbirds also are nocturnal migrants, it is unlikely that one Rufous Hummingbird would be able to follow another to a wintering area. Second, juvenile Rufous Hummingbirds initiate fall migration later than adults (Calder 1993), so little opportunity exists for naive birds to follow adults to wintering areas. Thus, there is no helping hand from adults except perhaps the hand that is extended in the genetic legacy to offspring. Third, Rufous Hummingbirds are extremely pugnacious in migration and on the wintering grounds (Calder 1993), making it unlikely that one individual would follow another. Finally, Rufous Hummingbirds rapidly colonized a vast area of the southeastern United States (from eastern Texas to the Carolinas), with isolated birds appearing in many widespread locations every year. If the novel migratory behavior was spreading by a follow-the-leader effect, one would expect the establishment of one or a few initial wintering sites with the population then spreading outward from those points. As mentioned above, however, Rufous Hummingbirds exhibit clumping within their winter range in the Southeast. Thus, even though cultural transmission seems inconsistent with some aspects of the migratory behavior of Rufous Hummingbirds, more data are needed to fully evaluate this hypothesis.

The second hypothesis involves a rapid evolutionary change in innate migratory behavior. As documented for several passerine species (Berthold and Helbig 1992, Berthold 1993), Rufous Hummingbirds may have an innate ability to get to their wintering grounds (i.e. they may have a genetically based tendency to orient in a particular compass direction and travel for a set distance). The distance between breeding areas in the Pacific Northwest and winter-

ing areas in Mexico is about the same as that from the breeding areas to wintering areas in the southeastern United States. Therefore, all that is potentially required for the observed change in migratory behavior is a change in the direction of orientation (Diamond 1982).

A small proportion of virtually every species of migratory bird makes "mistakes" in the timing, distance, or direction of migration, thus providing extralimital or out-of-season rarities (Diamond 1982). Undoubtedly, Rufous Hummingbirds occasionally have wandered into southeastern North America for as long as the species has existed. Until recently, however, the hardwood and pine forests of southeastern North America provided unacceptable habitat for wintering Rufous Hummingbirds. With the massive environmental changes that have followed colonization by Europeans—particularly the conversion of hardwood and pine forests to yards and gardens that provide a more accessible supply of insects and some winter flowers, and the increasing popularity of maintaining hummingbird feeders in winter—the Southeast now provides abundant food for hummingbirds in the winter. As a result, Rufous Hummingbirds that inherited a tendency to move southeast rather than south in the fall now might have a good chance of surviving and passing along the genes for migration to the southeastern United States. One possible explanation for the rapid increase in Rufous Hummingbirds wintering in this region is that genes for a new migratory pathway are spreading rapidly in the Rufous Hummingbird population.

Perhaps the best support for the idea that the increase in Rufous Hummingbirds in the Southeast results from rapid evolutionary change in innate migratory behavior comes from a detailed study of the Blackcap (*Sylvia atricapilla*), a European passerine that has undergone a change in winter distribution similar to that of the Rufous Hummingbird. Blackcaps are common breeders in Britain and Ireland, but until the 1950s they rarely occurred there in winter (Stafford 1956). Beginning in the 1950s, observers began to notice that more Blackcaps were being recorded each winter (Stafford 1956). By 1986, about 3,000 Blackcaps were wintering in Britain and Ireland (Bland 1986). Moreover, band recoveries showed that Blackcaps that wintered in the British Isles were not part of the local breeding population, but rather migrated from breeding areas in central Europe (Langslow 1979).

The similarity between the rapid changes in migratory behavior in Rufous Hummingbirds and Blackcaps is all the more interesting in light of an elegant set of experiments conducted on Blackcaps by Berthold and his co-workers. Berthold et al. (1992) speculated that the change in migratory behavior in Blackcaps reflected a rapid evolutionary change in innate migratory tendencies. To test the idea, they

captured Blackcaps wintering in England and Blackcaps breeding in Germany (most of which still migrate to Africa in the winter). When orientation was measured during the fall migratory period, German-caught birds oriented toward the southwest (toward Gibraltar), and British-caught birds oriented almost due west (toward the British Isles; Berthold et al. 1992). Moreover, the captive-born offspring of both the German-caught and British-caught birds, which had no opportunity to learn migratory behavior, oriented like their parents (Berthold et al. 1992). Thus, the experimental evidence indicates that the change in migratory behavior of Blackcaps reflects a rapid evolutionary change in the central European population (Berthold et al. 1992). It is possible that a similar change is affecting Rufous Hummingbirds in North America.

Berthold and Terrill (1988) proposed two advantages for Blackcaps that winter in the British Isles instead of Africa: (1) a relatively high probability of survival, and (2) a shortened migration route. Feeders in the British Isles provide a stable and reliable source of food that supplements natural food sources (Bland 1986). At the same time, historic wintering areas in Africa are being degraded or destroyed by human activities, lowering the probability of overwinter survival of Blackcaps (Berthold and Terrill 1988). Consequently, survivorship in winter probably is higher in the British Isles than in Africa. In addition, birds that winter in the British Isles as opposed to Africa travel about half as far in migration, reducing the risk of death, lowering the energetic cost of migration, and enabling Blackcaps wintering in the British Isles to arrive on their breeding grounds earlier in the spring (Berthold and Terrill 1988).

Rufous Hummingbirds wintering in the southeastern United States do not gain from a shortened migration route because distances between breeding and wintering areas in the southeastern United States and Mexico are about the same. Whether Rufous Hummingbirds are suffering reduced survival on traditional wintering areas in Mexico cannot be assessed without study. Deforestation is proceeding rapidly throughout the mountains of western Mexico, where Rufous Hummingbirds winter, but Rufous Hummingbirds may benefit, at least initially, when forests are opened and flowering forbs and shrubs proliferate (Calder 1993). However, the widespread environmental degradation that continues to unfold in the traditional wintering areas of the species may have reduced the carrying capacity for Rufous Hummingbirds in the region. In contrast, the winter food supply in the southeastern United States is substantial, and limited data suggest that overwinter survival of Rufous Hummingbirds in the region is high (R. R. Sargent and M. B. Sargent unpubl. data). In addition, winter densities of hummingbirds in the Southeast are very low such that little competition exists for food resources. In contrast, competition for

feeding territories is intense in wintering areas in Mexico (Montgomerie and Gass 1981).

A third hypothesis for the increased numbers of Rufous Hummingbirds in the Southeast is that birds are wandering north from Mexico in search of food. According to this hypothesis, Rufous Hummingbirds that end up wintering in the southeastern United States begin their fall migration by following traditional routes to Mexico. The resources in the traditional wintering areas, however, are inadequate to support the entire breeding population, and a proportion of the population begins to wander in search of better resources. A number of these birds make their way north and east into the southeastern United States where adequate resources are available. According to this hypothesis, the number of Rufous Hummingbirds wintering in the Southeast is increasing because individuals are returning (presumably back through Mexico) to sites where they found resources the previous year, and each year more birds are wandering from traditional wintering areas, perhaps due to habitat alteration as discussed above.

The main observation in support of this idea is a discontinuity in timing of the departure of Rufous Hummingbirds from the western United States and the arrival of Rufous Hummingbirds in the Southeast. Rufous Hummingbirds are essentially gone from the western United States by early September (Calder 1993), and yet the majority of wintering Rufous Hummingbirds in the Southeast do not arrive until November or December. The missing six or eight weeks could be accounted for by birds moving to Mexico and then wandering northward. Problems with this hypothesis include how birds that cannot find resources on traditional wintering grounds are able to travel 1,500 km to better areas in the Southeast and how so many birds gravitate to the same region to winter. It is also possible that Rufous Hummingbirds are following a U-shaped migration route through Mexico that is genetically based and that is spreading through the population, but this would require a much more complex change in migratory behavior than a simple change in compass direction.

The first test of these hypotheses should come as Rufous Hummingbirds banded in the Southeast in the winter are recovered elsewhere at other times of the year. Such recoveries will provide insight into migratory routes and timing of movements. A definitive test of whether an evolutionary change in innate migratory behavior has occurred may require laboratory experiments such as those conducted with Blackcaps.

*The future.*—The increase in numbers of Rufous Hummingbirds wintering in the Southeast shows no sign of abatement. All indications are that Rufous Hummingbirds only recently have entered a stage of exponential population growth in the Southeast (Figs. 1 and 2). Although wintering Rufous Hummingbirds are now vastly more common in the

Southeast than they were 20 years ago, they currently occupy only a small fraction of what appears to be suitable winter habitat. We predict that over the next decade, the number of Rufous Hummingbirds wintering in the southeastern United States will continue to grow exponentially until preferred habitat (i.e. suburban areas with feeders and nectar-producing ornamental plants) is saturated. Because a large and growing expanse of suburban habitat exists within the current winter range of the Rufous Hummingbird in the Southeast, a significant fraction of the total North American population could be affected by this shift in wintering range. The ultimate influence that such a change will have on winter populations in Mexico and on breeding populations has not been considered, but the rapid change in migratory behavior of Rufous Hummingbirds currently being documented provides a tremendous opportunity to investigate questions regarding population dynamics and orientation behavior.

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