THE MIGRATIONS OF ALLEN'S AND OTHER HUMMINGBIRDS[1]

ALLAN R. PHILLIPS
Delaware Museum of Natural History
P.O. Box 3937
Greenville, Delaware 19807

Migrations occur in bewildering number and variety, but tend to follow the sun. Thus, in either hemisphere, spring migrations are away from the Equator. To be sure, a few shorebirds without parental cares start back just before the vernal equinox (cf. Phillips et al. 1964, on female Wilson's Phalaropes, *Steganopus tricolor*). Yet data presented herein show that one North American land bird actually migrates southward in numbers in late spring; further, its route soon veers away, geographically and ecologically, from the northward return route used chiefly in winter.

Allen's Hummingbird (*Selasphorus sasin*) is remarkable in that it breeds only in California, barely overlapping that State's borders, and normally (at least until recent years) only in a narrow coastal strip. Of the few endemic California species, it is the *only* wholly migratory one! This distinction belongs to the northern, nominate race. The southern *S. s. sedentarius* Grinnell has the opposite distinction of being the only virtually *sedentary* hummingbird or nectar-feeder of any kind in the continental United States (see below).

These amazing, somewhat elliptical migrations at the wrong seasons remain unappreciated because of: (1) the few records, mostly unpublished, between early September and mid-February; (2) reluctance to admit migrations in Californian endemics or ignorance in official check-lists (cf. for example, Swarth 1914:38, 90, on both Allen's and Anna's Hummingbirds, *Calypte anna*, in Arizona); (3) their seasonal displacement; and (4) failure to distinguish age/sex classes, or even the species (vs. the extremely similar Rufous Hummingbird, *Selasphorus rufus*), whose migrations are asynchronous. Authorities disagree widely on migrations and winter ranges (see A.O.U. 1931, 1957, Berlioz 1932, Friedmann et al. 1950).

Loye H. Miller first pointed out (in Willett 1933:97) that even adult males of Allen's Hummingbird are not always safely distinguishable in color. This important fact is still generally overlooked; Peterson and Chalif (1973), Robbins et al. (1966), and Stiles (1972:31) all described the back of adult male *S. rufus* as rufous, or "sometimes with scattered green feathers," thus not contrasting to the rufous tail and coverts as in *S. sasin*. But there is a wholly green-backed, fully adult male *S. rufus* in the Northern Arizona University collection from the San Francisco Peaks, Arizona, where *S. sasin* is unknown. Jean T. Craig (unpubl. data) caught two similar males and Miller must have seen others. Females and young are, of course, unidentifiable afield.

METHODS AND ABBREVIATIONS

For a number of years I have searched museums, as opportunity arose, for relevant specimens. My techniques were improved in October 1970, when I received refined criteria for all forms, ages, and sexes from F. G. Stiles. (I did not have the bill criterion of Ortiz-Crespo 1972.) Further, Jean T. Craig kept detailed records (as described below under "Seasonal Occurrence of Age and Sex Classes") of birds netted on Point Loma, San Diego, California, from June 1970 to May 1971 (most of the critical rectrices I later examined). She also checked specimens in the San Diego Natural History Museum (SD hereafter).

Collections seen since October 1970 include those in the following institutions: American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Dickey Collection, University of California at Los Angeles (LA), Los Angeles County Museum of Natural History (LAM), Moore Laboratory of Zoology, Occidental College (RTM), Museum of Comparative Zoology at Harvard University (MCZ), University of California Museum of Vertebrate Zoology (MVZ), Neotropical Ornithological Foundation (RSC), my own (ARP), that of Amadeo M. Rea (AMR), and the Santa Barbara Museum of Natural History. Rea kindly reexamined for me the University of Arizona (ARIZ) and other Arizona collections and supplied additional information. H. M. Stevenson sent data on specimens in Florida State University, Tallahassee (FSU).

Earlier I had seen the collections of J. Berlioz; the British Museum (Natural History) (BM); the late Lawrence N. Huber; Instituto de Biología, Universidad Nacional Autónoma de México (in 1954, MEXU; these birds disappeared before 1970); University of Kansas Museum of Natural History (KANU); Louisiana State University (Sheffler collection only, LSU); Bell Museum of Natural History, University of Minnesota; Museum of Northern Arizona; Northern Arizona University; Museum National d'Histoire Naturelle, Paris (P); and United States National Museum of Natural History (US). In these collections, some female *S. sasin* may have been overlooked. "FWS" refers to the collectors' files of the United States Fish

[1] This paper is dedicated with great pleasure to Loye H. Miller.

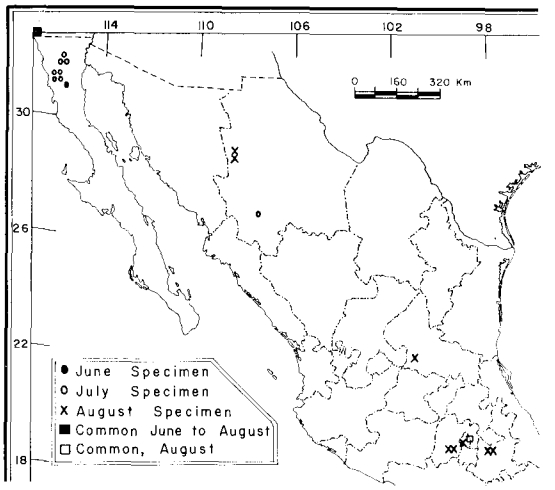

FIGURE 1. June to August records of S. *sasin* in and adjacent to México. (Los Coronados Is. excluded, as report there was not positive as to species; see Wright 1909.)

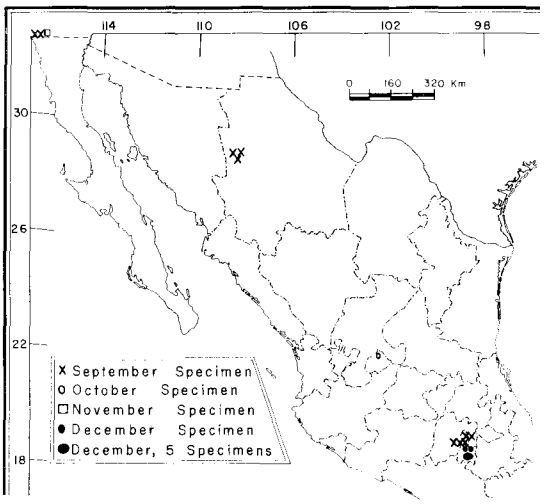

FIGURE 2. September to December records of S. *sasin* in and adjacent to México.

and Wildlife Service. I also checked the important notes of Helmuth O. Wagner on Mexican hummingbirds.

I have ignored sight records and reports, except records of adult male S. *rufus* by competent observers (cf. Van Tyne 1956), nor do I accept all specimen reports (see below).

IDENTIFICATION AND MOLT

This study reemphasizes the adage that, whatever one's interest, a naturalist must be a taxonomist. Complications arise here in females due to molt. Most males acquire adult-type rectrices, easily identifiable to species, at the first prebasic molt, probably about November to January. Due to scarcity of material, I have had to assume that molt (unless artificially speeded by accidental loss of feathers) will be similar in both sexes of immature birds. Immature females, then, would first acquire adult-type bodies and necks, then tails, judging by the molts of male S. *rufus*, which is represented more adequately in collections. Most of the primaries are replaced in late autumn (contra Aldrich 1956:131). The throat and forehead are among the longest-lasting juvenal feathers both in S. *rufus* and in *Calypte anna* (Aldrich 1956, Williamson 1956: 348).

A case in point is a female (RTM) taken near Lagos de Moreno, Jalisco, 4 November 1940 (C. C. Lamb 2752). Its throat seems to be immature, and as such it would qualify as S. *sasin* because of somewhat narrow rectrices and a fairly short wing. The tail measures 27 mm, however, and I consider it a rather short-winged S. *rufus* (the outermost primary is old) with new narrower, adult-type rectrices. Thus I exclude it from the discussion of S. *sasin*.

RESULTS

Outside of California, S. *sasin* has been found in abundance only in the Valley of México. Probably this reflects more past field work there and neglect of the rest of the country. All Mexican records to date are given in tables 1–2 and figures 1–3. The westward and northward route is there shown to be much like that of S. *rufus* (fig. 4); but the somewhat narrowed southeastward route and winter range reflect the narrow, more southwestern breeding range of S. *sasin*.

The easternmost records in the United States are for the Bradshaw Mountains, near Prescott, Arizona (ARIZ) and the Huachuca and Mule Mountains, southern Arizona. All records north of México are for southern or central Arizona or California except for a few northward along the Pacific lowlands, which will not be discussed here. These non-Californian data are too few to show age and sex variations.

SEASONAL OCCURRENCE OF AGE AND SEX CLASSES

At my request, Jean T. Craig collected the central and outer rectrices of most of the *Selasphorus* netted at Point Loma, San Diego, California, from June 1970 to April 1971. These she attached to a card with the date, description, and often measurements before releasing the bird; I later examined nearly all these cards (now in the Institut royal des Sciences naturelles de Belgique, Brussels).

TABLE 1. Mexican records of ♀ and immature S. *sasin*.

No. of specimens	Locality	Date	Collector	Museum[a]
1 [♀ im. ?]	Vallecitos, Sierra San Pedro Mártir, Baja California	23 June 1926	C. C. Lamb	MVZ
1	Laguna Hanson, Sierra Juárez, Baja California	10 July 1924	L. M. Huey	SD
3 ♂ im.	Piñón, W. slope of Sierra San Pedro, Mártir, Baja California	10 July 1905	Nelson & Goldman	US
1	Mountains above Jesús María, W'n Chihuahua	18 July 1884	R. R. McLeod	MCZ
5 (2 ♂ im. 3 ♀ im.)	Madera, Chihuahua	(25) Aug.— (10) Sep. 1921	W. W. Brown	AMNH
1 [♀ ad.]	Morales, San Luis Potosí	(2) Aug. 1923	W. W. Brown	AMNH
1 (♀)	Puebla, Puebla	Aug. 1933	Fuentes de María	Berlioz
8	"Valle de México"	"Aug. – Sept."	M. del Toro, P. Roveglia	RTM
7 (6 ♂ im. 1 ♀)	Cerro de la Caldera, México (at D. F. line SE. of Mexico City)	(22) Aug. 1937	Various	MEXU
3 (♂ im.)	do.	(29) Aug. 1937	Various	MEXU
1 (♀)	do.	Aug. 1937	C. Sánchez M.	Colln. Carlos Sánchez Mejorada
1 (♂ im.)	do.	"5 Sep. 1935"	P. Roveglia	Depto. de Conservación Fauna Silvestre, S.A.G., México, D.F.
2 (♀)	near La Cima, Distrito Federal	3 Sept. 1962	A. R. Phillips	ARP
2 (♂ im.)	near San Pedro Techuchulco (S. of Lerma), México	21 Aug. 1964	J. Nava S.	ARP
1 (♂ im.)	near Almoloya del Río (S. of Lerma), México	17 Sept. 1961	A. R. Phillips	ARP
1 ♀	San Jacinto, Aguascalientes	17 Oct. 1940	C. C. Lamb	RTM
3	Las Estacas, Morelos	"3–22 Dec. 1936"	M. del Toro A.	P
1 (♂ im.)	near Ticumán, Morelos	15 Dec. 1962	R. W. Dickerman	ARP
1 (♂?)	near Tepoztlán, Morelos	15 Dec. 1962	R. W. Dickerman	ARP
1 ♀ (?)	near Cuernavaca, Morelos	31 Dec. 1958	A. R. Phillips	ARP
1 "♂ im."	Tepames, Colima	20 Jan. 1959	*fide* Schaldach (1963)	
1 ♂ im.	Badiraguato, Sinaloa	12 Jan. 1937	C. C. Lamb	RTM
1 [♀]	14 km. E. of Concordia, SE'n Sinaloa	4 Feb. 1966	W. Bulmer	ARIZ
1 ♀	Sto. Domingo, Pac. coast at 30°45′ ± N., Baja California	22 Feb. 1925	L. M. Huey	SD
"seen commonly"[b]	San Quintín, Pac. coast at 30°30′ N., Baja California	25 Feb. 1925	(*fide* Huey, 1926)	
1 ♀	Isla Cedros, Baja California	"2 Mar. 1945"	[M. del Toro A.]	LA

[a] For abbreviations see Methods.
[b] May include all age-sex groups; also S. *rufus*?

The first two *Selasphorus* netted, on 4 June, were an adult and a young male of S. *sasin*. Adult male S. *sasin* predominated in early June, but none was netted after 2 August. Young males continued to enter the nets through August; the last two were captured on 1 September. No female was netted after 9 August (a probable female, certainly S.

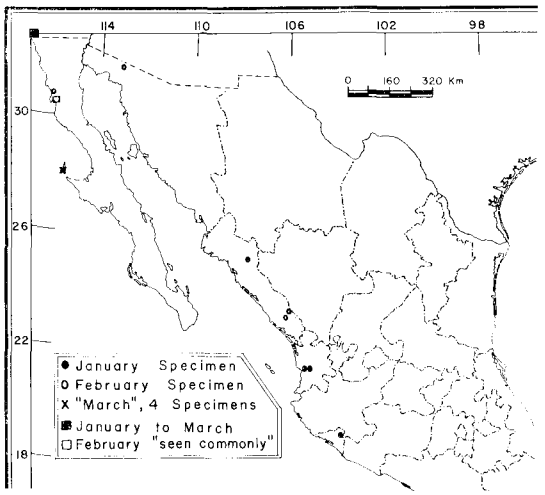

FIGURE 3. January to March records of S. *sasin* in and adjacent to México. (There are no Mexican records for April or May.)

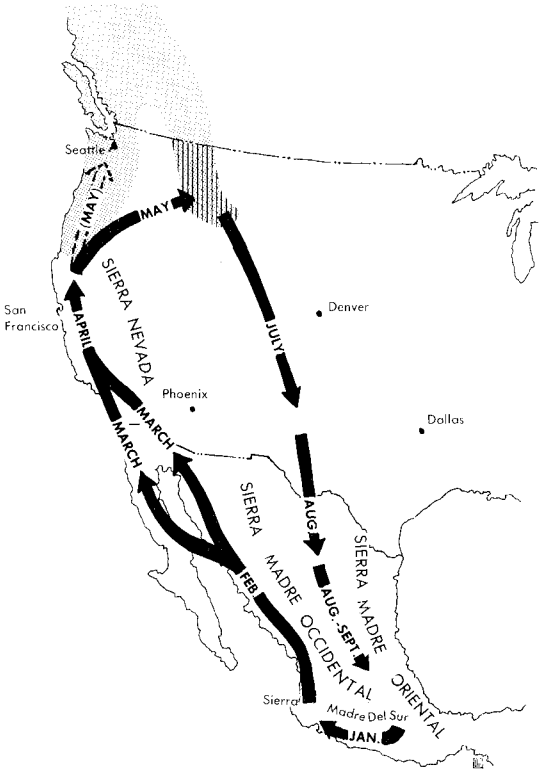

FIGURE 4. Apparent migrations of adult male S. *rufus* nesting in Montana and Idaho. Vertical lines show range of populations that have been mapped (solid arrows); stippling shows general breeding range.

sasin), unless one bird of uncertain identity on 25 August was an immature female S. *sasin*. S. *rufus*, of course, continued to occur into the autumn.

A build-up of S. *sasin* near the Mexican border in mid-June also occurred in 1894. E. A. Mearns (1907) was there all of early June, and collected three adult males and two immatures (US) at Laguna 18–19 June, but none earlier. In Los Angeles County, on his study area, Stiles (pers. comm.) later found adult S. *sasin* appearing from "late May onwards," but they were not common after mid-June, whereas immatures remained common in July. Farther north, in Kings Canyon, "fall" arrival is in mid-May as discussed below.

Museum specimens further demonstrate the predominance of immature males in the United States by mid-August. Adult males are almost unknown after 5 August; I have found only one, from Oroville, California, 12 August 1895 (Breninger, MCZ). A few mid-August females have equivocal measurements and may be small S. *rufus*. The only sure S. *sasin* females after 9 August are: immature, "Palmerlee" [= Huachuca Mountains], Arizona, 12 August 1905 (Marsden, AMNH); immature and adult, Los Angeles County, California, 16 and 19 August 1920 (Hornung, LAM); adult, Tejon Mountains, California, 17 August 1875 (Henshaw, BM); and an apparent female adult from Lost Palm Cañon, Riverside County, California, 22 October (!) 1945 (A. H. Miller 5689, MVZ; see Miller and Stebbins 1964:104).

Immature males, on the contrary, remain regularly in parts of coastal California in late August. In addition to Craig's, other records are: Highland Park, 17 August 1895 (W. B. Judson, MVZ); interior Los Angeles County, two 16 August, two 19 August, and two 26 August 1920, one 29 August 1919, two 29 August 1918, and one 2 September 1920 (all Hornung, LAM); near mouth of Klamath River, Del Norte County, four 27 August 1967 (Wm. F. Bowman, AMR and FSU); Echo, El Dorado County, one 28 August 1896 (P. O. Simons, AMNH); Maywood, Los Angeles County, one 1 September 1918 (Hornung, LA); San Pedro, one 27 August 1971 and one 22 September 1972, and probably one 1 September 1971 and one 3 September 1972 (Wells); and National City, San Diego County, one 18 September 1917 (Kimball, LA). Thus, as against only three certain females (all taken in the first few days) for the period 16 August through 22 September, I have records of at least 20 immature males in California—additional to Craig's. For the period 20 August to 1 October, the proportion of immature males among California S. *s. sasin* is close to 100%.

Other immature males are from Walker Basin, Kern County, California, 15 October

TABLE 2. Mexican records of ♂ adult *S. sasin*.

No. of specimens	Locality	Date	Collector	Museum[a]
2	Laguna Hanson, Sierra Juárez, Baja California	10 & 24 July 1924	L. M. Huey	SD
1	Piñón, Baja California	10 July 1905	Nelson & Goldman	US
1	Puebla, Puebla	Aug. 1931	Fuentes de María	Berlioz
(?)	near México, Distrito Federal	Aug. 1931	*fide* Berlioz (1932)	
1	San Pablo, Distrito Federal	(21) Aug. 1938	Santos Molina	MEXU
5	"Valle de México"	"Aug. – Sept."	Mario del Toro, Pablo Roveglia	RTM
1	Cerro de la Caldera, México	(29) Aug. 1937	Santos Molina	MEXU
1	do.	31 Aug. 1972	A. R. Phillips	ARP
1	do.	"15 Sept. 1930"	M. del Toro A.	P
1	Las Estacas, Morelos	"Dec. 1936"	M. del Toro A.	P
2	Cerro San Juan, W. of Tepic, Nayarit	26 & 29 Jan. 1955	L. D. Yaeger, A. R. Phillips	ARP
1	near Palmito, SE'n Sinaloa	19 Feb. 1964	R. S. Crossin	RSC
1	25 km. SW. Sonoyta, NW'n Sonora	22 Feb. 1955	J. T. Marshall, Jr.	LSU
3	Isla Cedros, Baja California	"2 Mar. 1945"	[M. del Toro A.]	LA

[a] For abbreviations see Methods.

1933 (R. M. Gilmore, MVZ), and Santa Catalina Mountains, Arizona, 23 August 1906 (Kimball, LA). Additional immatures taken by W. W. Brown (AMNH) are labeled Huachuca Mountains, Arizona, 17 June and 30 August 1919 (males), and Madera, Chihuahua, late August and September (2 males, 3 females in all); these data are approximate.

BIOLOGICAL VS. SEASONAL "SUMMER" AND "WINTER" RANGES

Practically all birds that breed in the northern hemisphere are on their breeding grounds from mid-June until early July, at least, although exceptions have been noted in populations of Bald Eagle (*Haliaeetus leucocephalus*) (Broley 1947) and Cassin's Sparrow (*Aimophila cassinii*) (Phillips 1944, 1973). The opposite, the southern or coastward portion of their range, is occupied at least from late December until early February. Northward migration usually takes place between February or March and May or early June. A bird that reaches an area on 11 or 14 May presumably is coming north to breed, especially if seen later gathering nest materials. Hence, Dixon (1943:210) was justified though apparently mistaken, in believing Kings Canyon National Park, California, to be within the normal breeding range of *S. s. sasin*. Grinnell and Miller (1944:222) likewise mapped this hummingbird as breeding south as far as the site where a female was taken on 15 June. All these records were possibly those of already southbound migrants; other dates presented herein show the annual cycle of *S. sasin* to be advanced over that of most birds by two or three months.

In this case, we must identify "summer" and "winter" ranges on biological grounds, not seasonal. Breeding begins in mid- to late winter; "fall" migration southward starts in late spring and may be nearly completed (at least by adults) before fall even begins. The southernmost ("winter") range seems to be occupied chiefly in late fall, and "spring" migration occurs chiefly in winter. Latitude and regular nesting show the range occupied chiefly in late winter and spring to be biologically the "summer" range.

COMMENTS ON PAST REPORTS

In central coastal California, *S. sasin* is common in spring, and collectors may feel they have enough by summer. Field studies based on birds in the hand, may suffer from a decline in interest as the season progresses and attention shifts to newer arrivals. This may account for the supposed local rarity of the relatively late-arriving *S. rufus*. Sight reports in mid- or late September have therefore been referred to *S. sasin* (Grinnell and Wythe 1927,

Bent 1940:417, Sibley 1952), as the supposedly "conservative" course. However, when Ortiz-Crespo (1971) investigated the situation, he found that S. *rufus* did occur in late fall, and indeed (unpubl. data) that "the departure of Allen's is all but finished by late July," though it does winter at least casually [immature males only?].

Apparently no specimens exist to support van Rossem's report (1909) of S. *sasin* as "very common" on Los Coronados Islands, Baja California, in April, nor Sams and Stott's (1959:22) possibly related statement, "Common . . . from February through May (northward) and in July and August (southward)" in San Diego County, California. More accurately, I believe, Pyle (1953) limited bulk passage of [male] S. *sasin* in southern California, in spring migration, to February and the first half of March; Stiles (1971:42) gave it as "between about mid-January and mid-March." Extreme dates at San Diego can be extended about another 10 days, according to Craig and Guy McCaskie (unpubl. data). None of Craig's April hummingbirds seems to me typical of S. *sasin*.

On the Mohave Desert, California, Cody (1968) studied a supposed male S. *sasin* and several possible females in late March and late April, as well as a male *Selasphorus platycercus* (Broad-tailed Hummingbird); but these species have never been proved to migrate there in spring, or even in any adjacent part of the Colorado River Valley (Phillips et al. 1964).

A female hummingbird (MCZ) from the Victoria Mountains, 26° N, Baja California, was reported as S. *sasin* by Brewster (1902) and Grinnell (1928); it now lacks most of its lateral rectrices and is nearer S. *rufus* by measurements, though small-winged (chord 42.5 mm; tail 26.4). It may have been a hybrid, but this can never be established, as neither author commented on the tail.

On the other hand, Grinnell (1928) identified as S. *rufus*, a female taken on 23 June at Vallecitos, northern Baja California; van Rossem (1934:439) reported as S. *rufus*: "Frazar, 1, Jesus Maria [Chihuahua], July 18, 1888." These last data are erroneous; the bird is actually a S. *sasin* taken by McLeod in the adjacent mountains 18 July 1884 and otherwise omitted by van Rossem. Similarly, Grinnell's bird, though more equivocal in measurements, is now considered S. *sasin* by Stiles. (Even a male, so early in June, would be unlikely to be S. *rufus* but I took a female S. *rufus* on 7 August as far south as northern Morelos.)

The Guanajuato bird described by Friedmann et al. (1950) as a probable S. *sasin* I find to be an imperfect skin of *Calothorax lucifer*.

The sedentary uniqueness of the other race, S. *s. sedentarius*, would be debatable if Anna's Hummingbird were also "essentially permanent resident" with a "limited range in California and Baja California" (Johnson 1972: 310). This old concept (cf. Swarth 1914:38, 90, Grinnell and Miller 1944) had long since been corrected (e.g. van Rossem 1945, Phillips 1947, Phillips et al. 1964, and Wauer and Rylander 1968). Actually, *C. anna* was found during the first serious autumn explorations of Arizona (Henshaw 1875), Sonora, and even southwestern Texas (Van Tyne and Sutton 1937); it is now spreading widely in range and season, having been taken in southern Chihuahua and Coahuila (Hubbard and Crossin 1974), for example.

COMPARISONS WITH OTHER BIRDS

As noted by Phillips et al. (1964), the migrations of certain far-western hummingbirds follow similar patterns. Except for the dates, relative abundance, and wider distribution, the migrations of S. *rufus* are much like those of S. *sasin*. The route of the Calliope Hummingbird (*Stellula calliope*) is similar, though rare east of Michoacán and Guerrero, so that its oval is narrower. The absence of all these (the only rufous-sided hummingbirds are occasional *Atthis heloisa*) in October from the mountains west of Tepic, Nayarit, is in striking contrast to their abundance and variety there in late January. The reverse—abundance in late summer and early fall vs. rarity in winter and spring—is equally striking about the Valley of México. Thus the pattern of S. *sasin* is repeated in other hummingbirds, with seasonal and other variations.

If the absence of these hummingbirds near the Mexican west coast in late summer and fall were an adaptation to avoid the hurricane-season storms there, why haven't "selective pressures" produced oval routes in many birds? Food is not scarce in fall. In fact, other migrant hummingbirds (the Ruby-throated, *Archilochus colubris*), certain swallows, Orchard Orioles (*Icterus spurius*), and Dickcissels (*Spiza americana*) are then rather common near Compostela, Nayarit, yet seem rare there in spring, whereas I know of no other bird with migrations similar, in Nayarit and

east, to those of these three northwestern hummingbirds.

These three are alike also in the early passage of adult males. For example, adult male *S. rufus* usually appear in Arizona about the first week or two of July; most are gone by early September, though other age/sex classes linger another five or six weeks. Occasional males appear in late June, or linger to mid-September; in Tucson I saw one on 16 September 1933, and my mother, Mrs. Alma J. Foerster, saw three males chasing, 21 September 1942. This was exceptional, as was also the male seen by E. A. Goldman (FWS) at Topock, Colorado River, 29 September 1917. (The 11 November report in Phillips et al. 1964 was an error on my part; the specimen is really a female.)

In spring both Rufous and Calliope Hummingbirds are largely limited, in Arizona, to the southwestern and (less commonly) central deserts, ranging up into the lower oaks and irregularly east to the Huachuca Mountains. Males are most common in March and are nearly gone by late April. The 3 male *S. rufus* supposedly taken in mid-May well inside New Mexico (Hubbard 1963) were suspiciously far from the mid-May range of male *S. rufus*. Their identification is correct, but their upper tail-coverts are badly frayed, as in July or August males; so I suspect that errors were made in their hastily written field tags. Even farther from authentic spring records is Mesa Verde, Colorado, where "several" *S. calliope* were "noted by Jean M. Pinkley May 9, 1949" (Bailey and Niedrach 1965:475). In the absence of suitable evidence, I doubt this report.

Field work is needed to clarify the status of *S. calliope* in Utah. Woodbury et al. (1949) gave no details in reporting it from 5 April to October. Behle kindly analyzed Woodbury's data and found the April records to be from extreme southwestern Utah, northeast only to Zion National Park; May records were concentrated in late May in the extreme north. Evidently this species skirts most of Utah, Arizona, and New Mexico in spring, taking a northwestward route very like that of Rufous (fig. 4) and Allen's Hummingbirds. The first two (northern) species then must fly *eastward* (fig. 4) to reach their breeding areas in the northern Rocky Mountains!

Exceptional records of hummingbirds wintering in the United States must not obscure the species' more regular northerly winter limits. In both *S. sasin* and *S. calliope*, these limits probably lie wholly south of the central Mexican transverse volcanic belt. *S. rufus* in Sinaloa supposedly "winters from 1100 to 6500 feet, K-d" [= RTM] (Friedmann et al. 1950), but the only Sinaloa specimen I could find taken between 23 August (on the Chihuahua border) and 19 February (at 700 ft) was an adult male from Badiraguato, 1100 ft, 5 January 1937. Possibly this species winters there no more regularly than in Arizona, whence there are November and January specimens (ARP), but there is a specimen from Durango, 27 November 1948 (RTM). There are December specimens from Guanajuato (RTM) and late January ones from Nayarit (ARP). Still, some *Selasphorus* linger until mid-November in the Valley of México; I think they are largely or wholly *S. rufus*, yet most or all disappear by early December. By late December most *S. rufus* may be as far south as *S. sasin*, some even farther south, for they are common in southwestern Oaxaca (ARP). Indeed, the late Mario del Toro A. showed me a single, young male *S. rufus* he had taken, with many *Archilochus colubris*, near Comitán, Chiapas, in October (ca. 1959). None of these was labeled then (30 June 1960), but he was clear in his recollection and was well aware of the exceptional nature of the record.

S. rufus evidently winters northwest at least to the mountains of southern Jalisco, where it was seen commonly in late December 1959 by W. J. Schaldach, Jr. and me. Thus its ranges and migration times are less restricted than those of *S. sasin*, not to mention the winter records in eastern North America and, recently, in California.

Although the arrival dates of the various species in México are unclear, it appears that only *S. sasin* and probably *A. colubris* occur at any great distance from the U. S. border before late July. The supposed female *S. calliope*, from near San Francisco, Chihuahua, 28 June 1957 (Thompson 1962; KANU) proves to be a small juvenile of some local species, not a migrant. Actual southern limits of migrant *S. calliope* in June seem to be much farther north: St. George, southwestern Utah, 21 June 1933 (*fide* Behle); Ash Meadows, southern Nevada, 24 June (Johnson and Richardson 1952); and Colorado, 30 June.

Not all western U. S. hummingbirds have parallel migrations. *Calypte anna* and *C. costae* move more nearly east and west (Huey 1926, Phillips et al. 1964); the less prominent southward component of their migrations seems to involve relatively few individuals. Yet none of these hummingbirds agrees well with the "general rule" (Thompson 1964:467) that temperate latitude birds that migrate

"early in spring tend to be late in autumn." Many other species and subspecies also deviate from this general tendency, but few, if any, depart so widely as does Allen's Hummingbird from Thompson's less flexible rules that the seasons of migration are spring and autumn, while winter in temperate latitudes is avoided by migration.

DISCUSSION

The most striking fact that emerges from the above listings of records (tables 1–2, fig. 1–3) is the inadequacy of our present knowledge about hummingbird migration. For almost the entire fall—mid-September to mid-December—there is but the merest handful of records of S. *s. sasin*, most of which are pretty surely of stragglers. If the records for the rest of the year are more representative, there is a distinct difference (as often happens) in the rate of spring and fall migrations. The latter is relatively leisurely, lasting from late May or June through at least mid-September, as a whole. Even for one age/sex class, young males, the birds are common in central México in the latter half of August, when some are still lingering all along the coast of California. "Spring" migration in México, on the other hand, seems from the present scanty data to be compressed into a 2-month period (early January to early March), which is within a month of the main flight through southern California; California and Sinaloa dates thus overlap widely. In "fall" migration, California and central Mexican dates show very little overlap within single age/sex classes other than immature males; I suspect that most females, at least, are concentrated in México somewhere north of the Valley of México during early August.

The seasonal displacement of the annual cycle of Allen's Hummingbird adapts it well to the Mediterranean climate of its breeding areas. In the more southern parts of these areas, mild and moist winters produce a bloom of flowers in late winter, at a time when in most years the mountains and higher deserts to the east and southeast are rather barren. The usual eastward limit of such winter storms as penetrate into the deserts almost corresponds to the eastward limits of Allen's, Rufous, and Calliope Hummingbirds in late winter and spring. At this time the higher, cold interior mountains are nearly or quite devoid of flowers. Here flowering swells to its peak with the melting of such snow as may fall, and the subsequent summer rainy season. In summer, hummingbirds swarm on these mountains, but Allen's seems to arrive there later than in the California mountains and at San Diego.

But why should the same coastal route be followed in spring by all the Rufous and Calliope Hummingbirds, including those that nest far inland in the Rocky Mountains (cf. fig. 4)? Surely there is *some* flowering in spring along the foothills and valleys of New Mexico and adjacent states, and in fact other hummingbirds do occur there in spring. Perhaps we underestimate the capabilities of these tiny creatures. Ecological correlations can be urged in this case also. Occasional spring storms do occur in late April or early May, even as far south as southern Arizona, blanketing the interior mountains with snow. The scarcity of insects at such times must be rather dramatic. The coastal route may afford a safer way to reach the breeding grounds with energy reserves for the exigencies of weather, territorial squabbling, etc. I am not aware, however, of detailed studies of spring foods of these birds, and other explanations are possible; for example, the following of an ancestral route, if they recently bred only along the coast and have spread east since the last glaciation.

Accurately determining the migration routes and dates for each species (including sex- and age-classes) will furnish merely a framework on which to build an understanding of the year-round activities of these amazing birds and to make interspecific comparisons. One cannot properly study interspecific behavior or possibly overlapping breeding ranges (not merely sporadic extralimital nestings), without knowing which species are involved.

SUMMARY

Allen's Hummingbird, *Selasphorus s. sasin*, migrates on an elliptical route that takes it southward and eastward in late spring and summer to its biological "winter range," westward probably about the time of the winter solstice, and northwestward to the breeding or "summer range" in the North Temperate Zone winter (figs. 1–3). More or less similar routes are followed a little later by Calliope and Rufous Hummingbirds (cf. fig. 4). Earlier published statements about these migrations are re-evaluated. These migrations are compared to those of other birds. The other race of S. *sasin*, S. *s. sedentarius*, is the only practically nonmigratory hummingbird in the United States.

Adult males precede females in all cases, but in S. *s. sasin* the most prolonged periods of

migration are those of *young males*, which linger in California about a month after the last adult males leave, and half a month after the last females. The possible ecologic basis of these migrations is discussed.

Sight records, except of adult male S. *rufus*, are considered useless in this group. Specimens in all museums combined are at present inadequate to clarify the whereabouts of Allen's Hummingbird in late summer, fall, and early winter. During this entire period, covering half the year, only two local concentrations are known: one in the Valley of México in August, and the other just south, in Morelos, in December. Even the latter is poorly represented in collections, and may not be a major gathering area. All Mexican records to date are listed (tables 1–2) and mapped (figs. 1–3).

ACKNOWLEDGMENTS

I wish to thank F. G. Stiles; Jean T. Craig, who kept detailed records; Robert W. Dickerman and Lewis D. Yaeger, who contributed important specimens; and others who have helped in many ways. Important information was supplied by Russell P. Balda, William H. Behle, Bruce G. Elliott, Gale Monson, Fernando I. Ortiz-Crespo, Van Remsen, and Shirley Wells. Collecting permits were issued by the late Ing. Luis Macías A. and Bernardo Villa-R. My museum work in 1966 and 1970 was aided by grants from the Frank M. Chapman Memorial Fund of the American Museum of Natural History.

LITERATURE CITED

ALDRICH, E. C. 1956. Pterylography and molt of the Allen Hummingbird. Condor 58:121–133.

AMERICAN ORNITHOLOGISTS' UNION. 1931. Check-list of North American birds. Fourth ed. A.O.U., Lancaster, Pa. 526 p.

AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds. Fifth ed. A.O.U., Baltimore. 691 p.

BAILEY, A. M., AND R. J. NIEDRACH. 1965. Birds of Colorado. Vol. II. Denver Mus. Nat. Hist., Denver, Col. P. 455–895.

BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. U.S. Natl. Mus. Bull. 176. 506 p.

BERLIOZ, J. 1932. Contribution à l'étude des Trochilidés du Mexique. Oiseau 2:120–132.

BREWSTER, W. 1902. Birds of the Cape Region of Lower California. Bull. Mus. Comp. Zool. 41: 1–242.

BROLEY, C. 1947. Migration and nesting of Florida Bald Eagles. Wilson Bull. 59:3–20.

CODY, M. L. 1968. Interspecific territoriality among hummingbird species. Condor 70:270–271.

DIXON, J. B. 1943. Birds of the Kings Canyon National Park area of California. Condor 45:205–219.

FRIEDMANN, H., L. GRISCOM, AND R. T. MOORE. 1950. Distributional check-list of the birds of México. Part I. Pacific Coast Avifauna 29. 202 p.

GRINNELL, J. 1928. A distributional summation of the ornithology of Lower California. Univ. Calif. Publ. Zool. 32:1–300.

GRINNELL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. Pacific Coast Avifauna 27. 608 p.

GRINNELL, J., AND M. W. WYTHE. 1927. Directory to the bird-life of the San Francisco Bay region. Pacific Coast Avifauna 18. 160 p.

HENSHAW, H. W. 1875. Report upon the ornithological collections made in portions of Nevada, Utah, California, Colorado, New Mexico, and Arizona during the years 1871, 1872, 1873, and 1874. Chapter 3 *in* Report Geogr. and Geol. Expl. and Surveys W. 100th Mer. by George M. Wheeler, 5:131–507, 977–989.

HUBBARD, J. P. 1963. Noteworthy records from New Mexico. Condor 65:236–239.

HUBBARD, J. P., AND R. S. CROSSIN. 1974. Notes on northern Mexican birds. An expedition report. Nemouria no. 14. 41 p.

HUEY, L. M. 1926. Notes from northwestern Lower California, with the description of an apparently new race of the Screech Owl. Auk 43:347–362.

JOHNSON, N. K. 1972. Origin and differentiation of the avifauna of the Channel Islands, California. Condor 74:295–315.

JOHNSON, N. K., AND F. RICHARDSON. 1952. Supplementary bird records for Nevada. Condor 54: 358.

MEARNS, E. A. 1907. Mammals of the Mexican boundary of the United States. A descriptive catalogue of the species of mammals occurring in that region; with a general summary of the natural history, and a list of trees. U.S. Natl. Mus. Bull. 56, part 1, 530 p.

MILLER, A. H., AND R. C. STEBBINS. 1964. The lives of desert animals in Joshua Tree National Monument. Univ. Calif. Press, Berkeley & Los Angeles. 452 p.

ORTIZ-CRESPO, F. I. "1971." Winter occurrences of Selasphorus hummingbirds in the San Francisco Bay region. Bird-Banding 42:290–292.

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

PETERSON, R. T., AND E. L. CHALIF. 1973. A field guide to Mexican birds. Houghton Mifflin Co., Boston. 298 p.

PHILLIPS, A. R. 1944. Status of Cassin's Sparrow in Arizona. Auk 61:409–412.

PHILLIPS, A. R. 1947. Status of the Anna Hummingbird in southern Arizona. Wilson Bull. 59: 111–113.

PHILLIPS, A. R. [1973]. Avian breeding cycles: are they related to photoperiods? Anal. Inst. Biol. Univ. Nal. Autón. México 42, Ser. Zool. (1):87–98, "1971."

PHILLIPS, A., J. MARSHALL, AND G. MONSON. 1964. The birds of Arizona. Univ. Ariz. Press, Tucson. 220 p.

PYLE, R. L. 1953. Annotated field list of the birds of southern California. Los Angeles Audubon Soc., Los Angeles, Calif. 40 p.

ROBBINS, C. S., B. BRUUN, AND H. S. ZIM. 1966. Birds of North America. Golden Press, New York. 340 p.

SAMS, J. R., AND K. STOTT, JR. 1959. Birds of San Diego County, California: an annotated check-list. Occ. Papers San Diego Soc. Nat. Hist., no. 10. 49 p.

SCHALDACH, W. J., JR. 1963. The avifauna of

Colima and adjacent Jalisco, México. Proc. West. Found. Vertebr. Zool. 1 (1). [i], 100 p.

SIBLEY, C. G. 1952. The birds of the South San Francisco Bay region. [San Jose, Calif., mimeogr.] 42 [+2] p.

STILES, F. G. 1971. On the field identification of California hummingbirds. Calif. Birds 2:41–54.

STILES, F. G. 1972. Age and sex determination in Rufous and Allen Hummingbirds. Condor 74: 25–32.

SWARTH, H. S. 1914. A distributional list of the birds of Arizona. Pacific Coast Avifauna 10. 133 p.

THOMPSON, A. L. ED. 1964. A new dictionary of birds. Nelson, London, and McGraw-Hill, New York. 928 p.

THOMPSON, M. C. 1962. Noteworthy records of birds from the Republic of Mexico. Wilson Bull. 74:173–176.

VAN ROSSEM, A. J. 1909. Some unrecorded species from Los Coronados Islands, México. Condor 11: 208.

VAN ROSSEM, A. J. 1934. Critical notes on Middle American birds. Bull. Mus. Comp. Zool. 77: 387–490.

VAN ROSSEM, A. J. 1945. The eastern distributional limits of the Anna Hummingbird in winter. Condor 47:79–80.

VAN TYNE, J. 1956. What constitute scientific data for the study of bird distribution? Wilson Bull. 68:63–67.

VAN TYNE, J., AND G. M. SUTTON. 1937. The birds of Brewster County, Texas. Univ. Mich. Mus. Zool., Misc. Publ. 37. 119 p.

WAUER, R. H., AND M. K. RYLANDER. 1968. Anna's Hummingbird in west Texas. Auk 85:501.

WILLETT, G. 1933. A revised list of the birds of southwestern California. Pacific Coast Avifauna 21. 204 p.

WILLIAMSON, F. S. L. 1956. The molt and testis cycles of the Anna Hummingbird. Condor 58: 342–366.

WOODBURY, A. M., C. COTTAM, AND J. W. SUGDEN. 1949. Annotated check-list of the birds of Utah. Univ. Utah Bull. 39, no. 16, Biol. Ser. 11, no. 2. 40 p.

WRIGHT, H. W. 1909. An ornithological trip to Los Coronados Islands, México. Condor 11:96–100.

Accepted for publication 27 September 1974.