

# Phenology, sex ratios, and population trends of *Selasphorus* hummingbirds in central coastal California

Steve N. G. Howell and Thomas Gardali<sup>1</sup>

Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970 USA

Received 17 September 2001; accepted 6 February 2002

**ABSTRACT.** From 1980 to 2000, we mist-netted 2412 Allen's Hummingbirds (*Selasphorus sasin*) and 203 Rufous Hummingbirds (*S. rufus*) at a site in central coastal California. Adult Allen's occurred from late January to early August and juveniles from early April to early September. Overall ratios of female to male Allen's were 2.5:1 for adults, 1:1.1 for juveniles. The breeding season female-to-male ratio for adult Allen's of 6.2:1 probably reflected net placement at riparian edges between nests and feeding areas for females. Adult Rufous occurred as transients from mid-February to early May and late June to mid-August and juveniles from mid June to late September. Overall ratios of female to male Rufous were 2.3:1 for adults in spring, 1:1.1 for juveniles. For adults, there was little evidence for a spring migration peak in Allen's, but a fall migration peak was marked. In contrast, adult Rufous showed a spring migration peak but were rare in fall. The two species' main southbound routes in California (coastal for Allen's, interior for Rufous) may, in combination with temporal separation, help partition nectar resources. Capture rates for both age groups of Allen's Hummingbirds indicated a stable population. Juvenile Rufous showed a significant decline in capture rates, reasons for which are unknown.

**SINOPSIS. Fenología, tasa de sexos y tendencias poblacionales de *Selasphorus* spp. en la parte central de California**

De 1980 al 2000 atrapamos con redes de niebla individuos de varias especies de colibríes en una localidad de la parte central costanera de California. Se atraparon 2412 individuos de *Selasphorus sasin* y 203 de *S. rufus*. Adultos de *S. sasin* se atraparon de finales de enero hasta principios de agosto y juveniles desde principios de abril a principio de septiembre. La tasa de sexos para esta especie fue de 2.5:1 (hembras por machos) en adultos y de 1:1.1 en los juveniles. La tasa de hembras a machos durante la época de reproducción fue de 6.2:1, lo que probablemente es un reflejo de la localización de las redes en habitats riparios que quedan entre las áreas de anidamiento y lugares de alimentación de las hembras. Por su parte los adultos de *S. rufus* son transitorios a la localidad de mediados de febrero a principios de mayo y de finales de junio a mediados de agosto, y los juveniles de mediados de junio a finales de septiembre. La tasa de sexos para ésta otra especie fue de 2.3:1 (hembras a machos) para los adultos y de 1:1.1 para los juveniles. Se encontró poca evidencia de una migración pico durante la primavera para los adultos de *S. sasin*, pero hubo un pico marcado para la migración otoñal. En contraste los adultos de *S. rufus* mostraron un pico migratorio en la primavera, pero resultaron ser raros en el otoño. Las rutas particulares para éstas especies en California (costanera para *S. sasin* y por el interior para *S. rufus*) pueden (en combinación con una separación temporal), producir una separación del uso del recurso néctar. No se encontró cambio en la tendencia de captura de *S. sasin*, por lo que su población se considera estable. Sin embargo, se notó una reducción significativa en la captura de juveniles de *S. rufus* y se desconocen las razones para éste fenómeno.

*Key words:* Allen's Hummingbird, Rufous Hummingbird, migration

The Allen's Hummingbird (*Selasphorus sasin*) is virtually endemic as a breeding species to California. Of the two described subspecies, nominate *sasin* breeds in California and southern Oregon and migrates to Mexico for the non-breeding season, while *sedentarius* is largely resident in southern California (Grinnell and Miller 1944; Mitchell 2000). The Rufous Hummingbird (*S. rufus*) occurs as transient throughout much of California and has bred in the north of the state (Grinnell and Miller 1944; Talmadge 1953; Calder 1993). These

two species are notoriously difficult to distinguish in the field (Howell 2001, 2002) and can be problematic to separate even in the hand (Pyle 1997). Consequently, their status in many regions of California is poorly understood (e.g., Garrett and Dunn 1981; Hamilton and Willick 1996), and Mitchell (2000) noted that large-scale banding studies could help unravel details of *Selasphorus* migration routes and timing. Based on 21 years of mist-net captures, we document phenology, sex ratios, and annual capture rates of Allen's (nominate *sasin*) and Rufous hummingbirds at a site in central coastal California.

<sup>1</sup> Corresponding author. Email: tgardali@prbo.org

## METHODS

From 1980 to 2000, 2412 Allen's Hummingbirds and 203 Rufous Hummingbirds of known age and sex were captured, measured, and marked at the Palomarin Field Station of the Point Reyes Bird Observatory (PRBO), located in the Point Reyes National Seashore, Marin County, California (37°56'N, 122°45'W). For a description of the site, see DeSante and Geupel (1987). Birds were caught in an array of 20 12-m mist nets, 14 of which (30 mm mesh) were set along the edge of riparian woodland in a mixed evergreen forest, with the remaining six (36 mm mesh) located in adjacent coastal scrub. Nets were opened 15 min after local sunrise and left open for 6 h (weather permitting), thus accumulating 120 net h per day. Two to three hummingbird feeders were maintained year-round at the field station buildings, within 10–20 m of one of the mist net locations. We examined the possibility that captures in the nets nearest hummingbird feeders might bias captures and sex ratios. Birds were identified to species, age, and sex by a combination of measurements, plumage characters, and extent of bill grooving (Stiles 1972; Pyle 1997; Yanega et al. 1997). A few birds (<1%) were unidentifiable and are omitted from our data set. We grouped records for all years by age and sex for early (1–10th), mid (11–20th), and late (21st–end) month. Because Allen's Hummingbirds breed at Palomarin, distinguishing transients from breeders was problematic. We considered the main adult migration periods to be February and June–July (Phillips 1975; Mitchell 2000; Howell 2002), and the breeding season to be March to May (Pitelka 1951; PRBO, unpubl. data).

During 1980–88 nets were run three days/week December–March and seven days/week April–November; during 1989–2000, nets were run three days/week December–April and six days/week May–November. Using the program STATA (Stata Corp. 1997) we examined population trends by linear and curvilinear regression, using number of birds captured per 1000 net h to standardize capture rate by netting effort. Net hours were calculated separately for each species by age class between the earliest and latest dates captured (e.g., adult Allen's from 29 January to 3 August). Trends in captures for Allen's Hummingbirds were analyzed

by two time periods to address the change in netting protocol. Adult Rufous Hummingbird captures were considered too few for population trend analysis. Captures of juvenile Rufous were log-transformed to normalize model residuals. We used chi-square tests to examine whether our observed female-to-male sex ratios differed significantly from an expected ratio of 1:1 (Mulvihill et al. 1992). Significance was set at a level of  $P < 0.05$ .

## RESULTS

**Allen's Hummingbird.** *Phenology.* The earliest capture dates for adults ( $N = 121$  males, 309 females) were 29 January (male) and 1 February (female), and there was little evidence of a spring migration peak (Fig. 1a). Captures of adult males increased in mid to late April, were highest during June, and then tapered off sharply; adult female captures increased through April and May, with a second peak in June (Fig. 1a). The latest adult female was caught on 21 July, the latest adult male on 3 August. Juveniles, caught mostly from mid-April onwards, were commonest from mid-May through July, and their numbers dropped off sharply in August (Fig. 1b). Date spans for juveniles were 11 April–1 September (males;  $N = 1031$ ) and 3 April–29 August (females;  $N = 931$ ). Mean latest capture dates for juveniles were 8 August for males and 7 August for females; females were recorded later than males in nine of 21 years.

*Sex ratios.* The overall sex ratio of adults was 2.5 females:1 male, but this varied seasonally. Although the two nets nearest to the feeders contributed 19% of all adult captures, the female to male ratio for adults in those nets was 2.6:1, similar to that for all adult captures. The female to male ratio of 2.3:1 in spring migration (February;  $N = 20$ ) was not significantly biased, but then increased to a significantly biased 6.2:1 ratio in the breeding season (March to May;  $N = 230$ ;  $\chi^2 = 119.97$ ,  $P < 0.05$ ), and dropped to a not significantly biased ratio of 1.2:1 in fall migration (June–July;  $N = 178$ ). The juvenile ratio of females to males appeared more balanced at 1:1.1 but was significantly male biased ( $N = 1766$ ;  $\chi^2 = 4.00$ ,  $P < 0.05$ ). Interannual variation in sex ratio of juveniles was 0.6–1.9 males:1 female and favored males in 13 of 21 years.

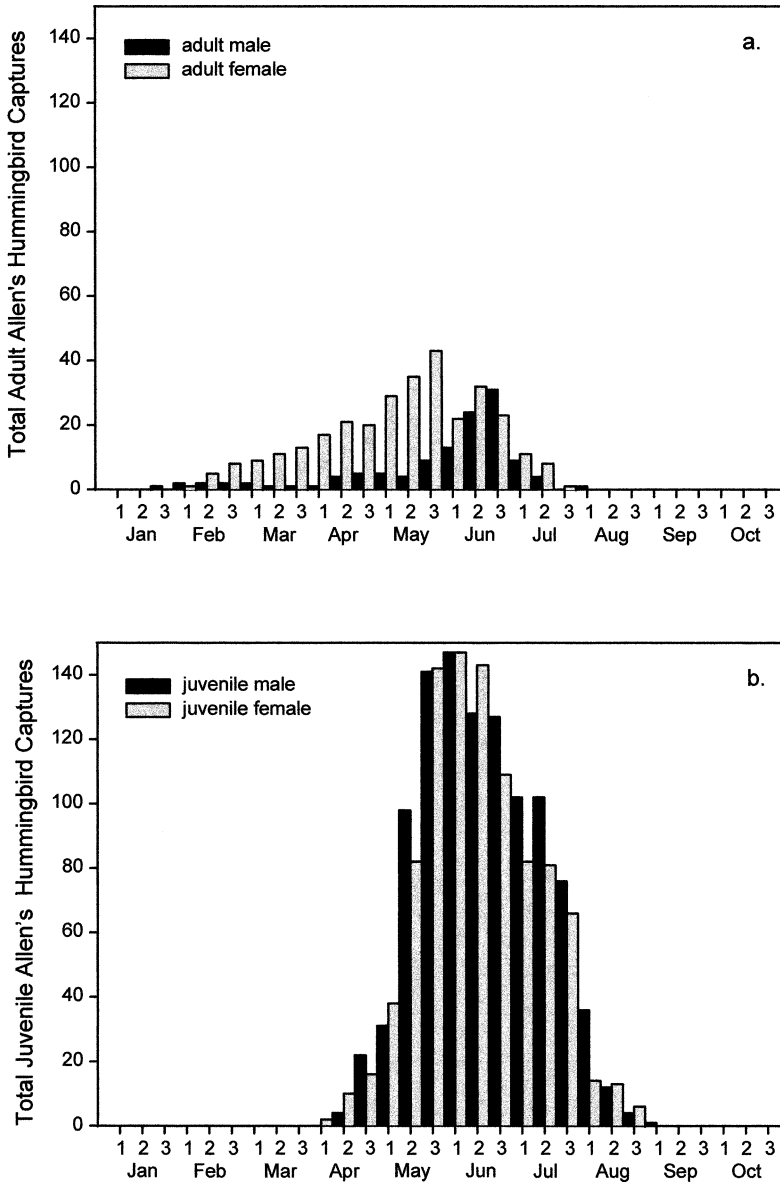


Fig. 1. (a) Total numbers of adult Allen's Hummingbirds captured at Palomar, by 10-day periods, 1980–2000. (b) Total numbers of juvenile Allen's Hummingbirds captured at Palomar, by 10-day periods, 1980–2000. Totals by period are paired either side of tick marks.

*Inter-annual variation and population trends.* Numbers of adults captured per year ranged from 8 to 40 (0.59–1.91/1000 net h) and juveniles from 16 to 216 (0.95–10.32/1000 net h). Annual captures of adults and juveniles were positively correlated ( $r = 0.44$ ,  $P = 0.04$ ). No significant trend was found for adults or juveniles in either time period (Table 1). Over the

entire period, however, juveniles showed a significant decline (Table 1), driven by low capture rates in 1999 and 2000.

**Rufous Hummingbird.** *Phenology.* Adults were caught 2 March–10 May (males;  $N = 17$ ) and 18 February–5 May (females;  $N = 39$ ), with only six fall captures, 24 June–30 August (Fig. 2a). Juveniles (Fig. 2b) occurred 23 June–

Table 1. Regression statistics for adult and juvenile Allen's Hummingbirds at the Palomarin Field Station, Marin County, California, for the time periods 1980–88, 1989–2000, 1980–2000, and for juvenile Rufous Hummingbirds during 1980–2000. Capture data for Rufous Hummingbirds were log-transformed and trend was quadratic.

	1980–88			1989–2000			1980–2000					
	Slope	SE( $\beta$ )	adj. $R^2$	P	Slope	SE( $\beta$ )	adj. $R^2$	P	Slope	SE( $\beta$ )	adj. $R^2$	P
Adult Allen's	-0.056	0.065	-0.03	0.42	0.058	0.038	0.11	0.15	0.007	0.017	-0.04	0.69
Juvenile Allen's	-0.333	0.345	-0.01	0.37	-0.322	0.180	0.17	0.10	-0.20	0.083	0.19	0.03
Juvenile Rufous	—	—	—	—	—	—	—	—	-0.005	0.004	0.25	0.03

23 September (males;  $N = 75$ ) and 18 June–18 September (females;  $N = 66$ ).

*Sex ratios.* For adults in spring the female to male ratio was significantly female biased at 2.3:1 ( $N = 56$ ;  $\chi^2 = 8.69$ ,  $P < 0.05$ ); the sample of fall adults was too small to provide a meaningful ratio. The female to male ratio for juveniles was 1:1.1 ( $N = 141$ ), identical to that for juvenile Allen's Hummingbirds but not significantly male biased due to a smaller sample.

*Inter-annual variation and population trends.* Numbers captured per year ranged from 0–10 adults (0–0.46/1000 net h) and 1–18 juveniles (0.06–0.85/1000 net h). Annual captures of Rufous and Allen's hummingbirds were positively correlated ( $r = 0.47$ ,  $P = 0.03$ ). Juveniles showed a significant curvilinear decline (Table 1, Fig. 3).

## DISCUSSION

**Allen's Hummingbird.** *Phenology.* Our data correspond broadly with what little has been published previously for central California (Ortiz-Crespo 1980; Pyle and Henderson 1991; Shuford 1993). For example, Allen's Hummingbirds typically return to Marin County from late January to early February (Shuford 1993), dates mirrored, but reflected poorly, by mist-net captures (Fig. 1). We have no evidence that males arrived earlier in spring than did females, as reported by Mitchell (2000), but our sample was small. Because of their loud wing buzz, spring males are much more conspicuous than the relatively silent females, and this could account for a perception that males arrive earlier; more data are needed to address this issue. For juveniles we did not detect a tendency for males to remain later than females (Fig. 2), as suggested by Phillips (1975) and Mitchell (2000).

The low number of spring captures for adults, especially males, indicates that few migrate along the immediate coast at this season. Captures of adults increased noticeably in mid-April for males and throughout April and May for females (Fig. 1a). These increases occurred during the breeding season and before what is generally considered the start of fall migration, in mid to late May (Mitchell 2000). Because fall migration dates for migratory Allen's (e.g., Phillips 1975; Mitchell 2000) have been derived from occurrences outside the geographic

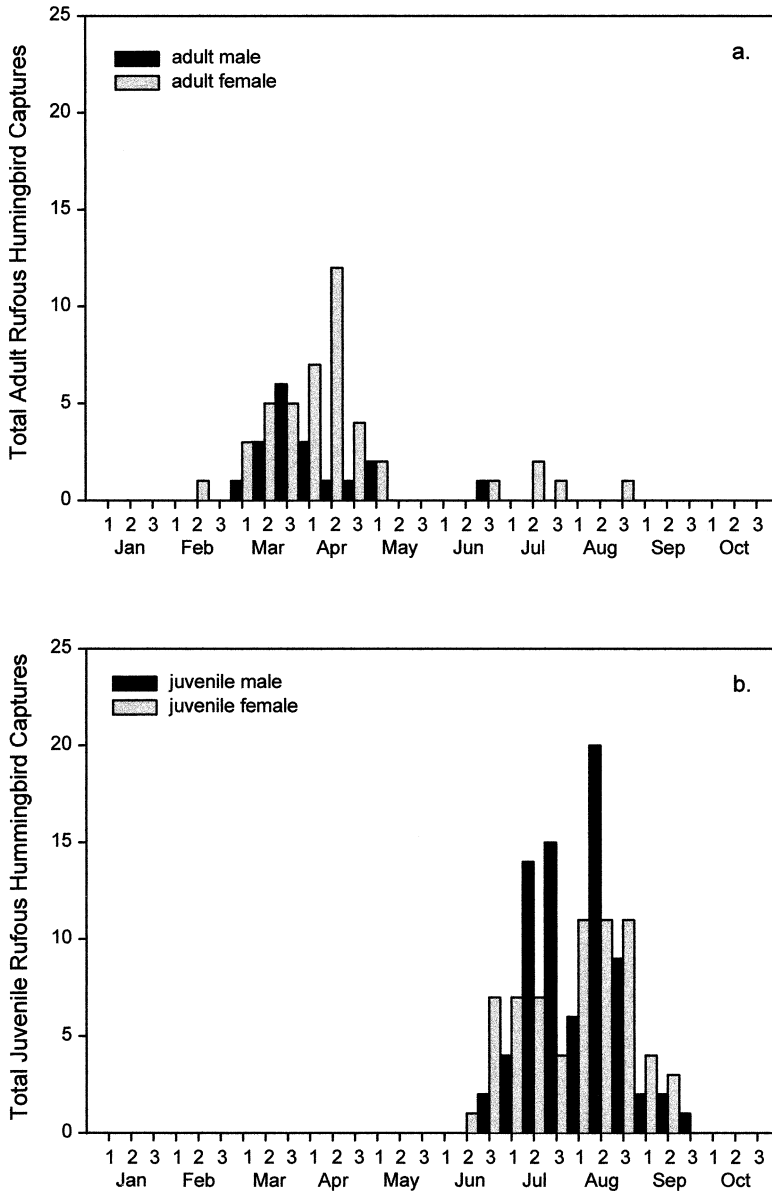


Fig. 2. (a) Total numbers of adult Rufous Hummingbirds captured at Palomarin, by 10-day periods, 1980–2000. (b) Total numbers of juvenile Rufous Hummingbirds captured at Palomarin, by 10-day periods, 1980–2000. Totals by period are paired either side of tick marks.

breeding range, it is possible that southward migration could start within the breeding range in late April and early May. Adult male Allen's typically maintain display territories into early or mid-May (Ortiz-Crespo 1980; S. Howell, pers. obs.), however, which argues against an April increase in male captures being due to migration. The apparent increases from April

onward may be partly due to change in netting protocol (see Methods), i.e., some adults that occurred before April were not captured. The increase in adult male captures also corresponds to the start of juvenile fledging in mid-April, resulting in a greater frequency of agonistic encounters and associated greater mobility of territorial birds at this time (Ortiz-Crespo 1980),

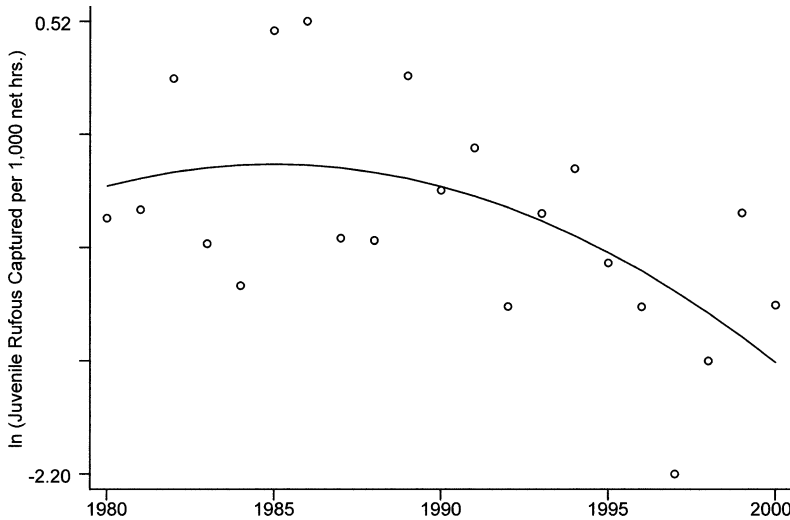


Fig. 3. Trend for juvenile Rufous Hummingbirds at Palomarin Field Station, 1980–2000. Each circle represents log-transformed data for one year; regression line is curvilinear.

which could increase captures. Another consideration could be the changing spatial distribution of flower resources over time. Adult male captures (unlike those of adult females) peaked during the conventional period of southward migration, in June (Fig. 1a).

The peak in adult female captures in May corresponded to the tail end of the main nesting period (Pitelka 1951; PRBO, unpubl. data). It may reflect increased numbers of adults moving to find food for their nestlings, perhaps in combination with an influx of post-breeding (and migrant?) females from adjacent riparian areas where they nested. The coastal scrub at Palomarin has a high density of flowers in May and June that could attract nomadic, post-breeding female Allen's from adjacent habitats with fewer nectar resources. Also, as with adult males, increased agonistic encounters related to the presence of juveniles competing for food resources may have increased captures of adult females. The second peak in adult female captures, in mid-June, corresponded to the conventional southward migration period.

Typically, very few adults of other locally breeding Neotropical migrants are captured at Palomarin in fall migration, e.g., Warbling Vireo (*Vireo gilvus*), Swainson's Thrush (*Catharus ustulatus*), and Wilson's Warbler (*Wilsonia pusilla*) (Johnson and Geupel 1996; Chase et al. 1997; Gardali et al. 2000). Relative to these

species, adult Allen's Hummingbirds showed high fall capture rates, perhaps reflecting the prolonged local flowering season caused by a humid climate moderated by coastal fog.

Phillips (1975) reported on the elliptical migration routes of Allen's and other hummingbirds but did not discuss at which point southbound Allen's move east. Quoting Grinnell and Miller (1944), Mitchell (2000) reported that the fall migratory route of Allen's Hummingbird follows mountains south to take advantage of the summer bloom. Our data show that in central California, many Allen's Hummingbirds migrate south along the coast, and we suspect that most do not swing east until they reach southern California (around 36° south). This accords with Gaines (1988) and D. DeSante (pers. comm.), who have found Allen's Hummingbirds very rare to absent in California's Sierra Nevada. Recent banding studies in the southern Sierra Nevada, however, have found female and immature Allen's to be rare but regular migrants there (D. Mitchell, pers. comm.). Thus while adult males may migrate south through California by a primarily coastal route, the more numerous and later-migrating females and immatures appear to spread inland, presumably in response to late-summer flowering in the mountains (Mitchell, pers. comm.). Birds may then stage during June to July in the mountains of southern California and northern

Baja California, Mexico, before they cross to the Sierra Madre Occidental of northwestern Mexico.

**Sex ratios.** Few data for sex ratios are available for other hummingbird species. For adult Ruby-throated Hummingbirds (*Archilochus colubris*) caught in mist nets, Mulvihill et al. (1992) reported 1.4–4.1 females:1 male, depending on season. Together with our data for Allen's (e.g., 1.2–6.2 females:1 male), this suggests that adult females may genuinely outnumber adult males. However, various factors can contribute to perceived versus real sex ratios. Differential behavior, habitat use, mist-net mesh size, feeder bias, and perhaps migration routes can all influence the sex ratio of captures (Mulvihill et al. 1992).

At Palomarin, adult male Allen's Hummingbird breeding territories were mainly in coastal scrub away from mist-net locations, helping to explain the low incidence of late January to early April captures. Adult females commuted from riparian nesting sites—where there was a high nesting density (PRBO, unpubl. data)—to feeding sites in more open habitats, including feeders, thus crossing the riparian edge where most nets were set. This may help explain the extremely high female:male breeding season ratio. Sex ratios during migration may be more representative of the adult population.

Our spring sample of adults was relatively small but showed a sex ratio of 2.3 females:1 male, compared to the fall ratio for adults of 1.2 female:1 male. This could be interpreted as higher mortality for females than males during the breeding season, the opposite of what Mulvihill et al. (1992) hypothesized for Ruby-throated Hummingbirds. Those authors suggested that relative to females, the male Ruby-throated's smaller size combined with territory defense and display might exact higher tolls during the breeding season. Adult females also expend energy on aggression during feeding, however, and experience the total cost of producing eggs and rearing young. While factors affecting interspecific mortality may differ between Allen's and Ruby-throated hummingbirds, we suggest that sex ratios derived from mist-net captures can be compromised by multiple factors and should be used with caution.

The juvenile sex ratio of 1.1 male:1 female ( $P < 0.05$ ) compares with 1.1 females:1 male for juvenile Ruby-throated Hummingbirds

(Mulvihill et al. 1992), indicating that sex ratios are closer to 1:1 for immatures than adults. For Ruby-throated and Allen's hummingbirds, sex ratios based on mist-net captures changed from close to 1:1 in fall immatures to favoring adult females by spring. This suggests that mortality in immatures is greater for males than females before their first breeding season. An examination of potential between-sex differences in behavior and ecology on the non-breeding grounds could address this possibility.

**Inter-annual variation and population trends.** The significant positive correlation in annual captures of adults and juveniles suggests that local factors, such as weather and flowering phenology, determine annual capture rates. Thus the wide range of variation of inter-annual captures probably does not reflect population status. From Breeding Bird Survey (BBS) data, Sauer et al. (2001) reported no trend survey-wide for Allen's Hummingbirds during 1966–2000. Mitchell (2000) noted, however, that hummingbirds may not be well sampled by the BBS (e.g., many routes are run after male Allen's have begun departing from the breeding grounds). Our data show no significant trends for adult Allen's Hummingbirds, and only a weak negative trend for juveniles.

**Rufous Hummingbird.** *Phenology.* Other authors have reported this species as commoner in spring than fall in coastal California (e.g., Garrett and Dunn 1981; Pyle and Henderson 1991). This was true for adults in our data set, but overall we found more Rufous Hummingbirds in fall ( $N = 147$ ) than spring ( $N = 56$ ). This discrepancy may be due to the difficulty of identifying immatures to species in the field. The Palomarin spring date span of 18 February to 10 May compares to that of 15 February to 21 May for Rufous Hummingbirds on Southeast Farallon Island, 32 km off the coast from Palomarin (37°42'N, 123°00'W; Pyle and Henderson 1991). A Farallon report for 4 June (Pyle and Henderson 1991) may be in error (P. Pyle, pers. comm.). The spring migration peak at Palomarin contrasted with the pattern shown by adult Allen's Hummingbirds, while in fall adult Allen's showed a marked migration peak at Palomarin but adult Rufous were very rare (Figs. 1a, 2a). This supports the use of an inland (mostly montane) southbound route for most Rufous Hummingbirds (Phillips 1975; Calder 1993). The two species' main south-

bound routes in California (coastal for Allen's, interior for Rufous) may, in combination with temporal separation, help partition nectar resources.

The fall date span for captures at Palomarin (18 June–23 September;  $N = 147$ ) compares with 19 July–10 October ( $N = 156$ ; only one in October) for Rufous Hummingbirds recorded on Southeast Farallon Island (Pyle and Henderson 1991). The relatively early arrival dates for juveniles at Palomarin are noteworthy. During 18–29 June there were ten carefully documented records of juvenile Rufous Hummingbirds from Palomarin, in five different years from 1980 to 1988. In most years, however, arrival dates were in mid July, which agrees with Farallon data and other sources. For example, Grinnell and Miller (1944) noted that adult male Rufous Hummingbirds appeared in numbers in California in late June, followed in two to three weeks by females and young.

*Sex ratios.* Our samples for this species were relatively small, but spring adults showed a significantly female-biased ratio of 2.3 females:1 male ( $P < 0.05$ ), the same as the non-significant ratio of spring adult Allen's Hummingbirds. For juveniles, the non-significant sex ratio of 1.1 male:1 female Rufous is the same as the significantly male-biased ratio for juvenile Allen's.

*Inter-annual variation and population trends.* The positive correlation of annual captures of all Rufous and Allen's hummingbirds supports local factors as the cause of large-scale inter-annual variation in numbers of birds netted (see above).

Sauer et al. (2001) noted a significant survey-wide trend for Rufous Hummingbirds of  $-2.6\%$  per year ( $P = 0.01$ ) during 1966–2000. Our data indicate that juveniles appear to be declining at Palomarin (Table 1). Reasons for a potential decline are unknown. Calder (1993) noted that increased deforestation should yield more food resources in successional habitats, which might be expected to increase numbers of this species. Although successional habitats are used for male territories and by feeding birds (S. Howell, pers. obs.), deforestation may degrade wooded nesting habitat, which could adversely affect populations. Studies of Rufous Hummingbirds on the breeding grounds could address habitat-related issues relative to population density and nesting success.

#### ACKNOWLEDGMENTS

We thank the numerous field biologists who collected data; David F. DeSante and Geoff Geupel for directing the long-term mist-netting program at the Palomarin Field Station during the years of this study; the Point Reyes National Seashore for their continued support and cooperation; and Dorothy Hunt and the members and board of PRBO for financial support. Peter Pyle provided data from Southeast Farallon Island, and Wilma Follette contributed helpful discussion concerning flowering phenology in California. The manuscript benefited by discussion and review from Grant Ballard, Ryan Burnett, Dan Barton, David F. DeSante, Geoff Geupel, Aaron Holmes, Donald E. Mitchell, Peter Pyle, W. Dave Shuford, and Jennifer D. White. This is PRBO contribution number 979.

#### LITERATURE CITED

- CALDER, W. A. 1993. Rufous Hummingbird (*Selasphorus rufus*). In: The birds of North America (A. Poole, and F. Gill, eds.), no. 53. Academy of Natural Sciences, Philadelphia, PA and American Ornithologists' Union, Washington, D.C.
- CHASE, M. K., N. NUR, AND G. R. GEUPEL. 1997. Survival, productivity, and abundance in a Wilson's Warbler population. *Auk* 114: 354–366.
- DESANTE, D. F., AND G. R. GEUPEL. 1987. Landbird productivity in central coastal California: the relationship to annual rainfall, and a reproductive failure in 1986. *Condor* 89: 636–653.
- GAINES, D. 1988. Birds of Yosemite and the East Slope. Artemesia Press, Lee Vining, CA.
- GARDALI, T., G. BALLARD, N. NUR, AND G. R. GEUPEL. 2000. Demography of a declining population of Warbling Vireos in coastal California. *Condor* 102: 601–609.
- GARRETT, K., AND J. DUNN. 1981. Birds of southern California: status and distribution. Los Angeles Audubon Society, Los Angeles, CA.
- GRINNELL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. *Pacific Coast Avifauna* 27.
- HAMILTON, R. A., AND D. R. WILLICK. 1996. The birds of Orange County, California: status and distribution. Sea and Sage Press, Irvine, CA.
- HOWELL, S. N. G. 2001. Field identification of female Allen's and Rufous hummingbirds. *Western Birds* 32: 97–98.
- . 2002. Hummingbirds of North America: the photographic guide. Academic Press, San Diego, CA.
- JOHNSON, M. D., AND G. R. GEUPEL. 1996. The importance of productivity to the dynamics of a Swainson's Thrush population. *Condor* 98: 133–141.
- MITCHELL, D. E. 2000. Allen's Hummingbird (*Selasphorus sasin*). In: The birds of North America (A. Poole, and F. Gill, eds.), no. 501. The Birds of North America Inc., Philadelphia, PA.
- MULVIHILL, R. S., R. C. LEBERMAN, AND D. S. WOOD. 1992. A possible relationship between reversed sexual size dimorphism and reduced male survivorship

- in the Ruby-throated Hummingbird. *Condor* 94: 480–489.
- ORTIZ-CRESPO, F. I. 1980. Agonistic and foraging behavior of hummingbirds co-occurring in central coastal California. Ph.D. dissertation, University of California, Berkeley, CA.
- PHILLIPS, A. R. 1975. The migrations of Allen's and other hummingbirds. *Condor* 77: 196–205.
- PITELKA, F. A. 1951. Ecologic overlap and interspecific strife in breeding populations of Anna and Allen hummingbirds. *Ecology* 32: 641–661.
- PYLE, P. 1997. Identification guide to North American birds, part 1. Slate Creek Press, Bolinas, CA.
- , AND R. P. HENDERSON. 1991. The birds of Southeast Farallon Island: occurrence and seasonal distribution of migratory species. *Western Birds* 22: 41–84.
- SAUER, J. R., J. E. HINES, AND J. FALLON. 2001. The North American Breeding Bird Survey, results and analysis 1996–2000, version 2001.2. U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD.
- SHUFORD, W. D. 1993. The Marin County breeding bird atlas: a distributional and natural history of coastal California. Bushtit Books, Bolinas, CA.
- STATA CORP. 1997. Stata Statistical Software: Release 5.0. Stata Corporation, East College Station, TX.
- STILES, F. G. 1972. Age and sex determination in Rufous and Allen's hummingbirds. *Condor* 74: 25–32.
- TALMADGE, R. R. 1953. Rufous Hummingbird nesting in California. *Condor* 55: 155–156.
- YANEGA, G. M., P. PYLE, AND G. R. GEUPEL. 1997. The timing and reliability of bill corrugations for ageing hummingbirds. *Western Birds* 28: 13–18.