

## FEMALE-BIASED SEX RATIO IN A WINTERING POPULATION OF RUBY-CROWNED KINGLETS

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**ABSTRACT.**—Many avian species have demonstrated differential wintering of the sexes, either latitudinally across their wintering range or by habitat. We examined the large numbers of wintering Ruby-crowned Kinglets (*Regulus calendula*) captured as part of a long term constant effort mist-netting program in coastal California to determine if such a pattern was evident in this population. Data from 1976 to 1997 revealed a consistent and significant female bias, with a mean of 2.13 ( $\pm$  0.31 SE) females caught per male. We evaluated the possibility that this bias resulted from differential capture probabilities of the sexes, and found no difference in recapture probabilities between males and females. The sex ratio was biased toward females in both scrub and mixed evergreen forest habitats, but significantly more skewed in the former (3.68:1 versus 1.91:1). We also examined captures over a two-year period from nearby stations in riparian forest; the sex ratio was least skewed in this habitat (1.37:1). Considered together with the latitudinal differential distribution of this species observed in eastern and central North America, our data suggest that Ruby-crowned Kinglets may not only be geographically but also ecologically segregated according to sex across their wintering range. Received 28 Sep. 2000, accepted 29 Aug. 2001.

Loss and degradation of wintering habitat has been proposed as a limiting factor for many of North America's migratory passerines (Rappole and McDonald 1994). However, little is known about the distribution and ecology of many species on their wintering grounds. Differential distribution of males and females across their winter range may result from geographic or habitat segregation. Such differential distribution may lead to differences in survival between the sexes (Marra and Holberton 1998). If females (or males) are excluded from prime habitat, such exclusion may result in poorer condition or even higher mortality for individuals occupying the lower quality habitat.

Overwintering sexual segregation may be common but has been examined in few passerines (Lynch et al. 1985, Kerlinger and Lein 1986). Passerines that have exhibited sexual segregation on their wintering grounds include the Dark-eyed Junco (*Junco hyemalis*; Ketterson and Nolan 1976, Nolan and Ketterson 1990, Swanson 1992), House Finch (*Carpodacus mexicanus*; Belthoff and Gauthreaux 1991), White-crowned Sparrow (*Zonotrichia leucophrys*; Emlen 1943, Morton 1984), Snow Bunting (*Plectrophenax nivalis*; Smith et al.

1993), Hooded Warbler (*Wilsonia citrina*; Lynch et al. 1985), and American Redstart (*Setophaga ruticilla*; Marra et al. 1993). These include species that are segregated latitudinally (Ketterson and Nolan 1976, Belthoff and Gauthreaux 1991), by habitat (Marra et al. 1993, Lynch et al. 1985), and by altitude (Smith et al. 1993). For a review of the hypotheses that explain this spatial segregation, see Myers (1981) and Belthoff and Gauthreaux (1991).

Ruby-crowned Kinglets (*Regulus calendula*) are another species with a differential wintering distribution over at least part of their wintering range (Fairfield and Shirokoff 1978, Swanson et al. 1999). Along the West Coast, they winter from the Washington-Canada border to the southern tip of Baja California, Mexico (Ingold and Wallace 1994). Large numbers of Ruby-crowned Kinglets winter within the Point Reyes National Seashore in central coastal California, where this study took place. Most migrate to the area from the coniferous forests of Alaska and British Columbia (Phillips 1986). Understanding more about the wintering ecology of this species is of particular interest as substantial population reductions have been found to occur on the wintering grounds (Laurenzi et al. 1982).

We investigated the occurrence of a differential wintering distribution in this species using 21 years of capture data from an ongoing

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constant effort mist-netting operation in the Point Reyes National Seashore, California. We examined the overall sex ratio of total captures from this station and examined yearly and monthly variation. We addressed the possibility that the bias may have resulted from differences in capture probability between the sexes by examining recapture probabilities (i.e., probability a bird was recaptured during the same year as its initial capture). We then compared the sex ratios between the two habitat types (mixed evergreen forest and coastal scrub) in which the nets were located, and also examined the sex ratio of captures from nearby mist-netting stations in a third habitat type (riparian) for comparison.

### STUDY AREA AND METHODS

Constant effort mist netting was conducted between 1976 and 1997 at Point Reyes Bird Observatory's Palomarin Field Station (37° 56' N, 122° 45' W) in the Point Reyes National Seashore, Marin County, California. Twenty 12-m mist nets were permanently installed at 14 sites at or near an ecotone between forest and scrub. Eight net sites (30 mm mesh size, six consisting of two vertically stacked nets) were located in a mixed evergreen forest composed primarily of coast live oak (*Quercus agrifolia*), California bay (*Umbellularia californica*), Douglas fir (*Pseudotsuga menziesii*), and California buckeye (*Aesculus californicus*). The other six sites (36 mm mesh size) were located in the adjacent coastal scrub in which the predominant plant species were coyote bush (*Baccharis pilularis*), California sagebrush (*Artemisia californica*), bush monkeyflower (*Mimulus aurantiinus*), poison oak (*Rhus diversiloba*), and California blackberry (*Rubus ursinus*). Mesh size differed between forest and scrub because the species that generally are more common in the forest (e.g., kinglets, warblers, and chickadees) are smaller than those most common in the scrub (e.g., sparrows). Nets were operated 6–7 days per week, May through November, and 3 days per week, December through April. Nets were opened 15 min after local sunrise and remained open for 6 h, weather permitting. For early years (1976–1979), when nets occasionally were open longer, only the first 6 h of data were included in the analyses.

During the winters of 1995–1996 and 1996–1997, mist netting also was conducted at three riparian sites in west Marin County, one which was 4 km from Palomarin, and two that were 18 km away and within the Point Reyes National Seashore. Habitat was primarily deciduous willow (*Salix* spp.) and alder (*Alnus rubra*) riparian forest. Ten nets (36 mm mesh size) were operated once every 7–10 days at each of these sites; otherwise, protocol was consistent with that at Palomarin. Except when specified, all analyses included only data from the Palomarin Field Station.

Ruby-crowned Kinglets were sexed in the hand by the presence (male) or absence (female) of many red feathers in the crown (Pyle et al. 1987). Fewer than 1% of the total captures were not sexed and they were excluded from the analyses. Although differential wintering distributions also have been shown for age classes in some species (Gauthreaux 1978, Nolan and Ketterson 1990), we were unable to examine age specific effects as by arrival time on their wintering grounds most hatching year birds had completed skull pneumatization and were not differentiated from older birds, and relatively few individuals could be aged with rectrix shape criteria (Pyle et al. 1987).

We restricted our analyses to captures during the winter months (November through February) to reduce the influence of transient migrants on our results; some individuals captured during early November may still be migrating through the area (Small 1994). We included only initial captures of each individual in all analyses except the calculation of within-season recapture probabilities. We examined the overall, yearly, and monthly ratios of female to male Ruby-crowned Kinglets captured during the winter at the Palomarin Field Station from 1976 to 1997. We analyzed the sex ratio by determining for each month within each year the mean proportion of captures that were female, weighted by the monthly sample size. We then converted this proportion to a ratio of female captures per male for presentation.

Our preferred analytic method, where the sample size was large, was that of linear models (Neter et al. 1990); in this case, we used the monthly proportion of females as the unit of analysis. Such analysis assumed that each monthly ratio was statistically independent of ratios obtained for other months, which we feel is a reasonable assumption. We preferred not to make the assumption that each individual capture was statistically independent of all others, as would be required by the Pearson correlation or *G* test (Sokal and Rohlf 1995). Such an assumption would be violated if there were social or competitive interactions among individuals. However, in a few cases, monthly data were either unavailable or the number of data points (i.e., months) were few, as was the case when comparing nets in scrub and forest habitat with nets in riparian habitat (only eight months of riparian data available). In this case we report both results of linear models and *G* tests and present 95% binomial confidence intervals for the proportion of females captured, to examine departure from 50%. We used linear regression analysis to examine trends in sex ratio across months (for all years combined) and ANOVA to examine monthly variation. We used linear and quadratic regression to examine yearly trend in the sex ratio and ANOVA to test for unspecified variation among years. All statistical analyses were carried out with STATA 6.0 (Stata Corp. 1999).

A biased sex ratio may reflect sex specific differences in capture probability rather than an actual difference in the abundance of males and females. Because we could not measure capture probability di-

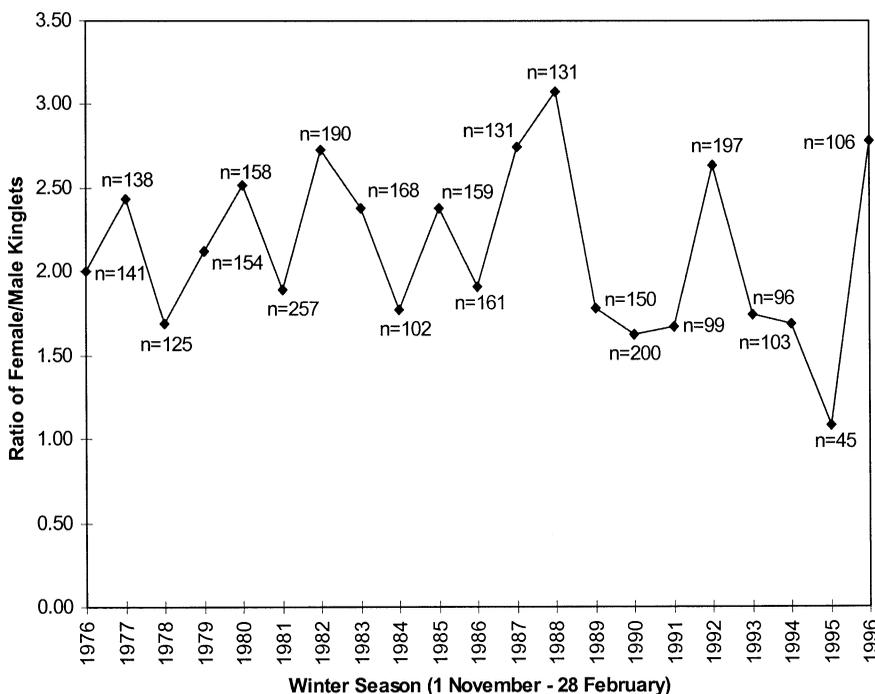


FIG. 1. Ratio of female to male Ruby-crowned Kinglets banded at the Palomarin Field Station, Marin County, California, during winter, 1976 to 1997. Year corresponds to November and December of each winter season.

rectly, we instead compared the observed same-season recapture probabilities of each sex with a  $G$  test (i.e., log-likelihood ratio test; Lebreton et al. 1992). Such analysis carried the assumption that the capture of an individual during a given winter was independent of whether other individuals also were recaptured.

We evaluated whether or not the female bias occurred in both habitat types (coastal scrub or mixed evergreen forest) at Palomarin, and compared the sex ratio of captures from each habitat using ANOVA (Neter et al. 1990). We used only 20 years of capture data for this analysis, as our records did not indicate habitat for net locations during the first winter (1976–1997). For the two winters in which riparian sites were monitored (1995–1996 and 1996–1997), we determined the proportion of captures that were female in riparian habitat, and then compared that proportion to those in Palomarin's coastal scrub and mixed evergreen woodland nets from those same two years. We also compared recapture probability of birds caught in nets in riparian habitat with birds captured in coastal scrub and mixed evergreen woodland habitat.

## RESULTS

Between 1 November and 29 February, 1976–1997, 1630 female (1.20/100 net-h) and 767 male (0.57/100 net-h) Ruby-crowned Kinglets were captured at the Palomarin Field

Station. The mean proportion of total captures that were female (over all years and weighted by monthly sample size) was  $0.680 \pm 0.010$  SE ( $t = 17.89$ ,  $df = 82$ ,  $P < 0.0001$  for deviation from 50% female captures). This is equivalent to a ratio of  $2.13 \pm 0.31$  SE females per male. In all years more females than males were captured (Fig. 1). We found no significant variation among the 21 years ( $F_{20,62} = 1.07$ ,  $P = 0.41$ ), nor any linear or quadratic trends among years ( $P > 0.6$  for each,  $F$  tests).

We found no significant variation in the sex ratio among the four months, either by pooling data across years ( $F_{3,79} = 1.69$ ,  $P = 0.18$ ) or by controlling for differences among years ( $F_{3,59} = 1.67$ ,  $P = 0.18$ ). Mean monthly ratios of capture during November, December, January, and February were fairly similar:  $2.08 \pm 0.04$  ( $n = 1462$ ),  $2.23 \pm 0.08$  ( $n = 431$ ),  $2.24 \pm 0.10$  ( $n = 316$ ), and  $2.13 \pm 0.09$  ( $n = 187$ ), respectively. No linear trend in sex ratio was apparent, by either pooling data across years ( $t = 1.48$ ,  $P = 0.14$ ) or by controlling for differences among years while testing for a trend across months ( $t = 1.66$ ,  $P = 0.10$ ).

TABLE 1. Sex ratio of Ruby-crowned Kinglets caught in coastal scrub and mixed evergreen forest nets at the Palomarin Field Station, Marin County, California, between November and February, 1977–1997.

	Habitat type of net location	
	Mixed evergreen forest	Coastal scrub
Number of females banded	1207	331
Number of males banded	633	90
Ratio females/male	1.91:1	3.68:1
Proportion ( $\pm$ SE) female	0.656 $\pm$ 0.011	0.786 $\pm$ 0.020
95% C.I.	0.633–0.679	0.747–0.825

Males and females did not differ significantly in their likelihood of being captured more than once within a winter season ( $G = 0.094$ ,  $df = 1$ ,  $P = 0.76$ ). Over the 21 years, 24.8% of female and 25.4% of male Ruby-crowned Kinglets were recaptured at least once within a season. The yearly recapture rate was 16.4–45.7% for females and 9.1–50.0% for males. During 11 years the percentage of males recaptured was higher than that of females, and during 10 years the percentage of females recaptured was higher. In only one of 21 years was this difference in percentages of male and female recaptures significant (1980), with proportionately more females than males recaptured (26.3% versus 9.1%;  $G = 6.35$ ,  $df = 1$ ,  $P = 0.012$ ). However, after correcting for multiple comparisons, the difference that year was not significant ( $P = 0.22$ ; Sidak correction).

While nets in both coastal scrub and mixed evergreen forest yielded a higher number of female than male Ruby-crowned Kinglet captures (Table 1), the female bias was nearly twice as great in the scrub than in the forest over the 20 years examined ( $F_{1,139} = 28.4$ ,  $P < 0.0001$ ). The female-biased sex ratio was significant for both habitats (forest:  $t = 7.96$ ,  $P < 0.001$ ; scrub:  $t = 9.13$ ,  $P < 0.001$ ).

In contrast, in the riparian habitat (7.31 cap-

tures/100 net-h) we found, for the two years examined, a female-biased sex ratio of 1.37 to 1, lower than that of both Palomarin habitat types over the 20-year study period, but nevertheless significantly different from 1:1 (95% C.I. for proportion of females was 0.509–0.644; Table 2). Examining those two winters only, we found a significant difference between the sex ratios in riparian and scrub captures ( $t = 2.46$ ,  $P = 0.032$ ) and between evergreen forest and scrub ( $t = 3.39$ ;  $P = 0.006$ ), but not between riparian and mixed evergreen forest ( $t = 0.30$ ,  $P = 0.77$ ). These statistical results were confirmed with  $G$  tests (Table 2). During one of those two years (1995–1996) the number of individuals captured and the sex ratio were lowest of all 21 years at Palomarin. Finally, we examined recapture probability for males and females in riparian nets: overall, 29.1% of females and 22.4% of males were recaptured ( $G = 1.45$ ,  $df = 1$ ,  $P = 0.23$ ), similar to what was observed for nets in the scrub and mixed evergreen forest habitat.

DISCUSSION

Significantly more female than male Ruby-crowned Kinglets were captured during winter at the Palomarin Field Station. We attempted to determine if the apparently skewed sex ra-

TABLE 2. Proportion of Ruby-crowned Kinglet captures that were female in the three central coastal California habitats during the winters of 1995–1996 and 1996–1997. Pairwise comparisons (all  $df = 1$ ): riparian forest versus mixed evergreen forest,  $G = 0.15$ ,  $P = 0.77$ ; riparian forest versus coastal scrub,  $G = 12.58$ ,  $P < 0.001$ ; mixed evergreen forest versus coastal scrub,  $G = 8.54$ ,  $P = 0.003$ .

Habitat	Number of captures	Proportion female	Number of months	95% C.I.
Riparian forest	218	0.578 (Ratio = 1.37:1)	8	0.509–0.644
Mixed evergreen forest	83	0.602 (Ratio = 1.51:1)	8	0.489–0.708
Coastal scrub	45	0.844 (Ratio = 5.41:1)	5	0.705–0.735

tio was influenced by factors other than a difference in abundance, as a biased capture ratio may result from greater movement of individuals of one sex throughout its wintering range, differences in daily activity levels between the sexes (Holloway and Edwards 1989), size dimorphism, or a vertical distribution of the sexes. Mesh sizes of nets at this station are unlikely to affect capture rates of this nearly monomorphic species (Ingold and Wallace 1994). The capture rate was nearly equal between the sexes at our two, single, lower unstacked forest nets, suggesting that the skewed ratio is not due to males foraging higher than females; however, sample size was low (40 females to 44 males).

Differences in overall sex ratio also could arise at hatching (Maynard Smith 1978), fledging, or a later stage of life (Spear et al. 1987). However, it would be unexpected for this passerine species to have as unbalanced an overall sex ratio as we report here (for review see Maynard Smith 1978). Our recapture results suggest that males and females have an equal capture probability. Thus, we conclude that the observed sex ratio reflects a true difference in the number of male and female Ruby-crowned Kinglets wintering in the area.

It is possible that the Ruby-crowned Kinglet population wintering in the Point Reyes National Seashore is not female biased, but that the males occur primarily in a habitat other than the ones studied. The difference in sex ratios observed between scrub and evergreen forest nets and between scrub and riparian forest nets can most parsimoniously be attributed to segregation. With respect to the geographical wintering distribution of this species in eastern and central North America (Swanson et al. 1999), the difference in sex ratio between habitats in coastal California suggests that male and female Ruby-crowned Kinglets may be not only geographically but also ecologically segregated across their wintering grounds. The habitats included in this study are the predominant habitat types in the area (DeSante and Geupel 1987, Shuford and Timossi 1989); we therefore believe that we are observing both geographical and habitat segregation at the local level. Although speculative at this point, it is possible that individuals of the dominant sex are excluding individuals of the other sex from higher quality habitat.

A similarly skewed ratio was found at a central coastal California winter banding site in Monterey County (1.84 females per male,  $n = 803$ , November through February, 1992–2001;  $G = 35.60$ ,  $df = 1$ ,  $P < 0.001$ ; Big Sur Ornithological Lab. unpubl. data). In contrast, a ratio near unity was found at another California site in Santa Clara County (1.17 females per male,  $n = 374$ , November through February, 1982–2001;  $G = 1.21$ ,  $df = 1$ ,  $P = 0.27$ ; San Francisco Bay Bird Observatory unpubl. data).

More study is needed to determine Ruby-crowned Kinglet migratory routes (Ingold and Wallace 1994) and to ascertain where the presumed male component to this population winters. This subject also is of particular interest as analysis of 21 years of fall migration data from the Palomarin Field Station revealed a significant negative trend in Ruby-crowned Kinglet captures (G. Ballard, G.R.G., and N.N. unpubl. data). Because human-induced change to wintering grounds has been suggested as a primary factor behind the decline of many migratory passerines (Rappole and McDonald 1994), more attention needs to be given to the wintering ecology of Ruby-crowned Kinglets and other songbirds.

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