

DIFFERENCES IN MIGRATORY TIMING AND ENERGETIC CONDITION AMONG SEX/AGE CLASSES IN MIGRANT RUBY-CROWNED KINGLETS

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ABSTRACT.—Ruby-crowned Kinglets, *Regulus calendula*, are small temperate zone passerine migrants that breed in conifer forests of Canada and the western United States and winter along the west coast and southern United States into Mexico. Previous studies have revealed that male kinglets precede females during spring migration and that females precede males during fall migration at various sites in eastern North America. We used mist net capture data to document sex/age structure, fat loads, and morphometrics of kinglets passing through southeastern South Dakota during spring and fall migrations from 1992–1995. Males migrated significantly earlier than females in spring; median passage dates differed by at least 8 days. These data are consistent with U.S. Geological Survey Bird Banding Laboratory records for central and eastern North America, which indicate that passage of males before females during spring migration is a widespread phenomenon. Bird Banding Laboratory data also indicate that males winter significantly farther north than females. We tested whether the differential winter distribution of the sexes could account for the differential pattern of spring migration and found that differential winter distributions do not fully account for the differential timing of spring migration between the sexes. Sex-specific migration rates do not differ over the entire spring migration route, so differences in the onset of migration apparently contribute to differential spring migration. Males migrated significantly later in the fall than females, with median dates in southeastern South Dakota differing by 7 days. We also examined whether differences in energetic condition were associated with differences in migratory timing. Visible fat scores did not differ between males and females in spring, although males had a significantly higher mean condition index (mass/wing chord). Sexes within the same age class did not differ in visible fat scores in fall, but adults tended to be fatter than juveniles, significantly so in some cases. No significant differences in condition index were apparent among sex/age classes in fall, although the adult-juvenile difference approached significance ($P < 0.09$), with adults having higher values. This tendency toward elevated fat and condition index in adults relative to juveniles in fall is consistent with more efficient foraging by adults than by inexperienced juveniles at migratory stopover sites, although differences in predation pressure or migratory routes and destinations might also be involved. Received 12 May 1998, accepted 24 Oct. 1998.

Differential timing of migration of sexes and/or age classes has been reported for numerous birds (see Gauthreaux 1982, Ramos 1988 for reviews). For passerine birds, males generally precede females in spring, but the timing of migration in fall is more complex and varied between sexes or age classes (see Hall 1981, Gauthreaux 1982, Francis and Cooke 1986, Ramos 1988, Nolan and Ketterson 1990, Hussell 1991, Winker and Rappole 1992). Earlier passage of males than females in spring presumably relates to advantages in territory acquisition that accrue to those individuals arriving early on the breeding grounds, regardless of whether this early arrival results from sexual differences in wintering areas, departure dates, or rates of migration (Myers 1981, Chandler and Mulvihill

1990). Differential timing of fall migration may result from differences in departure dates or rates of migration as a result of ecological or physiological factors (e.g., juvenile development, parental responsibilities, molt, fat deposition), and/or from differential distribution of age/sex classes throughout the wintering range (Gauthreaux 1982, Ketterson and Nolan 1976, Morton 1984, Prescott and Middleton 1990, Woodrey and Chandler 1997).

Ruby-crowned Kinglets, *Regulus calendula*, are small passerines breeding in coniferous or mixed coniferous-deciduous forests over most of northern and western North America and wintering throughout the western and southern United States, Mexico, and south to Guatemala (American Ornithologists' Union 1983). The winter range is apparently restricted to regions with a relatively mild winter climate (Lepthien and Bock 1976, Root 1988). Differential timing of migration in males and females has been reported from Iowa (Crim 1976) and Ontario (Fairfield and Shirokoff

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1978), but migration timing of sexes in the Great Plains has not been previously reported. In addition, male kinglets apparently winter farther north, on average, than females (Fairfield and Shirokoff 1978), but the extent to which differences in winter distribution affect differential migration is unknown. No previous study has been attempted to define the relative roles of geographic origin, departure dates, and rates of migration in shaping differential migration patterns in kinglets.

We used capture data from spring and fall migration periods from 1992–1995 in southeastern South Dakota to document patterns of migratory movement in Ruby-crowned Kinglets and to determine whether timing of migration and energetic condition differed between sexes in either season. We compared these results with banding data from the U.S. Geological Survey Bird Banding Laboratory (BBL) for central and eastern North America (east of 107° W longitude) to determine if patterns of migration between sexes in southeastern South Dakota are consistent with migratory patterns in Ruby-crowned Kinglets in eastern North America. We also tested the hypothesis that differential winter distributions could fully account for differential migratory timing.

METHODS

Collection of capture data.—Banding was conducted during spring and fall migration from 1992–1995 at four deciduous woodland study sites in southeastern South Dakota. Two sites were located in riparian habitats along the Missouri River (42° 45' N, 97° 00' W; and 42° 46' N, 97° 07' W), one study site was in a riparian woodland along the Big Sioux River (42° 45' N, 96° 37' W), and one study site included both riparian and upland woodlands along Brule Creek (42° 55' N, 96° 46' W), a tributary of the Big Sioux River. Riparian habitats along the Missouri River consisted of deciduous forest dominated by cottonwood (*Populus deltoides*), boxelder (*Acer negundo*), American elm (*Ulmus americana*), mulberry (*Morus alba*), and dogwood (*Cornus* spp.). The Big Sioux River site was dominated by boxelder, silver maple (*Acer saccharinum*), and cottonwood. The riparian forest at the Brule Creek site consisted mainly of boxelder and American elm, while the upland forest was dominated by bur oak (*Quercus macrocarpa*) with American elm and hackberry (*Celtis occidentalis*) also present. The Missouri River study sites have a generally west-east orientation, while the Big Sioux River and Brule Creek sites are oriented north-south. Extensive deciduous woodlands in this area of South Dakota, and indeed over

most of the northern Great Plains, are mainly restricted to river courses (South Dakota Ornithologists' Union 1991).

Kinglets were captured using mist nets during spring (15 April–26 May) and fall (5 September–2 November) migration periods. Capture dates were chosen to coincide with the major migratory movements for Neotropical migrants, not kinglets specifically, so the distribution of capture effort did not cover the kinglet migration evenly. However, the bulk of the kinglet migration through South Dakota occurs during our capture periods (South Dakota Ornithologists' Union 1991). From 15 April through 26 May in spring and from 5 September to 5 October in fall, nets were opened daily and cycled on a 4 day rotation among the four study sites so that each study site was sampled every 4 days. Later in the fall, nets were not opened every day and most capture effort was concentrated at the Brule Creek study site. We erected 2–7 mist nets (10 m × 2.6 m, 30 mm mesh) each day, depending on weather and available personnel. Net placement at the various study sites was consistent among seasons and years. We opened the nets at sunrise and nets remained open until approximately 11:00 CST during both spring and fall migration. Upon capture we measured the bird's mass to the nearest 0.1 g with an Ohaus Model LS200 balance, unflattened wing chord to the nearest 0.1 mm, and visible fat on a scale of 0–5 (Helms and Drury 1960). Fat scoring was performed by all three authors, but we regularly checked each other on individual birds to ensure that we were scoring fat similarly. During fall migration birds were aged by skull ossification as "after hatching-year" (AHY, adults) or "hatching-year" (HY, juveniles), although this method may be inaccurate after 1 October because some hatching-year birds may complete ossification after this date (Leberman 1970, Pyle et al. 1987). Retrix shape was not an effective measure of age in our population because most birds showed an intermediate condition (Pyle et al. 1987). Sex was determined by plumage differences in both seasons. Recaptures were very rare and were not included in our analyses.

We used banding data from the BBL from 1986–1995 to determine winter distributions and timing of spring migration in males and females. Data were grouped into 5° latitude zones for comparisons. Only banding records east of 107° W longitude were used in these comparisons to eliminate populations in western North America that breed at lower latitudes and winter at higher latitudes than populations in central and eastern North America. We considered records from 1 December–29 February as winter records, and from 1 April–31 May as spring records. Banding data were provided as number of captures for consecutive 5 day periods.

To determine whether differences in winter distribution of male and female Ruby-crowned Kinglets are sufficient to account for spring migration patterns, we used a method developed by Chandler and Mulvihill (1990) to calculate a predicted pattern of differential migration based on winter distributions of the sexes.

TABLE 1. Winter (December–February) abundance of male and female Ruby-crowned Kinglets in eastern and central North America from BBL records and results of χ^2 Goodness of Fit tests for equal abundance at each latitude.

Latitude ^a (°N)	Males	Females	% Males	χ^2	Significance
< 25	14	14	50.0	0.04	$P > 0.05$
25–29° 59'	30	28	51.7	0.02	$P > 0.05$
30–34° 59'	169	133	56.0	4.06	$P < 0.05$
35–39° 59'	54	17	76.1	18.25	$P < 0.001$

^a Latitudes north of 40° N had too few records ($n = 5$) to adequately assess distribution of sexes.

Chandler and Mulvihill (1990) assumed a linear change in the percentage of males in the population from the northern to the southern extent of the wintering range for their winter distribution; they predicted a linear change in the percentage of males in the population throughout migration from the first appearance to the last appearance of migrating males. They then used linear regression to calculate the predicted percentage of males throughout the migratory period and compared this regression against a linear regression of the observed percentage of males over the migratory period.

We used BBL data for wintering Ruby-crowned Kinglets to calculate a predicted differential pattern of spring migration between the sexes. The predicted percentage of males in the migratory population was calculated using the percentage of males in wintering populations from BBL data for 5° latitude zones over the entire kinglet wintering range in eastern and central North America (Table 1). We then divided the spring migratory period for males into an equal number of intervals (4 intervals at 5 days each) and assumed that the percent males during each successive 5-day interval (from first to last appearance) should equal the percent males in consecutive 5° latitude zones from north to south.

Statistics.—Median passage dates for sexes were compared by median tests (Zar 1996). Because capture effort was not evenly distributed over the entire kinglet migration period, median tests may be misleading. To control for uneven capture effort, we compared passage dates for sexes by Kolmogorov-Smirnov test for frequency distributions (Sokal and Rohlf 1995) as a function of cumulative net hours over all years pooled. Morphometrics, condition index [mass/wing chord (Winker 1995)], and visible fat scores for males and females in spring were compared by Student's *t*-test or, if sample variances were unequal (determined by *F*-test), Mann-Whitney test. In fall, morphometrics, condition index, and visible fat scores of sex/age classes were compared by one-way ANOVA, or by Kruskal-Wallis test if sample variances differed (*F*-test). Because skull ossification provides unreliable age distinction after 1 October in kinglets (Leberman 1970), fall comparisons of sex/age classes were conducted twice, excluding data after 30 September for birds with completely ossified skulls (aged AHY) and excluding all data (HY and AHY) after 30 September. If signif-

icant differences among sex/age classes were detected by ANOVA or Kruskal-Wallis tests, Student's *t*-tests or Mann-Whitney tests were used to identify which means differed with a sequential Bonferroni procedure employed for α -level adjustment to protect against inflated type I error rates in multiple comparisons (Rice 1989). This procedure involved six comparisons ($k = 6$) among the four sex/age classes for each variable measured (mass, wing chord, fat score, and condition index). For α -level adjustment, *P* values from individual *t*-tests for each comparison were ranked from smallest (P_1) to largest (P_6). The smallest *P* value was considered significant only if it was less than α/k (0.05/6 in this case). If P_1 was significant, then P_2 was considered significant only if less than $\alpha/k - 1$, P_3 was considered significant only if less than $\alpha/k - 2$, and so on, until the equality $P_i \leq \alpha/(1+k-i)$ was not met (Rice 1989). Once a *P* value was found to be not significant, all larger *P* values for that comparison were also considered nonsignificant.

For winter BBL data, distributions of males and females in 5° latitude zones were compared by 2-tailed χ^2 Goodness of Fit test with a null hypothesis of equal distribution (1:1) in each latitude zone. Bird Banding Laboratory data for timing of spring migration in males and females were compared by Kolmogorov-Smirnov test for frequency distribution as a function of cumulative captures during the migratory season pooled over all years (1986–1995). To determine whether winter distributions of sexes could fully account for differential migration in spring, predicted and observed percentages of males in the migratory population were compared by ANCOVA. Because neither the change in the percentage of males in the wintering population as a function of latitude nor the percentage of males in the migratory population through the spring migratory period varied in a linear fashion (Fig. 1), data for percent males were arcsine transformed prior to ANCOVA. In addition, we conducted Fisher's exact tests on observed versus predicted percent males for each 5 day interval over the spring migration of male kinglets. Statistical comparisons of mass, wing chord, condition index, and visible fat scores were conducted with Number Cruncher Statistical System (Version 4.1, Kaysville, Utah). Other statistical tests were performed with SAS (PC Version 6.03, SAS Institute 1988).

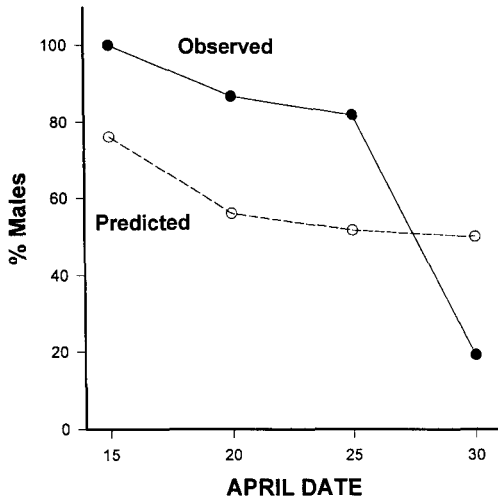


FIG. 1. Observed and predicted percentages of male Ruby-crowned Kinglets in the population during successive 5-day intervals over the spring migratory period as measured by capture data (first captures only). Predicted values were calculated based upon U.S. Geological Survey Bird Banding Laboratory data from 1985–1995 for wintering distributions of male and females kinglets east of 107° W longitude.

RESULTS

Southeastern South Dakota is not a part of the breeding range for Ruby-crowned Kinglets (South Dakota Ornithologists' Union 1991), so all birds in our samples were transients. Median passage dates for all years pooled for male and female kinglets in spring were 23 April and 1 May, respectively (Fig. 2). For fall migration, median passage dates for all years pooled were 29 September for females and 6 October for males (Fig. 2). Median tests indicated that males migrated significantly earlier ($\chi^2 = 45.74$, $df = 1$, $P < 0.001$) than females in spring and significantly later ($\chi^2 = 5.30$, $df = 1$, $P < 0.01$) than females in fall.

Total net hours (1 net hour = 1 net open for 1 h) were 2,081 in spring and 1,369 in fall. Our capture effort increased gradually over the spring migratory period (as days became longer) and similarly decreased gradually over the early part of fall migration (5 September–5 October). Capture effort was reduced after 5 October and only 12% of all fall net hours occurred after this date. This reduced capture effort late in fall migration may have reduced the relative number of captures of late migrating kinglets, mostly males, so the differ-

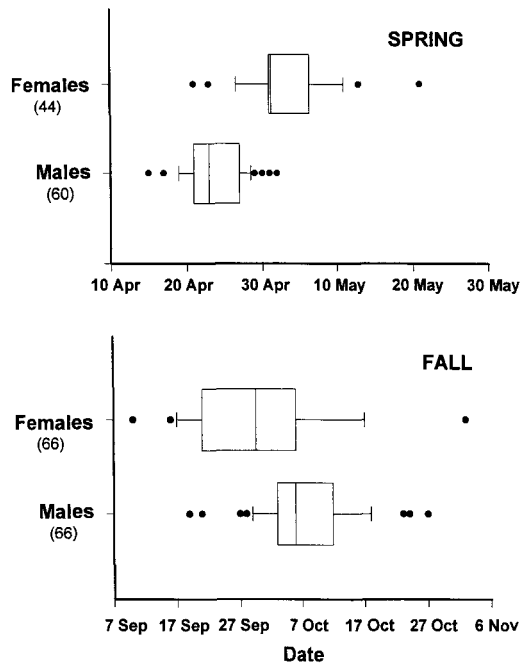


FIG. 2. Distribution of capture dates (first captures only) for male and females Ruby-crowned Kinglets during spring and fall migration. Box plots display the median (vertical line within box), the interquartile range (extent of box), the 10th–90th percentile range (extent of horizontal lines), and the data points falling below the 10th or above the 90th percentiles (dots). For spring females, the median passage date and the lower interquartile boundary were coincident on 1 May. The numbers included in parenthesis for males and females represent sample sizes for each season.

ence in median passage dates between sexes in fall that we report is probably conservative. Because capture effort was not even throughout migration periods, we tested whether frequency distributions of sexes differed as a function of cumulative capture effort. Again, these tests indicated that males migrated significantly earlier in spring (Kolmogorov-Smirnov test: $D = 0.673$, $n = 104$, $P < 0.001$) and significantly later in fall ($D = 0.425$, $n = 132$, $P < 0.001$) than females.

Data from the BBL indicated that at all latitudes males migrated significantly earlier in spring than females (Table 2). Median passage dates differed between the sexes by 10–15 days in the different 5° latitude zones. In winter, BBL data indicated that males had a significantly higher relative abundance than females at 30–35° N ($\chi^2 = 4.06$, $df = 1$, $P <$

TABLE 2. Median migration dates (5-day intervals) for male and female Ruby-crowned Kinglets in eastern and central North America from BBL records for April and May 1985–1996. Males migrated significantly earlier (Kolmogorov-Smirnov test: $P < 0.001$) than females at all latitudes. Sample sizes are given in parentheses.

Latitude ^a (°N)	Males	Females	<i>D</i>	<i>P</i>
30–34° 59'	6–10 April (69)	16–20 April (115)	0.333	< 0.001
35–39° 59'	16–20 April (275)	1–5 May (319)	0.566	< 0.001
40–44° 59'	21–25 April (1647)	6–10 May (1691)	0.502	< 0.001
45–50°	26–30 April (230)	6–10 May (297)	0.450	< 0.001

^a 5° latitude zones to the south and north of those above had too few total records (≤ 27) to adequately quantify medians for each sex.

0.05) and 35–40° N ($\chi^2 = 18.25$, $df = 1$, $P < 0.001$), but sexes were evenly distributed south of 30° N latitude (Table 1). Thus, male Ruby-crowned Kinglets winter farther north than females.

ANCOVA revealed that slopes for equations describing observed and predicted percent males in the spring migrant population differed significantly ($F_{1,4} = 9.46$, $P = 0.037$). Least-squares regression yielded the following equations:

$$\arcsin \text{ Predicted } \% \text{ Males} = 65.76 - 5.22(\text{Time Interval}) \quad (n = 4, R^2 = 0.99, P < 0.001)$$

$$\arcsin \text{ Observed } \% \text{ Males} = 111.05 - 19.54(\text{Time Interval}) \quad (n = 4, R^2 = 0.89, P = 0.05)$$

where Time Interval refers to successive 5-day intervals (1–4) from first (15 April) to last (2 May) capture of migratory males. For 20–24 April a higher percentage of males was captured than predicted (Fisher's exact test, $P = 0.039$) and for 30 April–4 May a lower percentage of males was captured than predicted (Fisher's exact test, $P = 0.04$); significant differences were not detected for other intervals. These data indicate that migratory passage of the sexes during the early season is more biased toward males than expected on the basis of their wintering distribution.

Rates of migration can also be estimated for males and females by dividing the distance between two successive 5° latitude zones (assuming 1° equals 111 km) by the number of days difference between median passage dates for each zone as determined from BBL data (Ellegren 1990, Woodrey and Chandler 1997). Estimating migration rates in this manner shows that both males and females increase migration speed as they near their breeding

grounds. For latitudes south of our study sites migration rates for males and females were 74 and 56 km day⁻¹, respectively, but for all latitudes overall migration speed was 83 km day⁻¹ for both sexes.

Male kinglets were significantly heavier than females ($t_{102} = 5.76$, $P < 0.001$) in spring. Visible fat scores did not differ significantly between males and females in spring, but spring males had significantly longer wings ($t_{102} = 9.49$, $P < 0.001$) and significantly higher condition index (Mann-Whitney test: $Z_{102} = 3.20$, $P = 0.001$) than spring females (Table 3). When age classes were pooled by sex in fall, males were significantly heavier than females ($t_{130} = 4.80$, $P < 0.001$) and had significantly longer wings ($t_{130} = 11.79$, $P < 0.001$). Neither visible fat nor condition index differed significantly between males and females in fall when age classes were pooled.

In fall, when AHY data after 30 September were excluded from comparisons, AHY males ($t_{38} = 3.39$, $P = 0.002$) and HY males ($t_{55} = 3.93$, $P < 0.001$) were both significantly heavier than HY females. Similarly, when all data after 30 September were excluded, AHY males were significantly heavier than HY females ($t_{24} = 3.035$, $P = 0.006$). Mass did not vary significantly among other sex/age classes in fall (Table 3). Visible furcular fat scores were significantly greater in AHY females than in juveniles in fall when AHY data after 30 September were excluded from comparisons (Mann-Whitney test: $Z_{49} = 3.14$, $P = 0.002$; $Z_{35} = 2.99$, $P = 0.003$ for HY females and HY males, respectively). Likewise, when all data after 30 September were excluded from analyses, AHY females carried significantly more furcular fat than HY females (Mann-Whitney test: $Z_{34} = 2.840$, $P = 0.005$).

TABLE 3. Means (\pm SD) of mass, wing chord, fat class, and condition index (mass/wing chord) in migrant Ruby-crowned Kinglets. Age classes (AHY = adults, HY = hatching-year) refer to fall migrants.

Sex/age class	n	Mass (g)	Wing chord (mm)	Furcular fat	Abdominal fat	Condition index
Spring males	60	6.6 \pm 0.6	57.7 \pm 1.3	2.2 \pm 1.1	2.1 \pm 1.4	1.15 \pm 0.10
Spring females	44	6.0 \pm 0.4	55.0 \pm 1.6	2.1 \pm 0.9	2.1 \pm 1.0	1.09 \pm 0.07
Fall males						
AHY	5	6.5 \pm 0.6	58.5 \pm 1.5	3.2 \pm 0.8	3.2 \pm 0.8	1.11 \pm 0.10
HY (before 1 Oct.) ^a	5	6.3 \pm 0.4	57.6 \pm 1.4	1.6 \pm 1.1	1.6 \pm 1.1	1.08 \pm 0.06
HY (all data) ^b	22	6.3 \pm 0.4	57.6 \pm 1.2	1.9 \pm 1.0	1.8 \pm 1.0	1.09 \pm 0.07
All males ^c	66	6.4 \pm 0.4	57.7 \pm 1.4	2.0 \pm 1.1	2.1 \pm 1.0	1.10 \pm 0.07
Fall females						
AHY	15	6.1 \pm 0.4	55.1 \pm 1.4	2.9 \pm 0.7	2.8 \pm 0.7	1.12 \pm 0.07
HY (before 1 Oct.) ^a	21	5.9 \pm 0.4	54.8 \pm 1.2	2.0 \pm 0.8	2.0 \pm 0.7	1.08 \pm 0.06
HY (all data) ^b	36	5.9 \pm 0.3	54.7 \pm 1.4	2.0 \pm 0.8	2.1 \pm 0.8	1.08 \pm 0.06
All females ^c	66	6.0 \pm 0.3	54.9 \pm 1.3	2.3 \pm 0.8	2.3 \pm 0.8	1.10 \pm 0.06

^a Data for HY birds prior to 1 October only.

^b Data for HY birds over the entire fall season.

^c Includes birds with completely ossified skulls after 30 September that were of indeterminate age.

Visible abdominal fat scores were significantly greater in AHY females than in HY birds when AHY data after 30 September were excluded from comparisons ($Z_{35} = 3.11$, $P = 0.002$; $Z_{49} = 2.84$, $P = 0.005$ for HY males and HY females, respectively). When all data after 30 September were excluded from comparisons, AHY females had significantly more abdominal fat than HY females ($Z_{34} = 2.695$, $P = 0.007$). The same trend occurred for AHY males, although differences were nonsignificant (Table 3). Neither furcular nor abdominal fat varied significantly between males and females within the same age class. No significant differences among age/sex classes were detected for condition index in fall, although when male and female data for each age class were pooled the adult-juvenile difference approached significance ($t_{73} = 1.74$, $P > 0.05$ when AHY data after 30 September were excluded; $t_{43} = 1.85$, $P > 0.05$ when all data after 30 September were excluded).

Wing chord did not differ significantly among age classes in fall, but males of both age classes had significantly longer wings than females when AHY data after 30 September were excluded ($P < 0.001$) and when all data after 30 September were excluded ($P \leq 0.005$, Table 3). Test statistics for between sex wing chord comparisons were: AHY males vs. AHY females ($t_{18} = 4.35$), AHY males vs. HY females ($t_{39} = 5.59$), HY males vs. AHY females ($t_{35} = 5.59$), and HY males vs. HY females ($t_{56} = 7.94$) for comparisons

with AHY data after 30 September excluded. For comparisons with all data after 30 September excluded, between sex wing chord comparison test statistics were: AHY males vs. AHY females ($t_{18} = 4.35$), AHY males vs. HY females ($t_{24} = 5.99$), HY males vs. AHY females ($t_{18} = 3.23$), and HY males vs. HY females ($t_{24} = 4.59$).

DISCUSSION

Male Ruby-crowned Kinglets migrated earlier in spring than females in both southeastern South Dakota and across eastern North America (Crim 1976, Fairfield and Shirokoff 1978, BBL data). Bird Banding Laboratory data indicate that median passage dates for the latitudes of our study sites (approximately 43° N) in eastern North America are 21–25 April for males and 6–10 May for females. These dates agree very closely with median passage dates for male and female kinglets from Iowa, which occurred from 20–25 April for males and from 5–10 May for females (Crim 1976). The median date for males in southeastern South Dakota was similar to median dates in Iowa and to median dates derived from BBL data for 40–45° N latitude in central and eastern North America (Table 2). The median date for females in our study is several days earlier than the median date from Iowa and from the median date derived from BBL data for the latitudes of our study sites. However, capture effort was not quantified in Crim (1976) and was not available for BBL

data, so median passage dates may not be directly comparable.

Earlier spring passage of males than females is a common pattern among passerines, presumably because of the advantages that early arrival provides to the sex establishing territory, which among passerines is usually the male (Gauthreaux 1982, Francis and Cooke 1986). Postponing arrival on the breeding grounds until after males have established territories might be beneficial to females if they compete for mates (Francis and Cooke 1986). Moreover, because temperatures and food availability increase throughout spring in northern latitudes, late arrival on the breeding grounds might also benefit females by providing more favorable conditions for breeding. Consistent with this latter argument, male kinglets were larger (i.e., heavier and longer wings), had higher condition index, and were more cold tolerant (Swanson and Dean 1999) than females in spring.

Because juvenile Ruby-crowned Kinglets may show complete skull ossification as early as 1 October (Leberman 1970), documentation of differential migration patterns of age classes in fall is problematic. In addition, we found retri shape (Pyle *et al.* 1987) to be unreliable for aging kinglets in our population. Thus, we were unable to compare passage dates for age classes during fall migration. However, males migrated significantly later than females during fall migration in southeastern South Dakota. This pattern of males migrating later in the fall than females is consistent with the observations of Fairfield and Shirokoff (1978) for Ruby-crowned Kinglets from Ontario.

Prescott (1980) found that adult female kinglets were fatter than adult males in fall in New Jersey, but sexes did not differ in fat scores during fall migration in our study. Adult kinglets in New Jersey (Prescott 1980) had a higher percentage of individuals with either no fat or heavy fat than juveniles, while juveniles had higher percentages of individuals with intermediate fat loads. In our study males were heavier than juvenile females in fall, but not adult females. Moreover, adults in our study carried more fat than juveniles in fall, significantly so for females. Woodrey and Moore (1997) reviewed several possible explanations for elevated fat levels in adults

compared to juveniles during migratory stop-over. These include: (1) less efficient foraging by juveniles at stopover sites because of inexperience or lower social status, (2) juveniles carry less fat to increase mobility for escape from predators because they may be more vulnerable to predation, and (3) possible differences in migratory routes or destinations affecting fattening.

Proximate factors regulating differential timing of migration among sex/age classes include differences in geographic origin, timing of the onset of migration, and rates of migration (Chandler and Mulvihill 1990). Fairfield and Shirokoff (1978) analyzed North American banding data from 1972–1975 and found that male kinglets winter farther north than females on average. Bird Banding Laboratory data from 1986–1995 also indicate that male kinglets winter farther north than females (Table 1) so different geographic origins undoubtedly contribute to differential migration of the sexes in the spring. However, passage of sexes during the early portion of spring migration is more biased toward males than expected on the basis of the differential wintering distributions. Sample sizes from BBL data for 1986–1995 for wintering populations of kinglets in eastern and central North America were relatively small, particularly south of 30° N latitude, even though kinglets regularly winter south of this latitude (AOU 1983, Ingold and Wallace 1994). Bird Banding Laboratory data indicate approximately equal numbers of males and females at southern latitudes in the wintering range, whereas females should outnumber males in the southern part of the wintering range, assuming equal sex ratios on breeding grounds. This could influence calculation of predicted percent males during the latter part of the spring migration of males, but should not affect comparisons during the early portion of the migration. Because a higher percentage of males was observed than predicted based on wintering distribution during the early part of spring migration, the small sample size from southern portions of the wintering range should not influence our conclusions that wintering distributions do not fully account for differential migration of the sexes in spring.

This suggests that males either migrate at a faster rate or initiate migration earlier than fe-

males. Calculation of spring migratory rates from BBL data revealed that male kinglets migrate at a faster pace than females south of 45° N latitude, but that rates over the entire migratory range do not differ between sexes. Thus, elevated rates of migration in males relative to females may contribute to their early arrival at our study sites, but not at higher latitudes. This suggests that the onset of spring migration is earlier in male Ruby-crowned Kinglets than in females and that this difference contributes substantially to differential spring migration of the sexes in this species.

For fall migration, where all sex/age classes presumably initiate migration from breeding grounds, differential timing of migration should reflect differences in onset or rate of migration, assuming that sex/age classes exhibit similar migration routes and that little postbreeding dispersal away from breeding sites occurs prior to southward migration. Fairfield and Shirokoff (1978) suggested that differential migration of the sexes in fall results from earlier departure of females from breeding grounds for two possible reasons. First, females are smaller and presumably less hardy than males, so they might depart before food availability and temperatures decline markedly in the fall. However, cold tolerance of male and female kinglets during fall migration through South Dakota did not differ significantly (Swanson and Dean 1999). Second, females might depart earlier than males because they winter farther south and, therefore, must travel farther. If we assume that all sex/age classes initiate migration from breeding grounds, then differential migration of sex/age classes might result not only from differences in departure, but also from differences in rates of migration (Chandler and Mulvihill 1990). Because Fairfield and Shirokoff (1978) did not directly test whether early departure or rates of migration differed between the sexes in fall, their suggestion must remain tentative. In our study males migrated later than females in fall but comparisons among age classes were confounded because juvenile kinglets could not safely be distinguished from adults after 1 October (Leberman 1970).

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Checklist of North American birds, sixth ed. Allen Press, Lawrence, Kansas.
- CHANDLER, C. R. AND R. S. MULVIHILL. 1990. Interpreting differential timing of capture of sex classes during spring migration. *J. Field Ornithol.* 61: 85–89.
- CRIM, G. B. 1976. Kinglets in Iowa. *Iowa Bird Life* 76:45–47.
- ELLEGREN, H. 1990. Autumn migration speed in Scandinavian Bluethroats *Luscinia s. svecica*. *Ringling & Migr.* 11:121–131.
- FAIRFIELD, D. M. AND P. A. SHIROKOFF. 1978. Migratory patterns and winter distribution in the Ruby-crowned Kinglet (*Regulus calendula*). *Blue Bill* (suppl.) 25:22–25.
- FRANCIS, C. M. AND F. COOKE. 1986. Differential timing of spring migration in wood warblers (Parulinae). *Auk* 103:548–556.
- GAUTHREAUX, S. A., JR. 1982. The ecology and evolution of avian migration systems. *Avian Biol.* 6: 93–168.
- HALL, G. A. 1981. Fall migration patterns of wood warblers in the southern Appalachians. *J. Field Ornithol.* 52:43–49.
- HELMS, C. W. AND W. H. DRURY, JR. 1960. Winter and migratory weight and fat field studies on some North American buntings. *Bird-Banding* 31:1–40.
- HUSSELL, D. J. T. 1991. Fall migrations of Alder and Willow flycatchers in southern Ontario. *J. Field Ornithol.* 62:260–270.
- INGOLD, J. L. AND G. E. WALLACE. 1994. Ruby-crowned Kinglet (*Regulus calendula*), no. 119. *In* The birds of North America (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C.
- KETTERSON, E. D. AND V. NOLAN, JR. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). *Ecology* 57:679–693.
- LEBERMAN, R. C. 1970. Pattern and timing of skull pneumatization in the Ruby-crowned Kinglet. *Bird-Banding* 41:121–124.
- LEPTEIN, L. W. AND C. E. BOCK. 1976. Winter abundance patterns of North American kinglets. *Wilson Bull.* 88:483–485.
- MORTON, M. L. 1984. Sex and age ratios in wintering White-crowned Sparrows. *Condor* 86:85–87.

- MYERS, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Can. J. Zool.* 59:1527–1534.
- NOLAN, V., JR. AND E. D. KETTERSON. 1990. Timing of autumn migration and its relation to winter distribution in Dark-eyed Juncos. *Ecology* 71:1267–1278.
- PRESCOTT, D. R. C. AND A. L. A. MIDDLETON. 1990. Age and sex differences in winter distribution of American Goldfinches in eastern North America. *Ornis Scand.* 21:99–104.
- PRESCOTT, K. W. 1980. Weight, fat class, and wing measurements of Ruby-crowned Kinglets during migration. *Inland Bird Banding* 52:1–7.
- PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.
- RAMOS, M. A. 1988. Eco-evolutionary aspects of bird movements in the northern Neotropical region. *Proc. Int. Ornithol. Congr.* 19:251–293.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- ROOT, T. 1988. Atlas of wintering North American birds. Univ. of Chicago Press, Chicago, Illinois.
- SAS INSTITUTE. 1988. SAS user's guide. SAS Institute, Inc., Cary, North Carolina.
- SOKAL, R. R. AND F. J. ROHLF. 1995. Biometry, third ed. Freeman, New York.
- SOUTH DAKOTA ORNITHOLOGISTS' UNION. 1991. The birds of South Dakota, second ed. Northern State Univ. Press, Aberdeen, South Dakota.
- SWANSON, D. L. AND K. L. DEAN. 1999. Migration-induced variation in thermogenic capacity in migratory passerines. *J. Avian Biol.* 30:In press.
- WINKER, K. 1995. Autumn stopover on the Isthmus of Tehuantepec by woodland Nearctic-Neotropical migrants. *Auk* 112:690–700.
- WINKER, K. AND J. H. RAPPOLE. 1992. The autumn passage of Yellow-bellied Flycatchers in South Texas. *Condor* 94:526–529.
- WOODREY, M. S. AND C. R. CHANDLER. 1997. Age-related timing of migration: geographic and interspecific patterns. *Wilson Bull.* 109:52–67.
- WOODREY, M. S. AND F. R. MOORE. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* 114:695–707.
- ZAR, J. H. 1996. Biostatistical analysis, third ed. Prentice Hall, Upper Saddle River, New Jersey.