

WINTERING BIOLOGY OF RUBY-CROWNED KINGLETS IN THE LOWER COLORADO RIVER VALLEY

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ABSTRACT.—The Ruby-crowned Kinglet (*Regulus calendula*) was studied from October–April during four years, 1975–1979, among six major plant communities in the riparian corridor of the lower Colorado River valley. Kinglets were most abundant in cottonwood-willow and least abundant in arrowweed. Within each community, the greatest density of kinglets generally occurred in areas of tall, dense vegetation. Density differed significantly among the four years in November, the month of peak abundance, and in February, winter's end. Populations decreased significantly through the winter in each year and decreases were not uniform among plant communities. Differences in relative abundances and winter population decreases were related to winter weather conditions. During the study period, kinglets were subject to marked seasonality as determined by decreases in average monthly minimum temperatures, changes in tree phenology, and changes in insect abundance and biomass. Kinglet responses to seasonality were most apparent in population dynamics, distribution among plant communities, foraging substrate utilization and choice of prey. Analysis of these data emphasizes the selective importance of the nonbreeding season ecology to kinglets and implies that these birds may be winter-limited.

Autecological approaches in bird studies have greatly advanced our knowledge not only of the particular species involved, but also of birds in general (Root 1967). Several researchers have recognized that a better understanding at the species level can yield more definitive statements at the community level (Holmes et al. 1979, Morton 1980). Most such studies in the avian literature have focused on the breeding season, yet the significance of ecological requirements in the nonbreeding season has become increasingly apparent (Lack 1966, Fretwell 1972, Wiens 1977, Keast and Morton 1980). The recent symposium on avian migrants in the Neotropics (Keast and Morton 1980), while elucidating the nonbreeding ecology of migrant birds, contains little information on those migratory species whose centers of winter distribution are essentially temperate (e.g., members of the Sylviidae, Certhiidae, and others). We need to increase our knowledge of nonbreeding-season ecology for many species over various geographic areas (Karr 1980).

Ruby-crowned Kinglets (*Regulus calendula*), hereafter referred to as kinglets, are common winter residents over much of southern Arizona (Phillips et al. 1964). They are abundant in the lower Colorado River valley, where they occur from October to April in all major riparian plant communities. Kinglets, because of their great numbers, widespread occurrence,

and duration of residency, are an ideal species in which to study the relationship of birds to their wintering environment.

In this report, we examine and discuss the relationship of kinglet densities, distributions, and habitat selection to plant community composition, vegetation structure, and weather conditions from October to April (1975–1979). Individual foraging behavior and diet are described and discussed in relation to seasonal changes in vegetation and food supply over a two-year period. Particular attention is directed toward the degree of seasonality present in the wintering environment of kinglets and the influence of seasonality, when present, on kinglet biology.

METHODS

Transects varying in length from 0.8 to 1.6 km were established in relatively homogeneous stands of riparian vegetation along the lower Colorado River from Davis Dam on the Arizona-Nevada border, south to the Mexican border. In the lower Colorado River valley six riparian plant community types were recognized, using dominant vegetation as a criterion: Cottonwood (*Populus fremontii*)-willow (*Salix gooddingii*) mixes, honey mesquite (*Prosopis glandulosa*), salt cedar (*Tamarix chinensis*), screwbean mesquite (*Prosopis pubescens*), salt

cedar-honey mesquite mixes, and arrowweed (*Tessaria sericea*).

All transects were censused two to four times monthly using the variable strip method (Emlen 1971). Average monthly population estimates were expressed as the number of birds per 40 ha within each plant community type. The number of transects censused varied between 55 in 1975 and 83 in 1978. For further details concerning vegetation classification and avian population estimates see Anderson and Ohmart (1977).

For vegetation analysis and a better understanding of bird-habitat relationships, each transect was subdivided into 150-m long intervals, with each 150 m \times 15 m lateral strip defined as a plot. The number of trees, foliage density, and foliage height diversity (FHD) measurements were recorded for each plot.

The number of trees was expressed as the average number per plot and the average number per hectare. Using the board technique (MacArthur and MacArthur 1961), two or three points per 150-m interval were sampled at heights of 0.15 m, 0.6 m, 1.5 m, 4.5 m, 6.0 m, 7.5 m, 9.0 m, and every 3 m thereafter, to obtain measures of foliage density. The mean for two or three points at each height was used to represent the foliage density profile in each plot. Patchiness Index (PI) for a given layer was the variance in mean foliage density for the 20 plots along a 1,500-m transect. Total PI was the sum of the variances for the layers: herb—0.0–0.6 m; shrub—0.6–4.5 m; and tree—>4.5 m (Anderson et al. 1978).

Data on foraging behavior were collected along transects in cottonwood-willow and honey mesquite communities. When an individual kinglet was encountered, we recorded foraging method (glean, hover, hawk), relative foraging height (lower, middle, or upper third of tree or shrub), foraging substrate (plant species and leaf, branch, trunk, flower, or other structural part), and perch size (≤ 1 cm, 1–5 cm, 5–15 cm, >15 cm). We attempted to record up to five moves per individual but usually were unable to do so because kinglets are so active. Data were recorded monthly from October 1976–March 1978 and were pooled seasonally in each year (fall, October–November; winter, December–February; spring, March–April). Spring data for honey mesquite were not included because of low kinglet densities.

Kinglet specimens ($n = 104$) were collected within the riparian corridor between December 1976 and April 1978 and their stomach contents were analyzed. Insect items were counted and identified to order and, when possible, to family. Because of fragmentation, the

minimum number of individual insects was estimated from counts of characteristic body parts. Lengths of prey items were estimated to the nearest millimeter by comparing the body parts present with the known body length of voucher specimens. Voucher specimens were obtained from foliage insect sweep samples in the study area. The minimum number of individuals per prey taxon per individual specimen was presented monthly and seasonally for each year and expressed as the average percent frequency of the total number of prey items eaten in a particular sampling period. Average length of items eaten was also estimated per bird specimen and was expressed as the average monthly individual mean prey size.

Insect sampling consisted of 2,000 or 4,000 sweeps with a 40-cm diameter net along a randomly walked route through a 20-ha study area within each community type. Sampling was done monthly between October 1976 and February 1978, except in January and April 1977 when no samples were collected. All collected insects were identified to family, counted, weighed to the nearest 0.001 g (dry weight), and measured to the nearest 0.5 mm. Data were summed for all communities and were recorded monthly.

Seasonal data are presented as fall (October–November), winter (December–February), and spring (March–April). The conventional designation of December–February as winter was substantiated somewhat by reference to 30-year weather data from lower Colorado River valley weather stations (Sellers and Hill 1974). The first day of frost typically occurs on November 28; December and January are the coldest months of the year and although February is warmer than the previous two months, it is not unusual for frost to be recorded.

We compared weather among the four study years using daily minimum temperature and average monthly precipitation data from three U.S. weather stations located in the lower Colorado River valley floodplain. Maximum temperature was not considered to be an important variable because daily temperatures usually exceeded 18°C throughout the winter. Nightly lows and the duration of cold (consecutive days of frost) determine the severity of a winter.

Differences in kinglet densities among plant communities in each year were determined using a Kruskal-Wallis one-way analysis of variance test (Siegel 1956). Communities were considered treatments and individual transect densities as cases within each treatment. This was done using both November (fall) and February (winter's end) kinglet densities. Among-year differences were tested in a similar manner using the Kruskal-Wallis test. Years were

considered treatments and individual transect densities as cases within each treatment for both November and February. Equality of November and February transect densities in each year was tested using Mann-Whitney *U*-tests (Siegel 1956). Comparisons were made between November and February within each community and with all communities combined. G-tests (Sokal and Rohlf 1969) served to compare frequency distributions of kinglet densities among communities in November and February of each year and among years during November and during February. Due to the large data set, presentation of seasonal changes in kinglet population densities and distribution was facilitated by reference to November and February data only. We felt that changes were likely to be manifested most strongly between November, a period of mild conditions (see Results) and peak kinglet abundance, and winter's end, February.

Relationships to habitat were initially explored in the cottonwood-willow community using Pearson product-moment correlations (Sokal and Rohlf 1969). We correlated monthly densities of kinglets on each transect with eight vegetation variables recorded for each transect (foliage volume $0 \leq 0.6$ m, foliage volume $0.6 \leq 4.5$ m, foliage volume >4.5 m, total foliage volume, FHD, total patchiness, patchiness ≥ 4.5 m, and numbers of cottonwood and willow trees). Data were normalized using \log_{10} transformations. Because of the difficulties in normalizing data, we made additional correlations in other plant communities using kinglet densities against vegetation variables with the aid of Spearman Rank correlation (Siegel 1956). Salt cedar-honey mesquite and arrowweed were excluded because these communities contained few transects.

Comparisons of frequency distributions of foraging observations in each foraging category were made using G-tests between years in a particular season, among seasons within a year, and between communities within each season. To avoid inflated Type I error rates associated with multiple-paired comparisons, a significant difference was initially determined among all replicates within each foraging category, a replicate being a season within a year. There were six replicates in cottonwood-willow (three seasons—two years), four replicates in honey mesquite (two seasons—two years), and eight replicates in the intercommunity comparison (two seasons—two years—two communities). Spring data in honey mesquite were not presented due to insufficient sample sizes. If a significant difference was obtained, the χ^2 value necessary to obtain significance in these G-

tests was used as the critical level in any subsequent paired comparison (Sokal and Rohlf 1969:582).

Welch's approximation (*t'*-test; Sokal and Rohlf 1969) was used to test for differences in length of prey eaten. The accepted level of significance was $P < 0.05$.

RESULTS

DENSITY AND DISTRIBUTION

Kinglets first appeared in the lower Colorado River valley in October; populations reached peak densities in November or December and then declined until April (Fig. 1). Although kinglet numbers increased in some communities during the four years, these increases were not significant, excluding arrowweed in 1975–1976 (Mann-Whitney *U*-test; Siegel 1956). Kinglets were present in significantly different densities in November, before the onset of winter and in February, winter's end, among the four study years (Kruskal-Wallis, one-way analysis of variance test; Siegel 1956).

Kinglets were most abundant in cottonwood-willow and least abundant in arrowweed communities. Densities were intermediate in honey mesquite, salt cedar, screwbean mesquite, and salt cedar-honey mesquite communities. Kinglet densities for all months, November through March, within all communities were highest in 1977–1978 and lowest in 1975–1976. Densities differed significantly among the six communities during November in each year. However, February densities showed a significant difference among communities in only 1975–1976 (Kruskal-Wallis test).

As with abundance, percent population decrease over the winter (November to February) varied from year to year and among communities. Overall densities (transect densities irrespective of community type) between November and February decreased significantly in each year (Mann-Whitney *U*-test). The largest percentage of decrease in overall kinglet density occurred in 1975–1976 and the smallest in 1977–1978. The largest decrease was in the year with the lowest peak abundance and the smallest decrease was in the year with the highest peak abundance. Kinglet density declined significantly in all plant communities in 1975–1976 and in all but screwbean mesquite during 1978–1979. In 1976–1977, kinglet densities in screwbean mesquite and honey mesquite showed a significant decrease. Densities in salt cedar and screwbean mesquite declined significantly in 1977–1978. Usually the percentage of decrease was smallest in cottonwood-willow communities and largest in

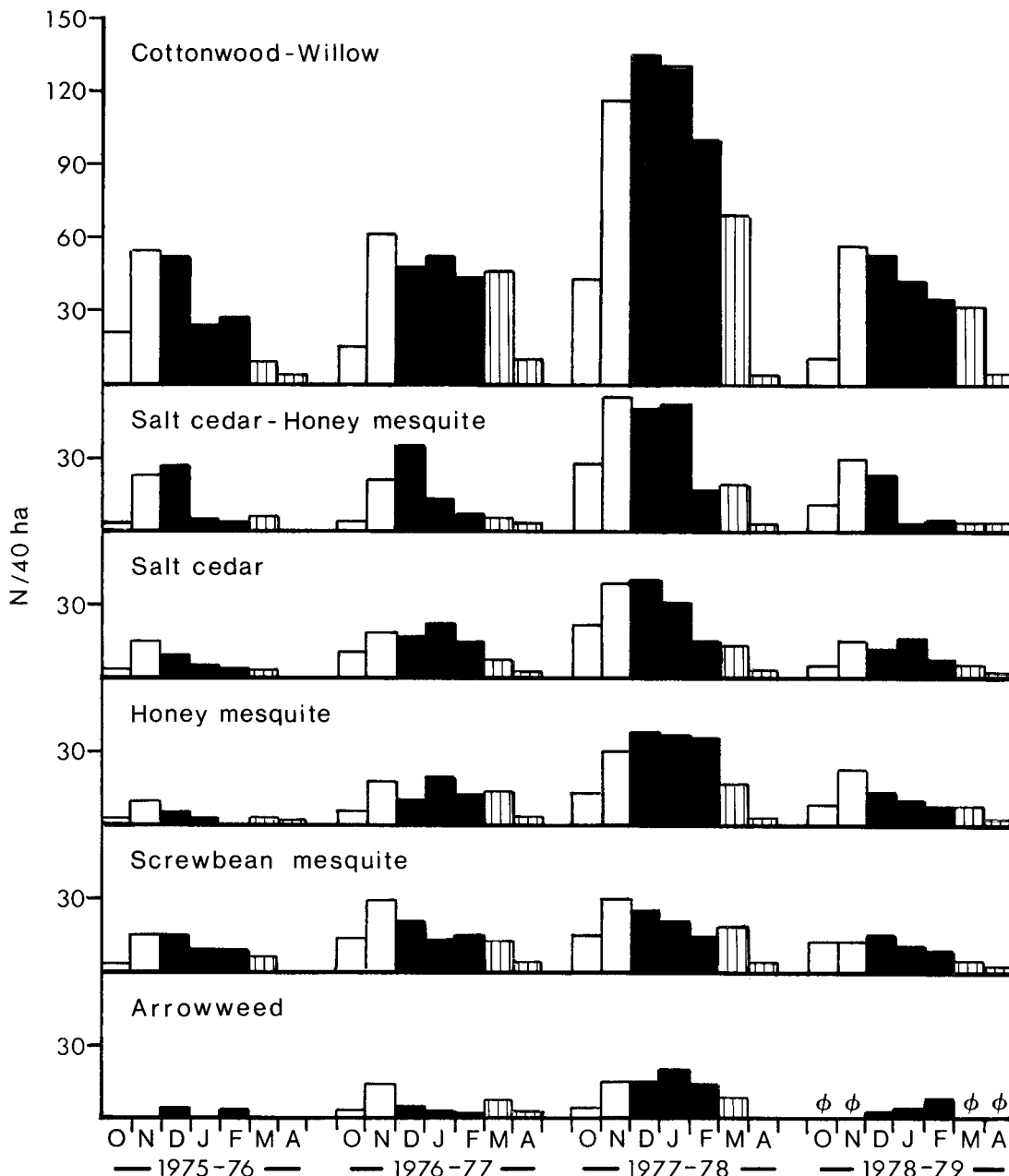


FIGURE 1. Monthly densities of Ruby-crowned Kinglets, expressed as number per 40 ha, among six riparian plant communities in the lower Colorado River valley during four years: 1975-79. Shading delineates seasons and ϕ indicates no data record.

salt cedar-honey mesquite. Unlike the other communities, densities in arrowweed were extremely erratic, with one winter (1978-1979) showing an increase in density through February.

The distribution of kinglets among plant communities in February was significantly different from the November distribution in three of four years (Fig. 2). Across the four years, the November distribution of kinglets among plant communities was not significantly different ($G_H = 15.921$; $G_{H(0.05,12)} = 21.096$) but

there was a significant difference in the February distributions ($G_H = 24.626$; $G_{H(0.05,12)} = 21.096$).

WEATHER

Of the four study years, 1977-1978 was the mildest winter, with no recorded frosts (Fig. 3). Winter monthly daily minimum temperatures averaged nearly 3°C warmer than comparative months in the other study years. Differences among other years were slight. In general, December and January temperatures

were cold, although February temperatures were somewhat more variable among years. Examination of other data (minimum temperature recorded, number of days of frost, or consecutive days of frost) did not reveal severe conditions in any one winter.

Conversely, precipitation varied substantially among years. In general, precipitation appeared to increase in each year. 1975–1976 was particularly dry, with little rain before October and little to none through February. The large increase in rainfall during February 1976 (Fig. 3) was a result of two consecutive storms during the last week of February. In contrast, 1978–1979 was extremely wet. That year Arizona experienced some of the worst floods in its recorded history (pers. observ.).

Significant correlations were obtained between January average daily minimum temperature and overall winter kinglet density ($r = 0.995$; $r_{(0.5,2)} = 0.950$), and between average January minimum temperature plus total November–January precipitation and overall kinglet density ($R^2 = 0.994$; $R^2_{(0.5,2,2)} = 0.975$).

CORRELATIONS WITH VEGETATION PARAMETERS

Kinglets were usually found to be most abundant in areas of tall, dense vegetation. Their highest densities consistently occurred on cottonwood-willow transects with a high forest canopy and a lush understory of young trees and herbaceous growth. Although kinglets in cottonwood-willow were correlated, at least once, with seven of the eight vegetation variables recorded, only five correlated significantly more often than by random chance (total foliage volume, foliage volume ≥ 4.5 m, FHD, Patchiness ≥ 4.5 m, and number of cottonwood and willow trees). This was determined using a binomial probability where each variable had a one-in-eight chance of a successful outcome (a significant correlation). Associated probabilities were calculated based on number of successful outcomes in 28 trials (seven months over four years). We interpreted the significant positive correlations of kinglet densities with these five variables as indicating the birds' preference for areas of tall, dense vegetation. Because of the high intercorrelation among these five variables we considered these variables as representative of a general vegetation structure and chose one variable as the best indicator of that structure. Relative foliage volume ≥ 4.5 m appeared to correlate most strongly for the other four variables and was used in correlations for kinglet transect density in three other plant communities. Cottonwood-willow was included for comparative purposes.

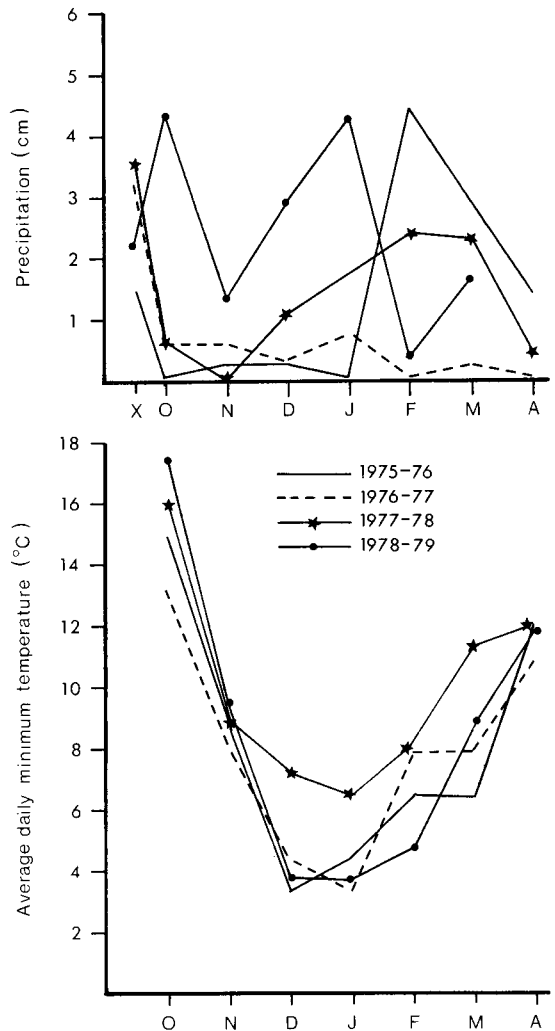


FIGURE 2. November and February distributions of Ruby-crowned Kinglets among the major riparian plant communities in the lower Colorado River valley in each of four years, 1975–79. G-statistics (Sokal and Rohlf 1969) indicate significant within year differences between the November and February distributions. Arrowweed was not censused in November 1978.

Kinglet density was correlated significantly with relative foliage volume ≥ 4.5 m at least one year in all communities (Table 1). In no plant community or year were significantly less correlations obtained than by random chance. An equal number of significant correlations were obtained in November and February.

FORAGING BEHAVIOR IN COTTONWOOD-WILLOW AND HONEY MESQUITE

Kinglets foraged primarily by gleaning but hovered often and hawked to a much lesser extent (Fig. 4). This was true for cottonwood-willow and honey mesquite communities in all seasons for both years. The degree to which kinglets employed these three foraging meth-

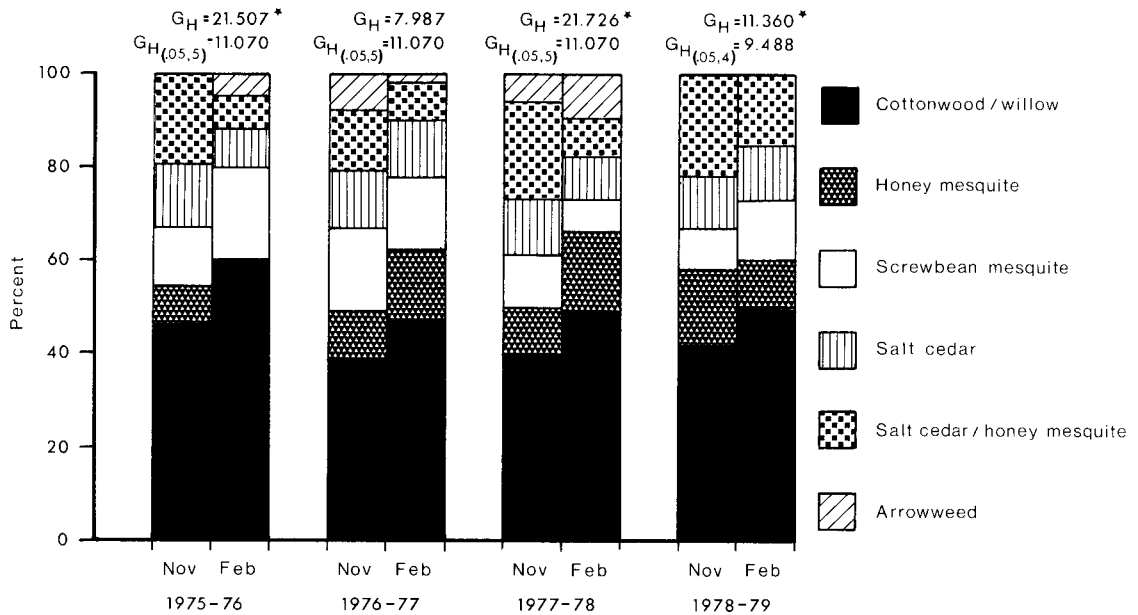


FIGURE 3. October–April monthly average daily minimum temperatures and monthly total precipitation values in the lower Colorado River valley during four years, 1975–79. Data averaged from three U.S. Weather Bureau Stations: Parker, Ehrenberg, and Yuma Valley, Arizona.

ods did not vary with time. We found no significant differences in the distribution of foraging method between seasons and years within each plant community or between plant communities (G-test, Sokal and Rohlf 1969).

The relative foraging height of kinglets varied between habitats; kinglets foraged in the upper third of the trees or shrubs in honey mesquite and in the middle third of trees and shrubs in cottonwood-willow. This difference

was significant only in winter 1976–1977 when kinglets foraged more often in the lower two-thirds of trees and shrubs in cottonwood-willow than in honey mesquite ($G_H = 37.029$, $G_{H(0.05,14)} = 23.685$). Within honey mesquite, kinglets foraged significantly more often in the lower one-third of the trees in the winter of 1977–1978 compared to the winter of 1976–1977 ($G_H = 13.161$, $G_{H(0.05,6)} = 12.592$). Within cottonwood-willow, there was a significant difference in relative foraging height between fall and winter of 1976–1977 ($G_H = 25.559$, $G_{H(0.05,10)} = 11.070$).

The size of perches used by kinglets was fairly restricted. We noted no significant shifts in the use of perch size between seasons, years, or communities. More than 90% of all gleaning occurred from a perch < 1 cm in thickness.

Kinglets showed the most variability in their use of foraging substrates leaf, bark, and other (flowers, fruit, and ground). We found significant differences between plant communities in fall 1977 ($G_H = 32.667$, $G_{H14(0.05)} = 23.685$) and both winters (1976–1977; $G_H = 24.182$, $G_{H14(0.05)} = 23.685$ and 1977–1978; $G_H = 94.245$, $G_{H14(0.05)} = 23.685$). In cottonwood-willow, significant seasonal differences in each year occurred as kinglets foraged on cottonwood and willow flowers in winter. This seasonal shift to flower substrate was consistent between years. In honey mesquite, kinglets foraged primarily on leaf surfaces. Significant differences were found in honey mesquite throughout the year in 1976–1977 but kinglets

TABLE 1. Spearman rank correlation coefficients between relative foliage volume ≥ 4.5 m for November and February Ruby-crowned Kinglet densities on transects in four of six major plant communities¹ in the riparian corridor of the lower Colorado River valley. * = $P < 0.05$; ** = $P < 0.01$.

Community	1975–1976	1976–1977	1977–1978	1978–1979
Cottonwood-willow				
November	.809**	.786**	.832**	.887**
February	.406	.835**	.814**	.544*
Honey mesquite				
November	.643**	.459*	.591**	.487*
February	.000	.511*	.436*	.652**
Salt cedar				
November	-.018	.374	.465*	.457*
February	-.815*	.549*	.726**	.366
Screwbean mesquite				
November	.635*	.325	.374	.393
February	-.412	-.104	.577**	-.094

¹ Salt cedar-honey mesquite mixes and arrowweed were excluded because of the small number of transects within these communities (three and four, respectively).

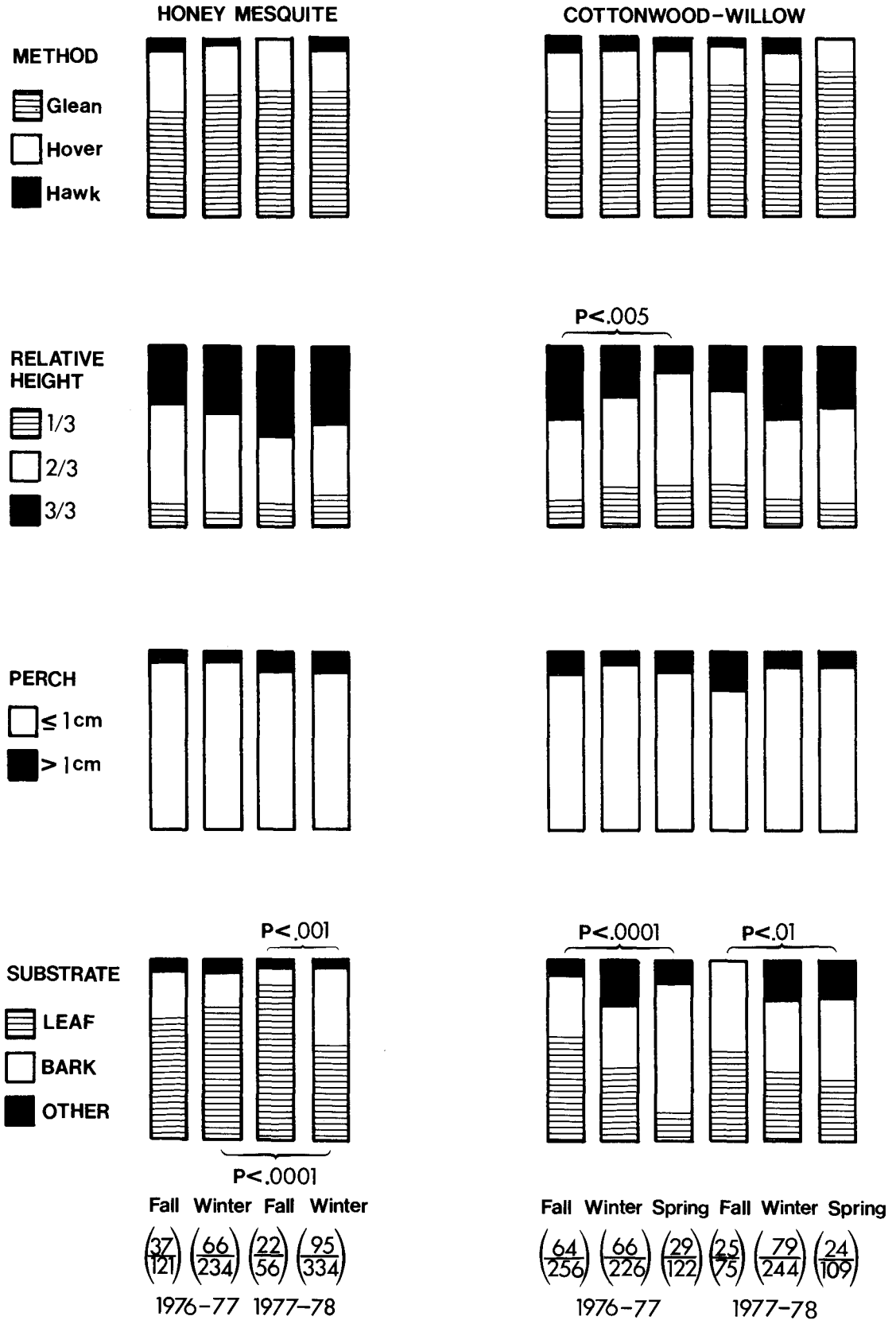


FIGURE 4. Percent of foraging observations of kinglets in each category presented seasonally for two years in honey mesquite and cottonwood-willow. G-tests, adjusted for Type I error rates (see Methods), determined significant differences. Statistics performed on original data. Parentheses below seasons indicate number of individuals observed per total number of foraging observations.

TABLE 2. Utilization (percent of total observations) of various foraging substrates by Ruby-crowned Kinglets in honey mesquite and cottonwood-willow riparian plant communities in the lower Colorado River valley. The numbers in parentheses below the months indicate number of individuals observed/total number of foraging observations recorded.

Substrate*	Honey mesquite (<i>Prosopis glandulosa</i>)							
	October–November		December		January		February	
	1976 (37/121)	1977 (22/56)	1976 (10/34)	1977 (25/83)	1977 (24/87)	1978 (31/124)	1977 (32/113)	1978 (39/127)
<i>P. glandulosa</i>								
Leaf	61	69	57	68	74	54	57	10
Branch	24	11	27	22	22	36	11	51
Trunk	0	0	0	0	0	3	0	0
Other	6	2	0	1	0	0	2	4
Other species								
Leaf	9	19	16	6	4	5	26	24
Branch	0	0	0	3	0	0	3	11
Trunk	0	0	0	0	0	0	0	0
Other	0	0	0	0	0	0	0	0
Substrate*	Cottonwood-willow (<i>Populus fremontii</i> - <i>Salix gooddingii</i>)							
	October–November		December–January		February		March	
	1976 (64/256)	1977 (25/75)	1976–77 (43/143)	1977–78 (38/100)	1977 (23/83)	1978 (41/144)	1977 (29/122)	1978 (24/109)
<i>P. fremontii</i>								
Leaf	12	11	2	5	12	4	6	7
Branch	9	3	3	2	0	9	5	7
Trunk	1	2	0	0	0	12	26	9
Other	0	0	24	17	0	0	0	2
<i>S. gooddingii</i>								
Leaf	34	23	25	20	30	16	13	25
Branch	22	11	22	23	14	19	20	22
Trunk	6	27	8	17	9	8	14	3
Other	0	0	0	0	28	19	7	19
Other species								
Leaf	16	17	10	14	7	10	5	6
Branch	1	8	7	1	0	3	0	2
Trunk	0	0	0	0	0	0	5	0
Other	0	0	0	0	0	0	0	0

* Trunk refers to all trunk portions and branches >10 cm; other refers to mesquite pods, mistletoe (*Phoradendron californicum*), and ground in the honey mesquite community, and flowers, fruits, and ground in the cottonwood-willow community.

showed a gradual shift to bark in winter during 1977–1978.

A more detailed approach to kinglet use of foraging substrate revealed a pattern closely tied to phenological events in the two communities (Table 2). In cottonwood-willow, kinglets increased their use of cottonwood flowers in January and willow flowers in February. Leaf drop begins in mid-November and continues through the winter in these two tree species. The greatest percentage of leaves have fallen by mid-December. Cottonwoods flower in early and mid-January, and new leaves appear in February. Willows follow the same pattern, but a month later, with flowering in February and leaf initiation in March. Kinglets did not differ in leaf-bark use despite subsequent leaf initiation in spring.

In the honey mesquite habitat, leaf drop began in mid-November and continued through the winter. Flowering or leaf initiation

did not occur until March. In the winter of 1977–1978 kinglets lessened their use of leaves and increased their use of bark throughout the winter. In February of both years they also made increased use of trees other than honey mesquite, primarily evergreen shrubs, such as salt bush (*Atriplex lentiformis*) and creosote bush (*Larrea divaricata*). In the winter of 1976–1977 kinglets did not shift from leaf to bark substrates. Leaf surfaces were used to a much greater extent throughout the winter. During September 1976 a great portion of the study area where honey mesquite occurs flooded, leaving large expanses of standing water that remained through September and October. This rain apparently caused honey mesquite trees to leaf out in November, a phenomenon not seen in any of the other three years. Although the trees never attained full leaf growth, many of them carried leaves through the winter, and these were used by kinglets.

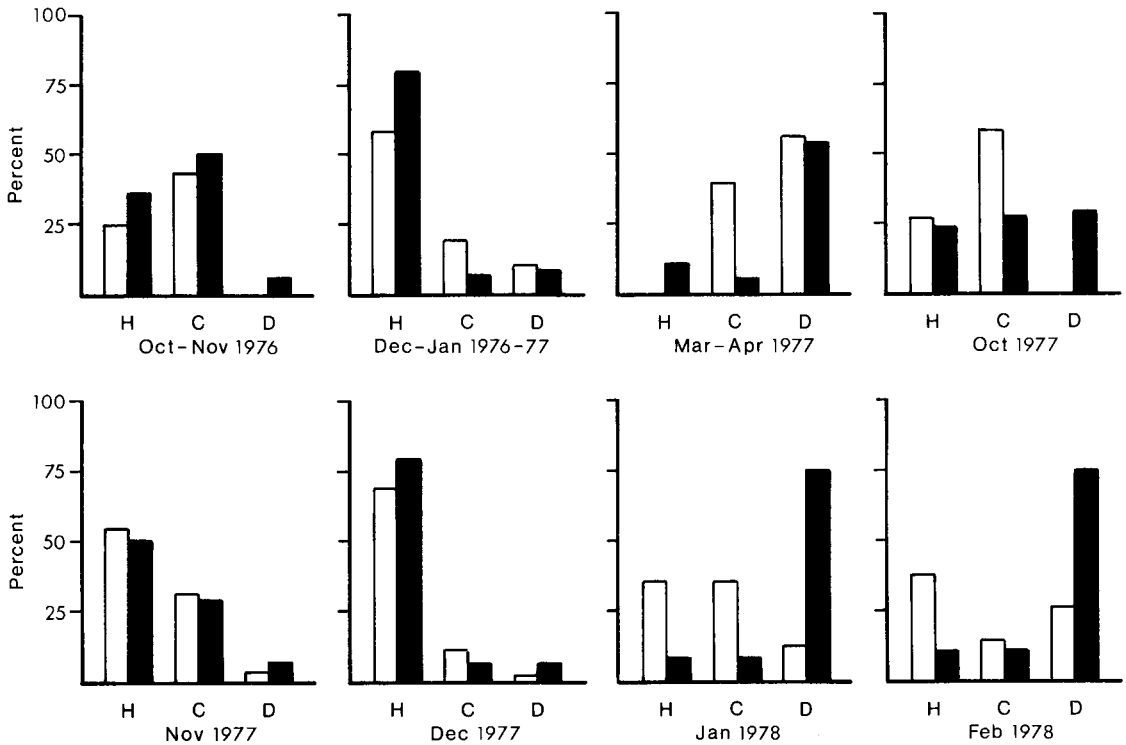


FIGURE 5. Percent of the total numbers of insects among three orders (H = Homoptera, C = Coleoptera and D = Diptera) in kinglet stomachs (open bars) and foliage sweep samples (closed bars) in the lower Colorado River valley during eight sampling periods.

DIET AND PREY AVAILABILITY

Kinglets ate arthropods almost exclusively; only three of 104 stomachs contained seeds. Two stomachs contained a small amount of plant matter, which was probably consumed while gleaning insects. Of the 16 insect orders found in foliage sweep samples, nine were present in kinglet stomachs. The seven orders not present accounted for less than 3% of the total number of insects collected in foliage sweep samples.

The majority of insects eaten were homopterans, coleopterans, and dipterans, which constituted from 50 to 100% of the total number of insects in the kinglet diet in any one month. These three orders also constituted from 67 to 95% of the total number of foliage insects collected in any one month in the sweep samples (Fig. 5). In general, an increase in the percentage of insects from a particular order in the kinglet diet paralleled the proportionate representation of that order in insect sweep samples, although this did not appear to be true of dipterans in January and February 1978 (Fig. 5). However, the percent occurrence of stomachs containing dipteran fragments increased from 20% in December to 47% in January to 69% in February.

Monthly mean prey size (average of indi-

vidual mean prey sizes) did not decrease through the winter (Table 3). There were no significant differences in mean prey size between any two successive months in either year, or between months of largest prey size eaten and smallest prey size eaten in either 1977 or 1978. Seasonal comparisons between fall and winter, fall and spring, or winter and spring within and between years also yielded no significant differences. The lack of a significant difference in any paired comparison, despite inflated Type I error rates due to multiple paired comparison tests, emphasizes the similarity in kinglet prey-size selection among sampling periods.

Ninety-five percent of the insects taken from stomachs of kinglet specimens were ≤ 4.5 mm in length. This size class accounted for most of the insects present in foliage insect sweep samples (Fig. 6).

Body length of foliage insects in sweep samples decreased through the winter in both years as did total biomass (Fig. 7). Numbers of insects increased through the winter of 1976-1977, but the biomass per individual insect decreased from 0.007 g/individual in November to 0.0007 g/individual in February. Insect numbers declined through the 1977-1978 winter as did biomass per individual insect, 0.0021

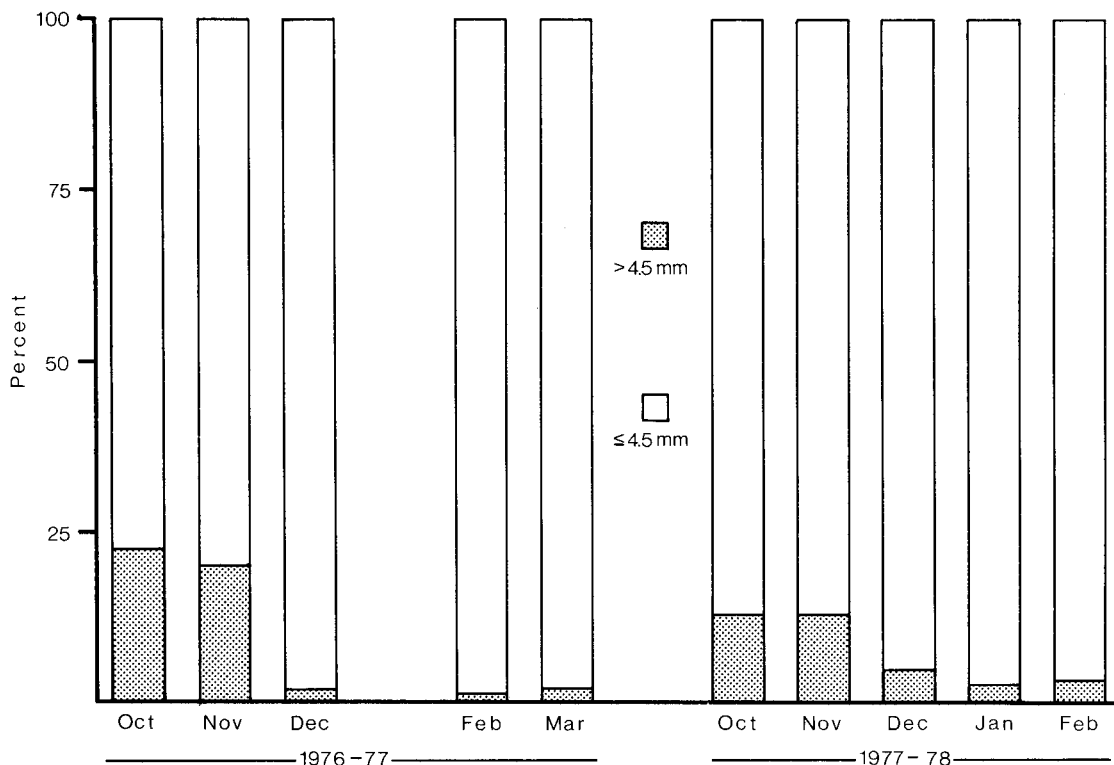


FIGURE 6. Percent of collected insects occurring in two size classes from monthly foliage sweep samples, October–March, during two years in the lower Colorado River valley. No samples were taken in January 1977.

g/individual in November to 0.0009 g/individual in February. During October–December 1977 more insects were collected than in the previous year at that time, but biomass

TABLE 3. Summary of stomach content analysis for 104 Ruby-crowned Kinglet specimens collected in the riparian corridor of the lower Colorado River valley. \bar{x} prey size represents averages of individual mean sizes in millimeters with SD.

Date	Number of stomachs	Number of insect orders present	\bar{x} Prey size \pm SD
March–April 1976	2	3	2.22 \pm 0.311
October 1976	1	3	2.80
November 1976	2	5	4.50 \pm 1.414
December 1976	4	6	3.33 \pm 2.083
January 1977	10	5	2.61 \pm 0.469
March–April 1977	5	4	3.20 \pm 0.843
October 1977	6	6	4.28 \pm 2.361
November 1977	23	8	3.11 \pm 0.572
December 1977	10	6	3.07 \pm 0.710
January 1978	16	7	2.92 \pm 0.714
February 1978	15	7	2.79 \pm 0.574
March–April 1978	10	5	2.81 \pm 0.883
Fall 1976	3	6	3.93 \pm 1.962
Winter 1976–1977	14	6	2.82 \pm 1.270
Spring 1977	5	4	3.20 \pm 0.843
Fall 1977	29	8	3.35 \pm 1.495
Winter 1977–1978	41	8	2.91 \pm 0.430
Spring 1978	10	5	2.81 \pm 0.883
Totals 1976–1978	104	10	3.04 \pm 0.976

was less as was biomass per individual collected when compared to the previous year.

DISCUSSION

The winter distribution of kinglets is predominantly Nearctic (Leptien and Bock 1976, Keast 1980a), which may be related to their Palearctic origin (Williams 1958). Their northern origin possibly enables them to winter farther north than many other small North American migrant insectivores. Keast (1980b) reported that kinglets at Prince Edward Point, Ontario, Canada, leave later and arrive earlier than any other small insectivores, except the Yellow-rumped Warbler (*Dendroica coronata*) and Golden-crowned Kinglet (*Regulus satrapa*). He attributed this to the greater cold tolerances of these species, which have a more northerly winter distribution compared to other migratory insectivores of similar size.

Despite the presumed tolerances of kinglets to a predominantly temperate wintering environment, data presented herein suggest that kinglets were strongly affected by the vicissitudes of a temperate winter. Substantial population decreases occurred over the winter in each year and marked seasonality was apparent during the nonbreeding period in the lower Colorado River valley.

In all four study years, kinglet numbers

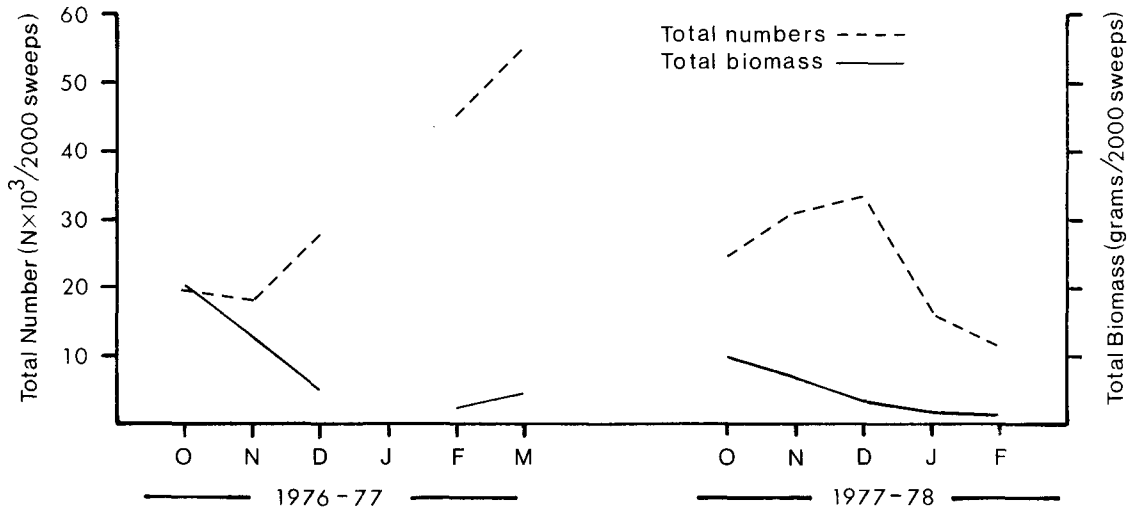


FIGURE 7. Total numbers and total biomass of insects collected in monthly foliage sweep samples in the lower Colorado River valley during two years. No samples were taken in January 1977.

decreased significantly between fall and the end of winter. Individual study sites were sufficiently numerous, between 55 and 83 20-ha plots, that we are confident these decreases did not merely reflect local redistribution (Wiens 1977). Additional data from other habitat types (i.e., residential, agricultural, and desert washes) exhibited an identical pattern of decreasing abundance through the winter (Anderson and Ohmart, unpubl. data). Some birds in November were probably in transit to more southerly habitats, so the degree to which these decreases reflect the harshness of the environment may be somewhat misleading. However, the greatest proportion of population decreases occurred over the entire winter. It was not possible to determine if the decreases were a result of kinglet mortality. Still, if the decreases were a reflection of mid-winter emigration, it is important to note that the lower Colorado River valley is essentially "a habitat island" surrounded on all sides by large expanses of sparsely vegetated desert. Any emigration by kinglets probably involved a flight of considerable distance. Considering the possible risks of migratory flight, particularly for immature birds (Greenberg 1980), mid-winter emigration may have also caused a substantial amount of mortality.

The significant correlations obtained between kinglet densities and two weather variables suggest that kinglet populations responded to changes in weather conditions. Lepthien and Bock (1976) also provided evidence that weather conditions influenced kinglet distribution. However, weather data often require subjective interpretation because of the manner in which various factors interact to produce a mild or harsh environment and the

difficulty in determining which are the most important factors.

In the four years of this study, 1977-1978 was clearly distinct from the other three years. Mild temperatures prevailed throughout the winter, rainfall was abundant, and, initially, insect sweep samples contained substantially more insects than the previous year. Kinglet densities were 50% greater than in any other year and underwent the lowest winter decrease. Numerous other wintering migrant birds were also more abundant that year (Anderson and Ohmart, unpubl. data). This was true for both the common wintering migrant, the Yellow-rumped Warbler, and those migrants usually seen in very low numbers during the winter, such as the Orange-crowned Warbler (*Vermivora celata*) and the House Wren (*Troglodytes aedon*).

Attributing the high densities of kinglets solely to the mild winter is questionable, however, because October and November densities of kinglets were also high. These months are typically mild and were not unusual in 1977. The high densities of kinglets may have been coincidentally related to factors outside the valley (e.g., a successful breeding season, favorable weather conditions for migration). Nonetheless, it is reasonable to assume that the small population decrease over the winter despite these high initial densities was due, in part, to the mild winter.

Of the other three years, 1975-1976 was both very dry and as cold as the other years. Kinglet numbers declined precipitously during that winter; the bulk of that decrease occurred between December 1975 and January 1976. January 1976 was the coldest of the four Januaries, and rain was virtually nonexistent. This

was in addition to eight previous months of dry weather. The severity of conditions was emphasized by the lack of a single kinglet detection in 60 censuses of 500 ha of honey mesquite in February 1976, a habitat that averaged 34 kinglets per 40 ha in February 1978.

Seasonal changes during the nonbreeding period were accompanied by changes in kinglet distribution among the plant communities. The consistency and distinctiveness of kinglet distributions among the habitat types in fall probably paralleled the environmental conditions during fall for these years. Temperatures were mild, frost did not occur until late in November, trees and shrubs had foliage, and insect biomass was relatively high. These habitat relationships, however, were not maintained through the winter. In February, kinglets were not distributed among the plant communities as they were in November, and the distinctiveness of these communities in relation to numbers of kinglets present (significant differences among communities) was not maintained in three of the four winters. This is not surprising considering the difference in winter temperatures, phenological events within plant communities, and the decrease in insect biomass through winter.

It may be that those cues used to determine habitat suitability in November involved both plant species composition and structure. By winter's end, only structure appeared to influence the distribution of kinglets among study sites. Kinglets were most abundant in the areas of tall, dense vegetation and were scarce or absent from areas with low foliage profiles (foliage volume ≤ 0.6 m, 0–0.6–4.5 m and total patchiness) or transects characterized as predominantly shrublike. These areas of tall vegetation are similar to types of riparian habitat that existed in the late 19th and early 20th centuries. Kinglets may be responding to these remnants of cottonwood-willow gallery forest and mesquite bosques described by early explorers (Grinnell 1914, Ohmart et al. 1977).

Changes in foraging behavior, while not specifically elucidating the impacts of a harsh winter, provided insight into the degree of seasonality present and the manner in which habitat quality may have differed between plant communities. During winter in honey mesquite, kinglets were limited to bark surfaces and persisting leaves. In cottonwood-willow, the birds were found to forage on four or more substrates. These differences were directly related to tree species phenology in each habitat. In addition, kinglets did not utilize large branches and trunks in honey mesquite (Table 2). Since they are able to hover, it seems likely

that the under-utilization of these substrates in honey mesquite communities was due to differences in prey occurrence on these substrates compared to cottonwood-willow rather than the availability of perches. The greater number of available foraging substrates in cottonwood-willow might be one way in which habitat quality differed between the two communities.

Kinglets also appeared to prefer flower and leaf substrates when available. This was shown in cottonwood-willow by the consistent tracking of cottonwood and willow flowering by kinglets in both years and in honey mesquite during the winter of 1976–1977 when leaves were present on honey mesquite all winter. The presence of leaves through the winter that year may have accounted for the increase in densities of kinglets in January. This was not a significant increase ($U = 262.5$; $P < 0.91$) but densities decreased on only 5 of 20 transects in January.

The significant shifts in foraging height were due primarily to an increased use of shrub substrates. In the cottonwood-willow community, use of salt cedar increased, and in the honey mesquite community there was an increased use of *Atriplex* spp. and creosote bush. These shifts appeared to be related to kinglet preference for leaf substrates. Salt cedar usually carries a great amount of dead leaves through the winter; *Atriplex* spp. and creosote bush are evergreen shrubs. All shifts were away from the canopy where little to no foliage was present during the winter.

Perch size selection did not vary seasonally and may be related to the inability of kinglets to grasp large branches. To use larger foraging substrates, the birds usually had to use a nearby small branch or a small piece of exfoliating bark, or to hover. In the few instances when kinglets were observed grasping a large branch, they appeared awkward and unstable. Physical ability was apparently limited by morphology and was not subject to seasonality. The proportion of gleans and hovers employed by kinglets is consistent with observations on foraging kinglets in pine-oak woodlands of southern Arizona (Austin and Smith 1972).

Foliage sweep samples indicate that in general insect numbers decreased through the winter. However, these samples varied highly between years. Insect biomass was greater through the winter in 1976–1977 than in 1977–1978. In addition, insect numbers collected increased dramatically in February and March 1977, whereas they decreased through the winter in 1977–1978. Assumptions on availability of food in light of environmental conditions without empirical data may be highly invalid.

Considering the mild nature of the winter in 1977–1978, one might have expected opposite results.

Optimal foraging theory would predict specialization when food is abundant (Schoener 1971, Emlen 1973). The kinglets' choice of prey items appeared relatively general and opportunistic. They ate a variety of insects from a number of orders and appeared to eat whatever was most abundant. Prey-size selection was very narrow, with most insects eaten being ≤ 4.5 mm in length; however, in fall more insects > 4.5 mm were eaten compared to winter. This corresponded to the greater number of insects > 4.5 mm in foliage sweep samples at that time. These larger insects were predominantly lepidopteran larvae and were eaten by numerous insectivorous birds (Anderson and Ohmart, unpubl. data).

Examination of data on biomass of insects ≤ 4.5 mm indicated that biomass per individual insect decreased in both years. Considering the lower winter temperatures and decreased biomass values of foliage insects collected, it is reasonable to assume that kinglets undoubtedly had to eat more insects in winter. Given the small size of insects eaten, it appears that kinglets might have been approaching the level at which energy gain per prey item would not compensate for the energy expended in obtaining that item. The energy expenditure may be very high for kinglets considering the degree to which they hover or need to hover because of their difficulties in finding perches of the proper size. Whether food was more limiting in winter than in fall is difficult to determine. More specific study is needed to determine the influence of increased insect density in compensating for lower biomass values per individual insect. In-depth studies are needed to determine the influence of environmental temperature in minimizing or exacerbating the impact of decreased insect biomass and density.

In summary, our findings support other research on migrant birds (Keast and Morton 1980, and references therein) in emphasizing the selective importance of nonbreeding season requirements. Our data suggest that kinglets may be winter-limited and that additional study should be directed toward integrating nonbreeding season ecology with knowledge of the breeding season to effectively understand the biology of kinglets and other bird species.

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RECENT PUBLICATIONS

Handbook of the Birds of India and Pakistan. Vol. 3. Second edition.—Salim Ali and S. Dillon Ripley. 1981. Oxford University Press, Delhi. 327 p. \$33.00. This volume continues the revision of the series (noted in Condor 78:574, 81:416, and 83:189). It covers Charadriiformes (Burhinidae through Laridae), Columbiformes, Psittaciformes, Cuculiformes, and Strigiformes. Minor changes have been made for many species. In order to maintain the original pagination, major additions are relegated to an appendix. These include five new species or subspecies for the region and a key to the calls of the seven cuckoo species there. The original color plates have all been retained except for four which have been replaced with new ones by F. P. Bennett, Jr.

Aves Brasileiras/Birds of Brazil/Identification Guide. Addendum.—Johan Dalgas Frisch. 1982. Dalgas-Ecoltec Ltda., São Paulo, Brasil. [25 p.], paper cover. This pamphlet, in English, is a supplement (rather than an addendum) to the guidebook, which is in Portuguese (noted in Condor 84:171). A new introduction explains the background, scope, and production of the book. The sections on nomenclature and on the chief characteristics of Brazilian orders and families of birds are translated. This material is fairly elementary and it contains several errors, perhaps introduced in translation. The chapters on watching, photographing, and recording birds have not been translated because they were deemed of limited value for foreign readers. Copies of the book that are sold in North America will presumably be furnished with this pamphlet. Individuals and libraries that already own the book should request a free copy of the supplement from the publisher.

Wintering Waders on the Banc d'Arguin, Mauritania/Report of the Netherlands Ornithological Mauritanian Expedition, 1980.—Wibe Altenburg, Meinte Engelman, Ron Mes, and Theunis Piersma. 1982. Communication Number 6 of the Wadden Sea Working Group. Krips Repro, Meppel, Netherlands. 283 p. Paper cover. L 6.00 by international money order from Netherlands Ornithological Mauritanian Expedition 1980, Semarangstraat 8A, 9715 JW Groningen, The Netherlands. This small volume is an ornithological sleeper. What began as a birdwatching expedition to the wintering shorebird concentrations on the west coast of Africa quickly became a major ornithological expedition. Some portions of the text remain narrative

and conversational. Others are detailed reports of systematic counts of birds and macrobenthos, and thorough ecological descriptions of the study area. Distribution of species among ecological zones, a partially successful correlation with available food organisms, and new information on foraging habits for some wader species are ecological highlights. Black-and-white photographs, line-drawings, and figures; maps; bibliography; summaries in French, Dutch, Frisian, Arabic.—J. Tate.

An Annotated Checklist of Peruvian Birds.—Theodore A. Parker, III, Susan Allen Parker, and Manuel A. Plenge. 1982. Buteo Books. 108 p. Paper cover. \$15.00. Source: Buteo Books, P.O. Box 481, Vermillion, SD 57069. While not quite an annotated checklist in the usual sense, this book nonetheless contains a great deal of information about birds and birding in Peru. Advances in understanding the diverse avifauna of northern and western South America are represented by nearly a full page of new and recently described species and races, along with their sources. The accounts of life-zones, descriptions of vegetation, and the reference photographs appear thorough and well done. The checklist, however, is more like those encountered at National Wildlife Refuges, being composed of symbols in a chart cross-referenced to the major life-zones. Unexpected, and welcome, are ten pages devoted to bird-finding in Peru. Cover painting by John O'Neill; black-and-white photographs, figures and maps; literature cited; additional reading; index to common names, and genera.—J. Tate.

Die Vogelarten der Erde. 7. Lieferung (Schluss).—Hans E. Wolters. [1982]. Verlag Paul Parey, Hamburg. 316 p. Paper cover. Subscription DM 150. Source: Verlag Paul Parey, Spitalerstrasse 12, 2000 Hamburg 1, Germany. Here is the final material for the author's list of living and recently extinct species of birds of the world. (Previously issued parts were noted in Condor 82:397 and 83:216.) It includes copious indexes, and pages to be put at the front of the volume (title page, introduction, and table of contents). Available too (at a cost of DM 12.80) is a hardboard cover for the entire volume and instructions for binding. This work is likely to become a major reference on the nomenclature, systematics, and breeding distribution of birds, especially for those groups that have not yet been treated in Peters' *Checklist*.