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SEQUENTIAL VERSUS INITIAL OBSERVATIONS IN STUDIES OF AVIAN FORAGING

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Abstract. During the breeding season, we compared sequential and initial observations of the foraging locations of five species of permanent residents in an oak-pine woodland of the western Sierra Nevada. Sequential observations were more dependent—that is, the conditional probabilities of occurrence of any locations were greater when from a sequence—than were initial observations. No visibility biases were associated with either method. Using bootstrap simulations, standard errors calculated for all observations (initial + sequential), without adjustment for dependency, underestimated the true standard error in 68% of the cases, with no difference in 32%. For common foraging locations, the mean proportions of used foraging sites and foraging substrates were similar with both methods, but initial observations gave more precise estimates of foraging locations than did all observations. The two methods differed in their estimates of means and standard errors for uncommon foraging locations. We also created a model using Markov chain analysis to investigate a larger population of sequential observations. Both Markov chain and bootstrap analyses resulted in similar implications. We prefer the use of initial observations in statistical tests that assume independence between observations and the use of statistical techniques that adjust for dependency with dependent, sequential observations. Suggestions for appropriate statistical analyses of sequential observations are given.

Key Words: Foraging; dependent observations; independent observations; statistical analysis; bootstrap; Markov chains.

Martin and Bateson (1986) emphasized that a common error in behavioral research is to treat repeated measures of an individual as though they were independent. One problem likely to result from analyses of such data is underestimation of sample variance. Although the problem of dependence is acknowledged by some students of avian foraging behavior, most have nonetheless used repeated observations from the same individual during the same period without testing for independence between observations from a single individual (but see Holmes et al. 1979b, Porter et al. 1985).

Researchers have used all sequential observations that they could obtain from an individual (Holmes et al. 1979b, Holmes and Robinson 1981, Sabo and Holmes 1983, Keeler-Wolf 1986), or have allowed sequential records of the same individual only after elapse of a specified period of time (e.g., Landres and MacMahon 1980, Wagner 1981a, Morrison 1984a, Porter et al. 1985) or after the bird moved to a new location (e.g., Hartley 1953, Root 1967, Peters and Grubb 1983). Hartley (1953) recorded the first observation on each separate plant while following the same bird. Root (1967) recorded up to three observations from the same individual, always separated by at least 2 min, and they were recorded only if the bird moved to a new substrate between records. Peters and Grubb (1983) recorded up to four observations of a given bird, but only after it moved to a new location for each record.

In addition to obtaining larger samples, many researchers prefer using all observations (initial + sequential observations) because they believe that initial observations are biased toward birds in conspicuous locations (e.g., Sturman 1968, Wiens et al. 1970, Austin and Smith 1972, Hertz et al. 1976). Wagner (1981a) and Morrison (1984a) both compared the results from initial observations with those from all observations. Wagner concluded that the method of data collection had an effect on her results but that different visibility biases were associated with each method. Morrison (1984a) concluded that similar results were obtained by the two methods for most measures, but he preferred sequential sampling because more rare behaviors were observed in his sequential data set. Bradley (1985) compared methods for biases in time-budget studies, concluding that counting only initial contacts was the least satisfactory of the four methods and was especially prone to discovery bias.

We studied the foraging behaviors of five species of birds—Scrub Jay (*Aphelocoma coerulescens*), Plain Titmouse (*Parus inornatus*), Bushtit (*Psaltriparus minimus*), Bewick's Wren (*Thryomanes bewickii*), and Brown Towhee (*Pipilo fuscus*)—in an oak-pine woodland in the foothills of the western Sierra Nevada. Our objectives were: (1) to test for independence among sequential observations of foraging sites and foraging substrates used by the birds, (2) to explore whether all observations gave the same information about foraging locations as did initial observations, and (3) to consider various analytical procedures that can be used to make appropriate adjustments in variance derived from sequential observations.

STUDY AREA AND METHODS

This study was done at the San Joaquin Experimental Range in March, April, and May 1980, and May 1982, during the breeding season. The Range is located approximately 32 km north of Fresno in Madera Co., California. Vegetation was characterized by intermixed patches of blue oak (*Quercus douglasii,* 5.4% cover) interior live oak (*Q. wislizenii,* 7.2% cover), gray pine (*Pinus sabiniana,* 12.5% cover), chaparral, mainly buckbrush (*Ceanothus cuneatus,* 18.6% cover), and annual grassland. Combined cover of the nine remaining tree and shrub species was 4.5% (J. Verner, unpubl. data). The climate is characterized by hot, dry summers and cool, wet winters.

Field observations were made on a 19.8 ha plot (300 × 660 m) gridded into 30-m quadrats, located in approximately 32 ha of foothill woodland that has not been grazed by livestock, burned, or otherwise disturbed since 1934.

BIRD OBSERVATIONS

Three observers recorded data in 1980 and five in 1982; two were the same observers in both years. Observers walked along alternate, numbered lines in the long dimension of the grid. Lines walked and the direction of travel were selected to ensure even coverage of all segments of the grid. Walking and stationary searches for birds were alternated approximately every 15 min. We attempted to obtain an equal number of observations of each species during each quarter of the daylight period, from sunrise to sunset, although sample sizes were smaller during the early afternoon quarter than during other quarters.

Only certain birds were selected for observation. Observers did not search out singing birds, as this would have biased our sample toward singing birds, although most birds sang or called during the period that they were observed. Only the first bird detected in a flock or pair was used as a subject, as locations of flock or pair members might not be independent. Further, a new individual of a given species was chosen as a subject only if the observer had traveled at least 30 m or unless 10 min had elapsed, since the last record of that species.

When a bird was accepted as a subject, we recorded its species and several aspects of its behavior and location. From the time of first detection, the observer counted slowly to 5 (approximately 5 s), allowing time to assess the bird's activity. Its activity at the count of "5" was recorded as an instantaneous sample. (We distinguish between the "state" of foraging, as being in the process of searching for and/or procuring food, and the "event" as actually procuring or attempting to procure a food item; see Altmann 1974, Martin and Bateson 1986.) If the bird was looking for food (in the state of foraging, but not the event of foraging) when the instantaneous sample was taken, but it did not appear to procure or attempt to procure a food item at that instant, the observer followed it visually until it appeared to procure or attempt to procure food. All subsequent locations of food procurement (sequential observations) were recorded, to a limit of 11 in 1980 and without limit in 1982.

In this paper we analyzed two measures of the location where a bird appeared to procure a food item, based on data obtained only in 1980: (1) foraging site (gray pine, blue oak, interior live oak, buckbrush, ground, or "other"); and (2) foraging substrate, the part of the plant or environs toward which a foraging maneuver was directed (air, twig [<5 mm in diameter], small branch [5 mm to 10 cm in diameter], large branch [>10 cm in diameter], flower bud, flower, catkin, cone, staminate cone, forb, fruit, ground, leaf bud, leaf, and trunk).

The effect of concealing cover on the detectability of a bird and the time between its subsequent foraging maneuvers were recorded only in 1982. Concealing cover for each observation was described as (1) little (the bird was completely in view), (2) moderate (vegetation obscured some of the bird), and (3) much (vegetation nearly obscured the bird). Observations ceased when the observer could no longer see the foraging behavior of the bird.

STATISTICAL ANALYSES

We used an alpha level of 0.05 for tests of significance.

Dependency among sequential observations

We created transition matrices and corresponding Pearson's contingency coefficients (Conover 1971:177) for the sequential observations to compare with matrices and coefficients for the initial observations used as a standard, assuming that initial observations were independent. These were then used to investigate dependency between sequential observations with zero, one, two, and three intervening observations, to compare values for sequential observations to those obtained from initial observations and to evaluate the effects of repetitive foraging habits on the Pearson's value that would be obtained from independent samples. The chi-square distribution provides a test of the significance of Pearson's contingency coefficients. To examine observations separated by one intervening observation, we compared the first observation to the third, the second to the fourth, and so on. A similar approach was used to compare observations separated by two and three intervening observations. For example, to examine observations separated by two intervening observations, we compared the first observation to the fourth, the second to the fifth, and so on. Pearson's contingency coefficients were corrected by dividing each coefficient by the maximum value possible for each contingency table.

Visibility bias

Places where birds were first observed may have been biased toward locations where they were most conspicuous. We tested this in two ways. First, we tested whether initial observations in certain sites or substrates more often resulted in records of subsequent observations. We used chi-square analysis to test whether the frequency of first observations differed by record length as a function of site or substrate at the initial location. Bonferroni adjustments (Miller 1981: 67) compensated for multiple comparisons.

Second, we used McNemar's test (Conover 1971: 127) to compare first and second observations from sequences. This test adjusted for dependency between observations, and Bonferroni adjustments compensated for multiple comparisons. Our sample size of matched pairs from third or later observations in sequences was too small for this test. Initial observations as a group could not be compared statistically to subsequent observations as a group, because not all records included the same number of observations (i.e., weighting problems and many unmatched initial observations; some initial observations did not have subsequent observations and some had many). Further, comparison of initial observations as a group with all observations as a group (as many researchers have done) is inappropriate, because the initial observations are a subset of all observations and often comprise a substantial proportion thereof, and unequal record lengths result in weighting and matching problems.

Estimating means and standard errors

Because they adjust for dependency within samples, bootstrap simulations (Efron and Gong 1983) were used to compare means and standard errors (precision) of the sample proportions of each class of site and substrate by initial observations and by all observations (initial + sequential observations). Five hundred random samples were drawn, with replacement, from the observed data.

To see whether large numbers of sequential samples would provide additional information, we used Markov chain analyses (Bishop et al. 1975:257–267, Isaacson and Madsen 1976) to compare differences in results based on initial observations and all observations. Assuming that our initial observations were independent of each other and that they approximated true proportions, our Markov chain model had characteristics similar to our data. We further assumed that the generation of successive observations in a sequence occurred according to a first-order Markov process. Transition matrices from sequential observations in the 1980 data set were estimated to approximate the true probability of change from one foraging site to the next and one foraging substrate to the next. Probabilities of the length of each sequential record were also estimated from our sample. Simulations of foraging records were then created from 500 runs for each species, drawing the same sample size as in the original data set for each species, and weighting each record length according to its proportion in the original data. Means and standard errors for initial observations as a group and all observations as a group were then computed for each simulation.

Both bootstrap and Markov chain analyses were also used to examine standard errors of all observations with and without adjustment for dependency among sequential observations. We compared the bootstrap estimate of standard error to the usual standard error created when assuming that all sequential observations were independent. From the Markov chain analyses, we compared the standard errors generated from each of the 500 simulations with the measure of standard error calculated from the mean estimate of proportions from all 500 simulations.

Because the means and standard errors generated by Markov chain analyses approximate the true values, based on the assumptions given, statistical comparisons are unwarranted. As a conservative criterion, we assumed that any difference between initial observations and all observations was biologically meaningful if the absolute difference exceeded 0.2 times the value from the initial observations. We used the same criterion to interpret bootstrap results.

RESULTS

The primary data set (1980) used in this study contained 1070 records of foraging events; 66% of those were of Plain Titmice and Bushtits, the two most commonly detected species on the plot. Sixty-five percent of all observations consisted of single records of foraging birds. We were seldom able to follow the same individual long enough to observe five consecutive foraging maneuvers, and records of eight or more consecutive behaviors were rare (Table 1).

In 1982, the only year we timed foraging sequences, the duration of a record was highly variable. For example, collective results from the five species gave a mean of 36 s (SD = 63; N = 173; range = 5 s to 6 min 38 s) to complete five consecutive maneuvers.

Our ability to record sequential observations differed among the bird species (Table 1). Sequential observations were obtained in 59% of the records of Brown Towhees but in only 31–34% of the records of the four other species. Data on the percent of sequences with 10 or 11 observations indicated that, if Scrub Jays, Plain Titmice, and Brown Towhees could be followed at all, they could be followed up to our self-imposed limit 7%, 7%, and 20% of the time, respectively. Bewick's Wrens changed foraging sites during 29% of the sequential observations, but the other species did so in only 6–10% of them. Thus we were more likely to get new information from sequential observations of Bewick's Wrens than from any other species.

DEPENDENCY AMONG SEQUENTIAL OBSERVATIONS

All analyses showed that sequential observations were highly dependent, with all values exceeding 0.64 and all but 4 of 40 values exceeding 0.81 (Table 2). For comparison, the Pearson's contingency coefficients that we created as standards using initial observations of foraging sites were 0.42 (Scrub Jay), 0.35 (Plain Titmouse), 0.38 (Bushtit), 0.57 (Bewick's Wren), and 0.52 (Brown Towhee); and of foraging substrates were 0.38 (Scrub Jay), 0.52 (Plain Titmouse), 0.59 (Bushtit), 0.42 (Bewick's Wren), and 0.39 (Brown Towhee). The transition matrix for foraging sites of Scrub Jays—for sequential observations with no intervening observation—had the highest Pearson's contingency coefficient (1.00) (Table

TABLE 1. Distribution of Records According to the Number of Foraging Maneuvers by an Observed Bird During a Continuous Observation (Proportions Shown below the Number of Records) in the 1980 Data Set

	Number of foraging maneuvers										
Species	1	2	3	4	5	6	7	8	9	10	11
Scrub Jay	117	13	15	4	6	1	1	1	0	12	0
	0.69	0.08	0.09	0.02	0.04	0.01	0.01	0.01	0.00	0.07	0.00
Plain Titmouse	230	40	19	15	5	6	2	1	2	23	0
	0.67	0.12	0.06	0.04	0.02	0.02	0.01	0.00	0.01	0.07	0.00
Bushtit	244	44	36	20	7	1	0	1	0	6	0
	0.68	0.12	0.10	0.06	0.02	0.00	0.00	0.00	0.00	0.02	0.00
Bewick's Wren	65	9	11	3	6	1	2	2	0	0	0
	0.66	0.09	0.11	0.03	0.06	0.01	0.02	0.02	0.00	0.00	0.00
Brown Towhee	41	10	9	6	9	3	1	0	0	16	4
	0.41	0.10	0.09	0.06	0.09	0.03	0.01	0.00	0.00	0.16	0.04
Totals	697	116	90	48	33	12	6	5	2	57	4
	0.65	0.11	0.08	0.05	0.03	0.01	0.01	0.01	0.00	0.05	0.00

3). The transition matrix for foraging sites of Bewick's Wrens—for sequential observations with three intervening observations—had the lowest coefficient for sequential data (0.65) (Table 4). Transition matrices created from initial observations for Scrub Jays on foraging sites (Table 3) and for Bewick's Wrens on foraging sites (Table 4) showed much less emphasis on transitions between the same foraging sites (visually depicted in the matrix as a high proportion of numbers on the diagonal from the upper left corner to the lower right).

VISIBILITY BIAS

The concealing cover of a bird when initially located apparently had no effect on whether it could be followed for subsequent observations. For example, a similar proportion of initial observations led to subsequent observations as did not, irrespective of the initial foraging site or foraging substrate. Only one of 105 comparisons had a significant chi-square value.

Percentages of observations in 1982 that were in little, moderate, and much concealing cover showed that first and subsequent observations were made in similarly difficult-to-see locations. For initial observations ($N = 130$), 19% were in little, 54% in moderate, and 27% in much cover. For subsequent observations ($N = 403$), 13% were in little, 61% in moderate, and 26% in much cover. No statistically significant differences appeared in any of the comparisons of the proportions of foraging sites and substrates that were used in the first and second maneuvers in a sequence. To convince ourselves that there were no differences, we set a standard for differences in proportion equal to 0.10 for the half-width of the 95% confidence interval and 21 of the 105 comparisons were inconclusive. We cannot reject the null hypothesis of no differences for these comparisons, but we cannot view it as confirmed either because of the large width of the confidence interval. Twelve of these 21 comparisons were for Bewick's Wrens.

ESTIMATING MEANS

All observations sometimes gave markedly different estimates of means than did initial observations, particularly in the case of uncommon foraging locations (defined here as representing 10% or less of the observations). Forty-two of 81 bootstrap comparisons met our criterion of a meaningful biological difference (Table 5). Thirty-seven of the 42 differences were on uncommonly used sites and substrates. When compared to initial observations, Markov chain analyses indicated that all observations overestimated the mean in 3% and underestimated it in 13% of the comparisons of foraging sites; all of these were on uncommonly used sites. All observations overestimated the mean in 25% and underestimated it in 31% of 51 comparisons of foraging substrates. Seventy-one percent of all comparisons of uncommon substrates satisfied our criterion of a meaningful biological difference, but only 15% of all comparisons of common substrates did so.

ESTIMATING STANDARD ERRORS: ALL OBSERVATIONS VS. INITIAL OBSERVATIONS

Bootstrap and Markov chain analyses differed slightly in their estimates of standard errors (Table 5). In bootstrap comparisons, initial observations estimated common foraging locations

TABLE 2. TESTS OF INDEPENDENCE OF SEQUENTIAL OBSERVATIONS OF FORAGING SITES AND SUBSTRATES WITH CORRECTED PEARSON'S CONTINGENCY COEFFICIENTS. A COEFFICIENT OF 1.00 IS THE HIGHEST POSSIBLE INDEX OF AUTOCORRELATION

Species	Number of intervening observations	Paerson's contingency coefficients[a]	
		Foraging sites	Foraging substrates
Scrub Jay	0	1.00	0.98
	1	0.93	0.97
	2	0.94	0.97
	3	0.99	0.97
Plain Titmouse	0	0.99	0.94
	1	0.90	0.88
	2	0.99	0.90
	3	0.99	0.84
Bushtit	0	0.97	0.92
	1	0.90	0.87
	2	0.99	0.91
	3	0.99	0.96
Bewick's Wren	0	0.93	0.79
	1	0.90	0.68
	2	0.92	0.78
	3	0.65	0.88
Brown Towhee	0	0.98	0.92
	1	0.93	0.87
	2	0.92	0.85
	3	0.83	0.82

[a] All values statistically significant at $P < 0.05$.

TABLE 3. TRANSITION MATRICES FOR FORAGING SITES OF SCRUB JAYS BASED ON SEQUENTIAL OBSERVATIONS WITH NO INTERVENING OBSERVATIONS (TOP) AND BASED ON INITIAL OBSERVATIONS ONLY (BOTTOM) (PROPORTIONS OTHER THAN 0 IN PARENTHESES)

Initial foraging site	Subsequent foraging site				
	Blue oak	Gray pine	Live oak	Ground	Other
	Sequential observations				
Blue oak	80	0	0	0	0
	(1.00)				
Gray pine	1	60	0	0	0
	(0.02)	(0.98)			
Live oak	0	0	7	1	0
			(0.88)	(0.13)	
Ground	1	0	0	50	2
	(0.02)			(0.94)	(0.04)
Other	0	0	0	1	50
				(0.02)	(0.98)
	Initial observations				
Blue oak	29	11	5	13	5
	(0.46)	(0.17)	(0.08)	(0.21)	(0.08)
Gray pine	10	1	4	7	1
	(0.43)	(0.04)	(0.17)	(0.30)	(0.04)
Live oak	4	2	1	3	2
	(0.33)	(0.17)	(0.08)	(0.25)	(0.17)
Ground	14	7	1	25	8
	(0.25)	(0.13)	(0.02)	(0.45)	(0.15)
Other	6	3	1	6	0
	(0.38)	(0.19)	(0.06)	(0.38)	

more precisely than did all observations in 59% of all cases, but less precisely in only 7%. Conversely, all observations estimated uncommon locations more precisely than initial observations in 46% of all cases and less precisely in 26%. In the Markov chain analyses, estimates of standard error from all observations differed from estimates from initial observations in 79% of the comparisons of common foraging sites and in 75% of the uncommon foraging sites; the estimates of standard error from all observations differed from those from initial observations in 46% of the comparisons of common foraging substrates and 82% of the uncommon foraging substrates.

ESTIMATING STANDARD ERRORS: ADJUSTED VS. UNADJUSTED DEPENDENCY IN ALL OBSERVATIONS

Both bootstrap and Markov chain procedures generally showed that standard errors estimated from all observations in the usual (unadjusted) way, assuming them all to be independent records, were smaller than true standard errors after adjustment for dependency. Using bootstrap, the usual standard error underestimated the adjusted standard error in 68% of all cases, using our criterion of a meaningful biological difference. The two estimates were similar in 32% of the cases, and in no case did the usual procedure overestimate standard error. Markov chain analyses showed that the usual procedure underestimated true standard error for foraging site by a mean of 45%, and 28 of 30 comparisons were underestimated. For foraging substrate, the usual procedure underestimated true standard error by a mean of 34%, and 42 of 53 comparisons were underestimated. The mean underestimate differed among species, but it was not significantly correlated with sample size (either for initial observations or for all observations).

DISCUSSION

Our results suggest that using dependent sequential observations is inadvisable for the estimation of proportions of foraging locations unless appropriate statistical analyses are used to adjust for autocorrelation. We were not able to obtain sequential records that were far enough apart in time to appear independent. We were seldom able to follow an individual long enough to obtain more than five sequential records of its foraging, and all analyses showed that the fifth observation in a sequence was dependent on the

TABLE 4. TRANSITION MATRICES FOR FORAGING SITES OF BEWICK'S WRENS BASED ON SEQUENTIAL OBSERVATIONS WITH THREE INTERVENING OBSERVATIONS (TOP) AND BASED ON INITIAL OBSERVATIONS ONLY (BOTTOM) (PROPORTIONS OTHER THAN 0 IN PARENTHESES)

Initial foraging site	Subsequent foraging site			
	Live oak	Buckbrush	Ground	Other
	Sequential observations			
Live oak	0	1 (0.25)	2 (0.50)	1 (0.25)
Buckbrush	1 (0.09)	7 (0.64)	0	3 (0.27)
Ground	0	2 (0.20)	8 (0.80)	0
Other	0	1 (0.33)	0	2 (0.67)
	Initial observations			
Live oak	8 (0.38)	6 (0.29)	0	7 (0.33)
Buckbrush	8 (0.21)	19 (0.50)	1 (0.03)	10 (0.26)
Ground	1 (0.11)	2 (0.22)	2 (0.22)	4 (0.44)
Other	5 (0.17)	10 (0.33)	6 (0.20)	9 (0.30)

TABLE 5. BOOTSTRAP AND MARKOV CHAIN ANALYSES FOR COMMON AND UNCOMMON (10% OR LESS OF OBSERVATIONS) FORAGING SITES AND SUBSTRATES. AO = ALL OBSERVATIONS (INITIAL + SUBSEQUENT OBSERVATIONS) AND IO = INITIAL OBSERVATIONS ONLY. DESCRIBED DIFFERENCES IN THE MEANS AND STANDARD ERRORS ARE THOSE FOR WHICH THE ABSOLUTE VALUE OF THE DIFFERENCE BETWEEN AO AND IO WAS GREATER THAN 0.2 IO

Differences	Bootstrap		Markov chain	
	Site	Substrate	Site	Substrate
Means				
Common locations				
AO > IO	1	2	0	1
No difference	13	9	14	11
IO > AO	0	2	0	1
Means				
Uncommon locations				
AO > IO	3	9	1	12
No difference	5	12	11	11
IO > AO	8	17	4	15
Standard errors				
Common locations				
AO > IO	10	6	11	4
No difference	4	5	3	7
IO > AO	0	2	0	2
Standard errors				
Uncommon locations				
AO > IO	4	10	8	14
No difference	5	10	4	7
IO > AO	7	18	4	17

first as indicated by a higher value than those created for initial observations. However, sequential observations of some species approached an equivalent level of independence to that obtained by the use of initial observations. For example, one of the contingency coefficients for sequential observations (0.65, Table 2) of Bewick's Wrens was nearly as small as that obtained from initial observations (0.57).

Dependency between observations in a sequence leads to inaccurate estimates of variance. Unadjusted standard errors from all observations were consistently less than those adjusted for dependency. One is thus more likely to conclude erroneously that two sample means are different with unadjusted standard errors that are artificially small due to the lack of adjustment for dependency.

The use of initial observations is preferable for estimating common foraging locations, but we are not sure which method is better for estimating uncommon foraging locations. As shown by bootstrap and Markov chain analyses, estimates of means of common foraging locations were similar with both methods, and initial observations more precisely estimated common foraging locations. However, the estimates of means and standard errors from uncommon foraging locations differed between the two methods, and we do not know which method estimates the true population parameters more accurately and precisely.

We had no conclusive evidence of a visibility bias in our habitat; however Recher and Gebski (this volume) found some evidence of a tendency for first-recorded prey attacks to be of particularly conspicuous individuals in their study in an open eucalypt woodland in Australia. We may not have detected any biases because we waited 5 s before recording any observations. Recher and Gebski concluded that the problem of overrepresentation of conspicuous behaviors or individuals might be minimized by rejecting initial observations. Rejecting initial observations may have the same effect as our 5-s waiting period. However, this solution may not be tenable in habitats other than eucalypt woodland. For example, we would not want to reject initial observations in our study, because we were unable to follow birds for sequential observations for 41–69% of our cases.

At least three solutions can be used to deal with problems of autocorrelation in sequential records. First, observers could record only initial

TABLE 6. SOME APPROPRIATE AND INAPPROPRIATE STATISTICAL TESTS FOR SEQUENTIAL DATA

Suggested analyses to examine or adjust for dependency among sequential records			Inappropriate analyses with dependent, sequential records
To compare proportions between initial and subsequent observations	To estimate variance of proportions for sequential records	To examine dependency among sequential records	(e.g., to compare proportions among foraging locations, to examine dependency among sequential records)
Categorical data (e.g., site, substrate)			
McNemar's test (Fleiss 1981:113–119)	Bootstrap Efron and Gong 1983)	Pearson's contingency coefficient (Conover 1971:177)	G-test (Bishop et al. 1975:125–130),
Cochran's *Q* (Fleiss 1981:126–133)	Jackknife (Efron and Gong 1983)	Runs test (Conover 1971:349–356)	Chi-square (Steel and Torrie 1960:346–387)
			Two-sample t-test (Steel and Torrie 1960:73–78, 82–83)
To compare means between initial and subsequent observations	To estimate variance of means for sequential records	To examine dependency among sequential records	(e.g., to compare mean values of foraging locations)
Continuous data (e.g., dbh, height)			
Paired t-test (Steel and Torrie 1960:78–80)	Bootstrap	Durbin-Watson *D* (Durbin and Watson 1951)	Two-sample t-test
	Jackknife		Analysis of variance (Steel and Torrie 1960:99–160, 194–276)

observations from each bird (e.g., Gibb 1954, Morse 1970, Lewke 1982, Franzreb 1985), or only second observations as Recher and Gebski (this volume) have suggested, and use a study design that ensures that all such records are independent. This method may not always be easy or practical for answering certain biological questions. For example, we designed this study so that we would rarely observe the same individual bird more often than once each day. Even if the design succeeded with this objective, however, the same individual was likely observed in the same territory repeatedly over a period of several days. Our primary objective was to study the changes in foraging behavior of a particular population over time. The extent to which obtaining foraging information from the same individuals over time may have biased results of the present analysis is unknown. The most obvious way to obtain completely independent records is to select new areas with new individuals for each observation, but many questions that students of avian foraging behavior choose to answer would not be compatible with this design.

Second, one could make sequential observations for extended periods in a pilot study, analyze for autocorrelations, and select a time interval between observations to ensure independence. Others have used intervals of 10 s (Wagner 1981a), 15 s (Landres and MacMahon 1980), and 60 s (Morrison 1984a). Because our average interval between the first and fifth sequential records was 36 s, we consider the 10-s and 15-s intervals probably insufficient to ensure independence. Porter et al. (1985) followed six individually marked Red-cockaded Woodpeckers (*Picoides borealis*) for extended periods and concluded that records separated by 10-min intervals were independent. But few species are so amenable to study; we could not have followed many individuals for 10 min, and most studies without individually marked birds would likely have the same difficulty. Further, the effects of within-season, seasonal, and annual variation on avian foraging should be considered when establishing appropriate intervals.

Third, as in this study, one could record all possible sequential observations from each individual and analyze the data with procedures capable of adjusting for autocorrelation. We recommend bootstrap or jackknife procedures, both of which can be used with sequential records of unequal length. However, the discrepancies in mean proportions for uncommon foraging locations found for all observations and initial observations in this study show that the two methods may give different estimates of proportions, and we do not know which method would produce a more accurate estimate of true proportions.

Airola and Barrett (1985) used sequential observations but treated each *sequence* as an equally-weighted independent sample. Each measure was expressed as a proportion of the total for that measure in the sequence, so each individual's record was weighted as one in the total sample. We question the validity of giving equal weight to records of unequal length, although the problem may be significant only for relatively short sequences where biases are high (J. T. Rotenberry, pers. commun.). A solution is to use only records greater than a standard length, for example, a 3-min minimum, although this would require rejection of all records shorter than the standard, and longer records may be biased toward more visible locations or more visible bird species or individuals.

Assumptions of statistical analyses have rarely been achieved in studies of avian foraging behavior. First, most errors in the application of statistics result from assumptions of independence among sequential records (see Table 6). Probably the most common example of such errors is the use of G-tests or chi-square tests (that assume independence between records) to examine differences in proportions of behavioral measures using sequential records without first establishing that the records within each sequence are independent. Further, when comparing initial observations with sequential observations, the two data sets must be perfectly matched, the sequential observations must be weighted equally, and a test that deals with matching must be used. For example, G-tests are commonly used incorrectly to compare initial observations with all observations to decide whether sequential data may be used.

Finally, sequential observations are useful, even essential, for certain ethological studies of foraging, such as transitions among various behaviors. They also allow one to include time as a measure to estimate rates at which birds make foraging strikes, move from substrate to substrate, and move from one tree or shrub to another. They may also help to correct for visibility bias, because birds in relatively concealed locations may not be detected as often by initial observations. Although our data did not provide evidence of such a bias, it is probably a valid concern in some habitats.

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