

EVALUATION OF FOUR METHODS FOR ESTIMATING PARROT POPULATION SIZE¹

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Abstract. We evaluated point transect, line transect, mark-resighting, and roost survey methods by comparing population estimates to a reference population of Green-rumped Parrotlets (*Forpus passerinus*) in the llanos of Venezuela. All four methods produced similar population estimates, reflected peaks in nesting and fledging, and almost always exceeded the known minimum population size. Congruence among the estimates decreased as the breeding season progressed. The mark-resighting method had the largest confidence intervals, but precision was similar for the other three methods. Point transect surveys appeared to underestimate the population in open habitat. Line transect surveys more accurately estimated the distribution of the population between habitats. Detection probability was more variable for point transects than for line transects. We recommend using line transect surveys rather than point transects when conditions allow. Roost surveys were complicated by the tendency of parrotlets to change roost sites often, and roost surveys underestimated populations during breeding. Roost surveys may be reliable during nonbreeding, and we recommend further development of roost survey protocol. Behavioral characteristics of Green-rumped Parrotlets allowed us to meet assumptions and requirements of all methods with the exception of mark-resighting. This success may not be replicated with other parrot species.

Key words: survey methods, parrots, *Forpus passerinus*, Green-rumped Parrotlet, Venezuela, Wild Bird Conservation Act.

INTRODUCTION

Many Neotropical parrot species are threatened by widespread habitat destruction and capture for the pet trade (Collar and Juniper 1992). Possible conservation approaches include *in situ* conservation programs and creation of reserves for endangered species, sustainable harvesting of common species, and international control of trade through legal mechanisms such as the Convention on International Trade in Endangered Species (CITES) and the Wild Bird Conservation Act (WBCA) of 1992 (Beissinger and Snyder 1992, Stoleson and Beissinger 1997). These conservation approaches require inexpensive and rapid survey techniques that are accurate and precise for determining the status of a species and for setting harvest levels when appropriate.

Parrot populations are difficult to estimate for several reasons. Parrots tend to fly long distances between nesting, roosting, and feeding areas

in large flocks that can be composed of several species (Chapman et al. 1989, Lindsey et al. 1991). Parrots often inhabit dense forests where visibility is poor, and their cryptic coloration and secretive behavior inhibit detection when they perch. Parrots often nest high in trees where it is hard to find and monitor nests. Finally, it is difficult to capture and mark parrots, so mark-resighting surveys rarely have been employed.

Three survey methods typically are employed to estimate parrot populations. Roost counts are used in small areas and on islands where most roosts can be found (Snyder et al. 1987, Gnam and Burchsted 1991). However, the assumption that all roosts are found is rarely tested, nor have estimators of variance been developed for roost-survey population estimates. Point transects and line transects (also referred to as variable distance point and line counts) also are used to estimate parrot population size (Desenne and Strahl 1991, Lambert 1993); these methods often produce large confidence intervals. For example, Lambert's (1993) 95% confidence intervals were 70,700–435,080 for the total population of Violet-eared Lorries (*Eos squamata*) in the North Moluccas, Indonesia. Such intervals are not precise enough for setting national harvest quotas.

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We present here the results of a study to assess the accuracy and precision of point transect, line transect, mark-resighting, and roost survey methods for estimating parrot population size. We compared estimates from each method to a reference population of banded Green-rumped Parrotlets (*Forpus passerinus*) that nested primarily in polyvinyl chloride (PVC) nest boxes installed from 1988 to 1989 (Beissinger and Waltman 1991, Beissinger and Bucher 1992). This small (25–35 g), seed-eating parrot is common in forest and savanna habitats of north-central South America (Forshaw 1989). Green-rumped Parrotlets exhibit typical parrot behavior: they defend a nest site, have no all-purpose territory, often forage in flocks, and roost communally (Forshaw 1989, Waltman and Beissinger 1992).

METHODS

All surveys were conducted between June and November 1994 at Hato Masaguaral, a working cattle ranch in the state of Guárico, Venezuela, 45 km south of Calabozo. Parrotlets have been banded at this 2-km² study site every year since 1988 as part of a long-term behavioral study (Beissinger and Waltman 1991, Curlee and Beissinger 1995, Stoleson and Beissinger, in press). As of May 1994, 3,363 parrotlets had been banded. Each parrotlet received a unique combination of colored plastic bands and an aluminum band or a metal ring with an identification number. During the 1994 breeding season (June–November) we re-banded adults that were missing plastic bands, banded 60 previously unmarked adults, and banded 516 nestlings.

Within the 2-km² study site, we established a 49-ha area that could be surveyed during a 3-hr period by one person on foot. The 49-ha area included forested (19 ha) and open (30 ha) areas (Fig. 1) that served different habitat needs of the parrotlets. Forested habitats (defined as “bajío” by Troth 1979) were dominated by deciduous trees on poorly drained soils that flooded throughout the rainy season (May–November) and included small areas of open water. Open habitats were grassland, generally higher in elevation and underlain by well drained sandy soils (defined as “médano” by Troth 1979), and included open swamps on poorly drained soils (defined as “estero” by Troth 1979). The open area was lightly grazed by cattle and included isolated tree islands.

We monitored 60 PVC nest boxes and 9 natural nest cavities in the 49-ha study area. Daily nest checks were used to determine the nesting population and number of nestlings that fledged during each of 11 survey periods. Each survey period lasted approximately 2 weeks. We estimated a minimum population size for each survey period from the number of adult parrotlets nesting and the number of nonbreeding banded parrotlets that we identified during each period. Unbanded parrotlets were not included to avoid double counting.

POINT AND LINE TRANSECT SURVEYS

We conducted point and line transect surveys following the variable distance methodology of Buckland et al. (1993). This approach uses counts of birds and their distance from the observer to model the probability that birds were detected around the point or line. Population density is estimated from the number of birds detected and the probability of all birds being detected.

We used a pilot study consisting of 15-min surveys at three randomly selected points to determine optimal length of count time per point (Scott and Ramsey 1981, Verner 1988) and optimal distance between sampling points. The total number of detections decreased after 5 min, and then increased after 10 min. This pattern suggested an inability to keep track of previously detected birds, or to detect birds flying into range. Therefore, we limited the count time to 10 min to maximize detections while minimizing error due to double counting or mistakenly counting birds flying into the sampling area.

Analysis of the pilot study data using the software DISTANCE (Laake et al. 1994) yielded an effective detection radius of 150 m. We chose a distance of 300 m between points to maximize the number of points in the study area and minimize possible double counting between points. Points were laid out at 300 m distances along two parallel lines (Fig. 1). The location of the southernmost point was determined randomly. This resulted in eight points within the study area. Four line-transects were mapped by connecting the points. The configuration was intended to leave a minimum of 300 m between parallel line transects. Each transect was approximately 300 m in length. The order and direction in which the points and lines were surveyed was determined randomly each day.

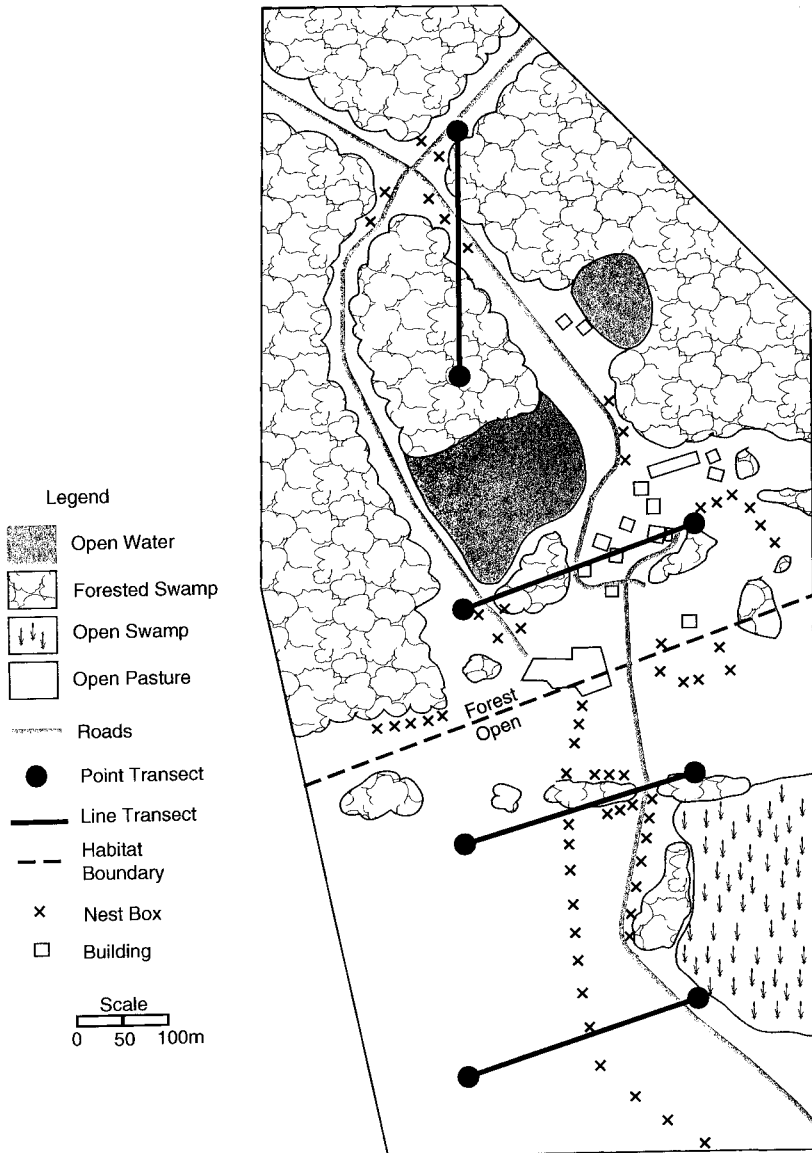


FIGURE 1. Map of the 49-ha study area located on Hato Masaguaral in the state of Guárico, Venezuela. The study area includes forested and open habitat. Point and line transect locations resulted from parallel lines placed randomly.

All surveys were conducted during fair weather between 07:30 and 11:00 when parrots were most active (Blake 1992). We recorded the location of clusters (relatively tight aggregations *sensu* Buckland et al. 1993) of parrotlets and the number of parrotlets in each cluster. We used 8x binoculars to insure correct species identification. Only perched birds detected at their initial locations were counted (Buck-

land et al. 1993). At the end of the 10-min count, we measured the distances to the observed clusters using a tape measure for distances less than 50 m and a range finder for distances greater than 50 m. All eight points were surveyed three times during each 2-week survey to yield a total of 24 point surveys. All four line transects were surveyed three times to yield a total of 3.6 km per survey. Distances

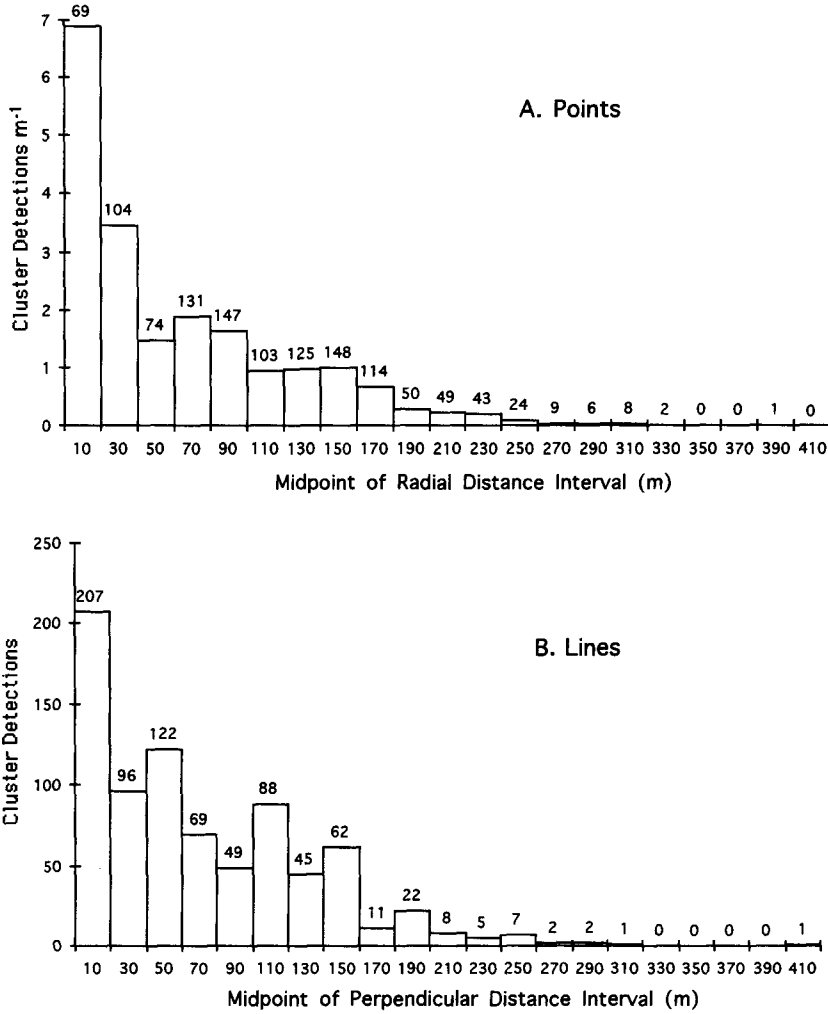


FIGURE 2. Total detections of Green-rumped Parrotlets for the 11 point and line transect surveys. Radial distance intervals reflect concentric circles around points. Perpendicular intervals reflect the distances perpendicular to line transects.

for line transects were measured from the point on the line that was perpendicular to the observed cluster (Buckland et al. 1993).

We tested for bias resulting from evasive movement prior to detection and failure to detect clusters at or near the point or line due to cryptic behavior. Such bias would be indicated by low probabilities of detection close to the observer (Buckland et al. 1993). We generated histograms of total cluster detections for the entire season to check for low rates of detection within the smallest distance classes (Fig. 2). For point surveys, the area surveyed increases geometrically with distance from the point. However, the data

can be analyzed as detections per meter (Fig. 2A), since detection probabilities are estimated from detections per meter (Buckland et al. 1993). The number of parrotlets detected was greater within the first 20 m than at all other distances, suggesting that parrotlets were neither evading detection near the observer nor moving evasively prior to detection (Fig. 2).

We estimated population size using the software DISTANCE. This software estimates the detection probability as a function of distance by fitting six possible probability functions to the data (Buckland et al. 1993). To reduce variability in detection probability and density esti-

mates, we selected probability functions and produced density estimates for the forested and open habitat strata independently. All detections were treated as clusters, and densities were estimated using mean cluster size. Detections beyond 300 m were excluded to eliminate isolated detections at great distances (Fig. 2) because outlier observations provide little information about density and are often difficult to model (Buckland et al. 1993).

We ran the program to select the optimal detection function based on Akaike's Information Criterion (AIC) for each stratum for the 11 surveys. All six possible detection functions were considered (Buckland et al. 1993). The estimator most commonly selected by the program for point transects (11 of 22 estimations) and line transects (13 of 22 estimations) was the hazard-rate key function with either polynomial or cosine series expansion. However, in two cases the population estimates were unreasonable ($N = 1$, $N > 900$) and highly imprecise ($CV > 100\%$). The second most commonly selected estimator for both point transects and line transects (6 of 22 estimations for each) was the half-normal key function with polynomial series expansion. We used the half-normal function to compute all density estimates, and found all of the estimates to be reasonable ($82 < N < 200$) and precise ($CV < 30\%$).

MARK-RESIGHTING SURVEYS

Estimates of population size using most mark-resighting methods assume that the marked population is known (Brownie 1987). In our case, the marked population size was unknown because of partial band loss and mortality of birds banded in previous years. Therefore, we used the methodology of Arnason et al. (1991) for a closed population with an unknown number of marked individuals. We assumed a closed population based on the relatively short survey interval (5 days). This methodology uses maximum likelihood theory to estimate population size and number of marked individuals in the population.

We walked random transects throughout the study area and attempted to identify every parrotlet encountered using binoculars and spotting scopes. We recorded color band combinations, sex, and whether the parrotlet was fully banded, partially banded or unbanded. We only included a sighting in the total count if we saw the par-

rotlet well enough that we would have seen its bands had they been present. Surveys were limited to 5 days during each of the 11 survey periods to ensure that the population was closed, and coincided with point and line transect surveys for comparison.

Arnason et al. (1991) found that data must be transformed before constructing confidence intervals because of small sample bias and because distributions of population estimates from this method tend not to be normal. Accordingly, we calculated confidence intervals using the inverse cube-root transformation method (Arnason et al. 1991).

An important assumption of the mark-resighting method is that individuals are sighted independently and with equal probability. We tested this assumption by performing a chi-square goodness-of-fit test on expected frequencies of sighting generated by maximum likelihood and observed frequencies (Arnason et al. 1991).

ROOST SURVEYS

We conducted 11 roost surveys to coincide with the other survey methods. We searched for all roosts in the 49-ha study area beginning 1 hr before sunset. Each of three surveyors patrolled a section of the study area, listening for parrotlets and watching for roosts. This often involved following parrotlets for short distances as they flew to their roosts. Each surveyor recorded the location of the roosts. These data were used to compute the average number of roosts (r) per night during the survey period.

It was not possible to count parrotlets entering the roosts in the evening because of the variability and rapid changes in roost location. Therefore, a randomly selected roost was counted by two surveyors on the following morning. Ideally, we would have counted every roost simultaneously, but this required more surveyors than were available. The surveyors arrived at 06:00 before the parrotlets began to leave. Because parrotlets tended to roost in isolated trees or small groves of trees, one surveyor was positioned on either side of the roost and counted parrotlets leaving from that side of the roost. These data were used to estimate an average roost size (s) during the survey period.

We estimated population size (N_R) for the study area using the equation

$$N_R = r \cdot s \quad (1)$$

where: r = mean number of roosts per night and s = mean roost size. This method assumes that: (1) all parrotlets roost communally during the survey period, (2) all roosts are found each night, and (3) counts of the number of parrotlets in each roost are accurate. The first assumption was the least likely to be met during the breeding season when some parrotlets spend the night in their nests (Beissinger and Waltman 1991).

It was not possible to estimate confidence intervals for all of the 11 surveys because the amount of data we were able to obtain was constrained by the amount of effort required to survey roosts. Roost locations moved very often and were difficult to find, and roosts sometimes moved during the night. Therefore, we pooled the data to produce four discrete population estimates with durations of 4 to 6 weeks.

We computed 95% confidence intervals by developing an estimator of variance that included variability of both roost size and number of roosts per night. Roost size (s) and number of roosts per night (r) would be dependent variables in a closed population. However, the length of the survey periods (4 to 6 weeks) probably precludes the assumption of population closure. Furthermore, since the roost to be counted was determined randomly each morning, we were sampling the variables independently. Therefore, the variance of the population estimate is

$$\widehat{\text{var}}(N_R) = \widehat{\text{var}}(r \cdot s) \quad (2)$$

and was computed by the equation

$$\widehat{\text{var}}(N_R) = \left[\left(\frac{1}{n_r} \sum_{i=1}^{n_r} (x_i^2) \right) \cdot \left(\frac{1}{n_s} \sum_{i=1}^{n_s} (y_i^2) \right) \right] - \left[\left(\frac{1}{n_r} \sum_{i=1}^{n_r} x_i \right)^2 \cdot \left(\frac{1}{n_s} \sum_{i=1}^{n_s} y_i \right)^2 \right] \quad (3)$$

where: x_i = the number of roosts observed on the i_{th} evening, and y_i = the number of parrotlets in the i_{th} roost. The derivation of this equation is presented in the Appendix.

COMPARATIVE ANALYSIS

We used Wilcoxon matched-pairs signed-ranks test (z ; Conover 1971) to test for differences among population estimates and population estimation parameters. Spearman rank correlation (r_s ; Conover 1971) was used to test for concordance among the population estimates to evaluate whether survey methods responded similar-

ly to overall trends in the population. We used nonparametric tests because true population parameters probably varied over the course of the 11 surveys and were not normally distributed. All statistical analyses were performed using SYSTAT (SYSTAT Inc. 1994).

We compared population estimates derived from the four methods to the known minimum population to determine if any of the estimates were unrealistically low. We also compared population estimates from the four methods to the nesting and fledging populations to determine if the population estimates reflected population trends.

RESULTS

POINT AND LINE TRANSECT SURVEYS

Density estimates from the point transect surveys yielded population estimates that always exceeded the known nesting population in the forested habitat (Fig. 3A). In the open habitat, however, population estimates were lower than the number of birds nesting there during three survey periods (Fig. 3B). Density estimates from point transect surveys were significantly lower for open habitat than for forested habitat ($z = 2.93$, $P = 0.003$). Lower density estimates for the open habitats resulted from the probabilities of detection as estimated by DISTANCE, and not from the total number of parrotlets sighted. On average, more parrotlets were detected in open (6.6 per point) than in forested habitat (3.6 per point). Probabilities of detection were significantly lower ($z = 2.93$, $P = 0.003$) for the forested habitat ($x = 0.15$) than for the open habitat ($x = 0.35$). Also, probabilities of detection produced by the point transect surveys were more variable for the forested habitat (CV = 53%) than for the open habitat (CV = 29%).

None of the line transect population estimates were lower than the nesting populations in the open or forested habitats (Fig. 3). Line transect density estimates were significantly lower for forested habitats than for open habitats ($z = 2.40$, $P = 0.016$). The probabilities of detection also were significantly lower for the forested habitats than for open habitats ($z = 2.70$, $P = 0.007$). Probabilities of detection were not particularly variable for the forested habitat (CV = 18%) or the open habitat (CV = 20%).

MARK-RESIGHTING SURVEYS

Mark-resighting results indicated that the following testable constraints outlined by Arnason

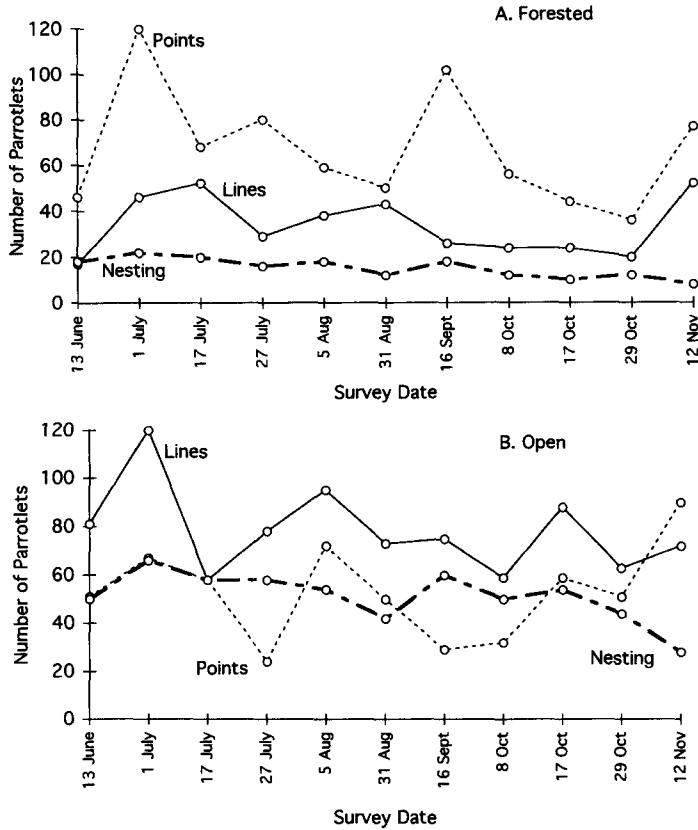


FIGURE 3. Point and line transect population estimates and the nesting populations of Green-rumped Parrotlets in forested and open habitats.

et al. (1991) were met (Table 1), with the exception of the minimum recommended number of observations. In every survey at least one parrotlet was seen twice, the estimate of marked population (M_{mr}) was greater than the total num-

ber of different marked animals seen (m'), and the estimate of the marked population was less than the total number of marked parrotlets ever released ($M_0 = 3,939$). The chi-squared goodness-of-fit test of observed and expected sight-

TABLE 1. Mark-resighting survey sightings, and estimations of banded and total population size.

Survey beginning	Total sightings (n)	Unique sightings (m')	Banded population estimate (M_{mr})	Total population estimate (N_{mr})	95% CI Total population	
					Low	High
13 June	25	12	70	135	17	1,064
1 July	60	21	84	210	33	319
17 July	40	28	77	99	45	147
27 July	39	28	77	97	45	147
5 Aug	59	32	86	124	47	183
31 Aug	61	38	74	103	52	111
16 Sept	63	30	84	143	45	183
8 Oct	60	30	80	137	49	138
17 Oct	60	27	96	156	26	1,207
29 Oct	56	33	79	113	49	138
12 Nov	51	28	82	127	44	179

TABLE 2. Roost survey population estimates (N_R) calculated from mean number of parrotlets in each roost (s) and mean number of roosts per night (r). n_r = the number of roost observation evenings, n_s = the number of roosts counted, and SE = standard errors.

Survey dates	Number of roosts			Roost size			Total population size	
	n_r	r	SE	n_s	s	SE	N_R	95% CI
13 June–26 July	4	1.75	0.25	9	94	7.5	165	135–195
27 July–29 Aug	9	1.67	0.29	5	57	15.1	95	57–133
3 Sept–16 Oct	11	2.45	0.25	14	34	6.8	82	55–109
17 Oct–19 Nov	13	2.23	0.39	8	77	5.9	172	124–220

ing frequencies indicated an independent and equal probability of being resighted throughout individual surveys ($\chi^2_2 = 0.35$, $P < 0.75$).

The computer simulation experiment of Aronson et al. (1991) indicated that acceptable precision required the total number of sightings (n) to exceed the true population (N) and should ideally be double N . The total number of sightings during each survey (Table 1) was never greater than or equal to the known minimum population during each survey. The low number of observations was partly due to the short survey period and resulted in large confidence intervals (Table 1).

ROOST SURVEYS

Roost surveys conducted during the mid-breeding season produced the lowest population estimates (Table 2). The roost survey population estimate for the period beginning 3 September was below the known minimum population. During this period, the average number of parrotlets in roosts (s) was lowest, and the average number of roosts (r) was highest. This may have increased the likelihood of not finding all of the roosts. In addition, during this period, incubating and brooding female parrotlets spent the nights in their nests instead of in communal roosts.

POPULATION FLUCTUATIONS

All survey methods generally reflected fluctuations in the population within the study area (Fig. 4). Breeding for the 1994 season began with egg-laying on 12 June and included two peak periods of nesting followed by two peaks in fledging (Fig. 4B). Many birds were seen prospecting for potential nest sites during the survey period beginning 1 July. Population estimates declined soon after pairs established nest sites. Estimates did not increase again until early August, when many young were fledged and second broods were being initiated. Point tran-

sect, line transect and mark-resighting population estimates increased during both onsets of nesting (beginning 1 July and 16 September) and during the first fledging peak (beginning 5 August), with the exception of the line transect method which decreased during the nesting peak that began 16 September. Population estimates decreased during the second fledging peak that began 29 October.

All but one population estimate exceeded the known minimum population as determined by nesting population and identification of non-nesting parrotlets (Fig. 4A). Only the roost survey population estimate for the period beginning 3 September was below the known minimum population for that period. Population estimates at the end of the breeding season indicated little change in population size from the beginning of the breeding season (Fig. 4A).

COMPARISON OF METHODS

All four methods produced population estimates with 95% confidence intervals that overlapped. The point transect survey method yielded estimates that commonly fell between the estimates of the other methods (Fig. 4A). There was no difference between point transect and line transect population estimates ($z = 1.25$, $P = 0.21$), point transect and mark-resighting population estimates ($z = 1.07$, $P = 0.29$), or line transect and mark-resighting estimates ($z = 1.69$, $P = 0.10$). However, point transect density estimates were significantly lower than line transect density estimates in the open habitat ($z = 2.60$, $P = 0.009$), and significantly higher than line transect density estimates in the forested habitat ($z = 2.93$, $P = 0.003$).

Conformity among the four methods was greater during the first half of the breeding season than later in the season after nestlings began to fledge and parents began second nesting attempts (Fig. 4). Mark-resighting survey popu-

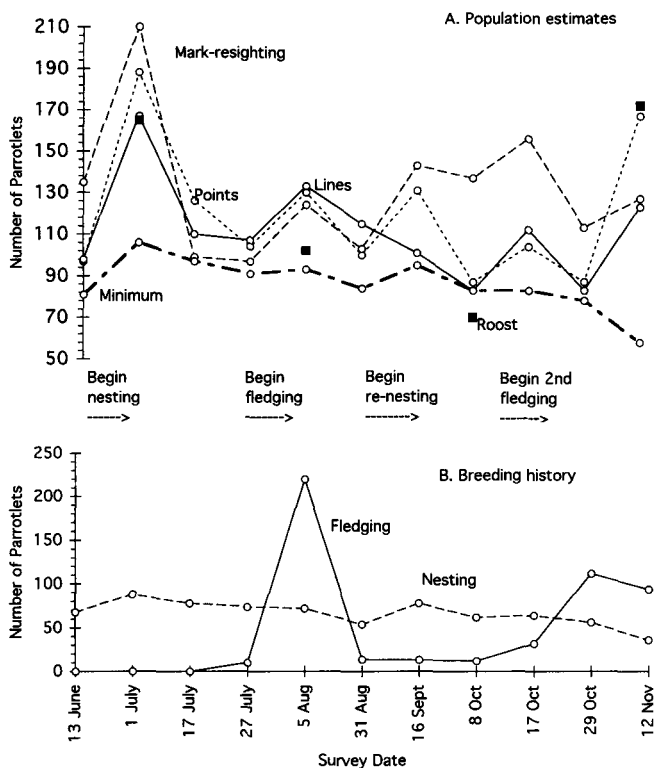


FIGURE 4. Survey population estimates using different methods, minimum population, and breeding history of Green-rumped Parrotlets for the 49-ha study area during the 1994 breeding season. Number of nesting parrotlets includes those with eggs or nestlings.

lation estimates were consistently higher than estimates from other methods during the second half of the breeding season. Line transect and point transect population estimates were significantly correlated ($r_s = 0.77$, $n = 11$, $P < 0.05$).

TABLE 3. Coefficients of variation for the population estimates produced by the four survey methods.

Survey beginning	Point transects	Line transects	Mark-resighting	Roosts ¹
13 June	0.21	0.26	0.91	0.09
1 July	0.19	0.30	0.55	—
17 July	0.23	0.15	0.30	—
27 July	0.19	0.13	0.30	0.21
5 Aug	0.17	0.12	0.34	—
31 Aug	0.17	0.14	0.19	—
16 Sept	0.18	0.17	0.35	0.17
8 Oct	0.14	0.24	0.22	—
17 Oct	0.13	0.22	0.87	0.14
29 Oct	0.17	0.18	0.26	—
12 Nov	0.15	0.25	0.35	—

¹ The 11 roost surveys were consolidated into four survey periods that began on the indicated dates.

Mark-resighting estimates were not correlated with either the line ($r_s = 0.14$, $n = 11$, $P > 0.10$) or the point transect estimates ($r_s = 0.29$, $n = 11$, $P > 0.10$), suggesting that these methods did not reflect population fluctuations similarly.

We examined precision of the methods by comparing the coefficients of variation (CVs) associated with population estimates (Table 3). Coefficients of variation were significantly higher for the mark-resighting estimates than for the point transect estimates ($z = 2.93$, $P = 0.003$) and the line transect estimates ($z = 2.85$, $P = 0.004$). The coefficients of variation for the point transect and line transect population estimates did not differ ($z = 0.93$, $P = 0.35$). Coefficients of variation produced by the roost surveys were similar to those of the point and line transect surveys (Table 3).

Precision was lowest for mark-resighting estimates even though we expended 84 person-hours on average to capture, band, and resight parrotlets during each 2-week period. This did

not include labor expended banding in previous years. Point transects and line transects required approximately 10.5 person-hours and 9 person-hours, respectively, per survey period. We expended an average of 30 person-hours on roost surveys during each 2-week survey period.

DISCUSSION

The point transect, line transect, mark-resighting, and roost survey methods all have the potential to estimate parrot populations reliably. All methods yielded estimates that generally reflected population fluctuations (Fig. 4). However, the survey methods may have underestimated parrotlet numbers when estimates were close to the minimum population, because minimum population values did not include partially banded or unbanded parrotlets. Furthermore, we have identified potential biases and limitations for each of the methods that should be considered in their application to parrots. Foremost among these is that obtaining reliable estimates of parrot populations requires that assumptions and requirements of the method being used are met. The high precision and similarity of population estimates between methods that we obtained resulted mostly from careful survey design and implementation, which allowed us to meet most method assumptions and minimize bias.

ABILITY TO MEET METHOD ASSUMPTIONS

Line and point transect theory assumes that objects are detected at their initial location and objects on the point or line are detected with certainty. Counting birds flying over, or into, the field of vision can bias estimates (Buckland et al. 1993). However, parrots often inhabit forests where visibility is poor, and cryptic coloration and secretive behavior inhibit their detection when they are perched (Snyder et al. 1987, Chapman et al. 1989). We often were able to count perched birds detected at their initial locations by relying on vocalizations. It may not be possible to replicate this result for other, less vocal parrot species. The resulting distribution of detections relative to distance (Fig. 2) indicated that parrotlets were not moving evasively prior to detection. Because parrots would be less likely to flush during point transects than during line transects, line transects would be preferred for cryptic nonvocal species.

Parrots often fly in flocks for long distances between nesting, roosting and feeding areas

(Lindsey et al. 1991), and counting birds that fly over a point or line without landing violates transect theory (Buckland et al. 1993). These factors can severely limit the ability to obtain enough parrot detections for estimation with DISTANCE. Small sample sizes can result in large confidence intervals (Buckland et al. 1993), such as those obtained by Lambert (1993). We used pilot data to establish sample size requirements by calculating CVs, and to identify optimal count duration and distance between points. Pilot studies for other parrot species may indicate that point or line transect surveys are not applicable.

Point and line transect surveys also require that the number of objects in a cluster be accurately counted. This can be difficult for large flocks of parrots composed of mixed species (Chapman et al. 1989). Green-rumped Parrotlets rarely travel in mixed flocks, which facilitated the estimation of cluster size.

Roost-survey population estimates depend on accurately counting roosts and meeting the assumptions that the entire population roosts communally and all roosts are found. Parrotlets tended to leave roosts in small groups during 20 to 30-min periods, and this facilitated counting. As a result, counts for each roost were probably accurate. The assumptions that all parrotlets roosted communally during the survey period and that all roosts were found each night were not met during the peak of the breeding season. It is more likely that all parrotlets roost communally during the nonbreeding season when nests are not occupied (Chapman et al. 1989, Waltman and Beissinger 1992). Assumptions probably were more closely met during the beginning and end of the breeding season, when roosts appeared to be consolidated and roost survey estimates tended to conform with population estimates from other methods (Fig. 4A).

Roosting behavior can vary substantially throughout the year and among species (Snyder et al. 1987, Chapman et al. 1989, Waltman and Beissinger 1992). Parrotlet roosts were difficult to find because birds congregated in small roosts, searched much of the study area in small groups before consolidating into a few roosts at dusk, and changed roost location often. Roost movement also has complicated survey attempts for other parrot species (Gnam and Burchsted 1991), although some species are more predict-

able in their roosting behavior (Snyder et al. 1987, Chapman et al. 1989).

BIAS

Results of other studies have suggested that point survey estimates are less reliable than line survey estimates (DeSante 1981, 1986, Bollinger et al. 1988). Our results also suggest that the point transect method is susceptible to bias when applied to areas with high visibility (Fig. 3). Point density estimates in the open habitat may have been too low because estimated probabilities of detection were too high. Counts of objects at greater distances usually are higher for point surveys than for line surveys (Buckland et al. 1993). However, it is observations close to the point or line that are most important for fitting estimation equations (Buckland et al. 1993). Greater visibility in the open habitat resulted in more sightings than in the forested habitat during the point surveys and significantly higher probabilities of detection. Our results suggest that detection probability estimation was more precise for line transects than for point transects. The probability of detecting a parrotlet was more variable for point transects in both the open ($CV = 29\%$) and forested habitat ($CV = 53\%$) than for line transects ($CV = 20\%$ and 18% , respectively).

Although the point transect method may be more susceptible to bias, it may sometimes offer logistical advantages over the line transect method. In most cases line transects are preferred because more time is spent sampling than traveling between points (Bollinger et al. 1988). However, line transect surveys may not be possible in impenetrable terrain, and they can be more dangerous since the surveyor can not watch the ground while walking. Point transects also may be preferable if a large area is being sampled and a motor vehicle is required.

PRECISION

The point transect, line transect and roost survey methods all yielded population estimates with acceptable confidence intervals and were similarly precise as measured by coefficients of variation (Table 3). Mark-resighting surveys resulted in the largest confidence intervals of the four methods and required the greatest amount of time, indicating the large effort that can be required to attain precision with this method (Shupe et al. 1987). We were unable to obtain the

minimum number of observations recommended by Arnason et al. (1991) due in part to the short length of our survey periods, which resulted in large confidence intervals. Also, it is difficult to catch and band parrots and to read bands because parrot tarsi are short. Given the amount of labor needed to overcome these difficulties, mark-resighting methods are less likely to be useful to estimate population size or trends.

Roost surveys yielded population estimates with small coefficients of variation (Table 3). This was because the number of roosts per night and number of parrotlets in each roost did not vary much within survey periods (Table 2), although they varied throughout the season. Our results suggest that roost surveys can be as precise as point and line transects, but they required an investment of three times as many person-hours. Roost surveys may be a reasonable alternative to point and line transects when parrots are too rare or widely dispersed to estimate probabilities of detection (Snyder et al. 1987).

CONCLUSIONS

The choice of method to survey parrot populations depends on the characteristics of the population, the terrain being surveyed, and logistical constraints. Mark-resighting is the least desirable method because large numbers of sightings are required. Line transect surveys are generally preferable to points because they are less susceptible to bias and fewer detections are needed to gain precision. Point transect surveys also may tend to underestimate population size in open habitats. Roost survey results suggest congruence with the other methods in the nonbreeding season. We encourage further development and evaluation of roost surveys, especially for species that are not amenable to point and line transect methods.

Our study also has important implications for monitoring sustainable harvesting programs under the WBCA. WBCA import regulations (Federal Register, 24 January 1996) require year-to-year population assessments conducted during the same season (breeding or nonbreeding) to monitor changes in population size. Our results suggest that such surveys should be conducted either before or after the breeding season, and that point, line or roost surveys would be appropriate if properly employed to meet assumptions.

WBCA regulations also allow harvest levels

to be set by estimating the number of young produced per year using the difference between prebreeding and postbreeding surveys conducted within the same annual cycle. None of the methods we tested are adequate alone for setting harvesting quotas this way. Although our study population produces hundreds of young each year, comparison of pre- and postbreeding season counts indicated little change in population size (Fig. 4). This occurred because our population acts as a source. Many young disperse out of the study population, sometimes at ages as young as 2 months (Beissinger, unpubl. data). Furthermore, local population estimates of species that have large home ranges and disperse widely may reflect the effects of regional population processes. Therefore, determining harvest sustainability requires direct estimates of mortality and productivity.

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LITERATURE CITED

- ARNASON, A. L., C. J. SCHWARZ, AND J. M. GERRARD. 1991. Estimating closed population size and number of marked animals from sighting data. *J. Wildl. Manage.* 55:716–730.
- BEISSINGER, S. R., AND E. H. BUCHER. 1992. Can parrots be conserved through sustainable harvesting? *BioScience* 42:164–173.
- BEISSINGER, S. R., AND N. F. R. SNYDER [EDS.]. 1992. *New World parrots in crisis: solutions from conservation biology*. Smithsonian Inst. Press, Washington, DC.
- BEISSINGER, S. R., AND J. R. WALTMAN. 1991. Extraordinary clutch size and hatching asynchrony of a Neotropical parrot. *Auk* 108:863–871.
- BLAKE, J. G. 1992. Temporal variation in point counts of birds in a lowland wet forest in Costa Rica. *Condor* 94:265–275.
- BOLLINGER, E. K., T. A. GAVIN, AND D. C. MCINTYRE. 1988. Comparison of transects and circular plots for estimating Bobolink densities. *J. Wildl. Manage.* 52:777–786.
- BROWNIE, C. 1987. Recent models for mark-recapture and mark-resighting data. *Biometrics* 43:1017–1019.
- BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, AND J. L. LAAKE. 1993. *Distance sampling: estimating abundance of biological populations*. Chapman and Hall, London.
- CHAPMAN, C. A., L. J. CHAPMAN, AND L. LEFEBVRE. 1989. Variability in parrot flock size: possible functions of communal roosts. *Condor* 91:842–847.
- COLLAR, N. J., AND A. T. JUNIPER. 1992. Dimensions and causes of the parrot conservation crisis, p. 1–24. *In* S. R. Beissinger and N. F. R. Snyder [eds.], *New World parrots in crisis: solutions from conservation biology*. Smithsonian Inst. Press, Washington, DC.
- CONOVER, W. J. 1971. *Practical nonparametric statistics*. John Wiley & Sons, New York.
- CURLEE, A. P., AND S. R. BEISSINGER. 1995. Experimental analysis of mass change in female Green-rumped Parrotlets (*Forpus passerinus*): the role of male cooperation. *Behav. Ecol.* 6:192–198.
- DESANTE, D. F. 1981. A field test of the variable circular-plot censusing technique in a California coastal scrub breeding bird community. *Stud. Avian Biol.* 6:177–185.
- DESANTE, D. F. 1986. A field test of the variable circular-plot censusing method in a Sierran subalpine forest habitat. *Condor* 88:129–142.
- DESENNE, P., AND S. D. STRAHL. 1991. Trade and conservation status of the family Psittacidae in Venezuela. *Bird Conserv. Int.* 1:153–169.
- FORSHAW, J. M. 1989. *Parrots of the world*, 3rd ed. Lansdowne Editions, Willoughby, Australia.
- GNAM, R. S., AND A. BURCHSTED. 1991. Population estimates for the Bahama Parrot on Abaco Island, Bahamas. *J. Field Ornithol.* 62:139–146.
- LAAKE, J. L., S. T. BUCKLAND, D. R. ANDERSON, AND K. P. BURNHAM. 1994. *DISTANCE user's guide*, version 2.1. Colorado Coop. Fish Wildl. Res. Unit, Colorado State Univ., Fort Collins, CO.
- LAMBERT, F. R. 1993. Trade, status and management of three parrots in the North Moluccas, Indonesia: White Cockatoo (*Cacatua alba*), Chattering Lory (*Lorius garrulus*), and the Violet-eared Lory (*Eos squamata*). *Bird Conserv. Int.* 3:145–168.
- LINDSEY, G. D., W. J. ARENDT, J. KALINA, AND G. W. PENDLETON. 1991. Home range and movements of juvenile Puerto Rican Parrots. *J. Wildl. Manage.* 55:318–322.
- SCOTT, J. M., AND F. L. RAMSEY. 1981. Length of count period as a possible source of bias in estimating bird densities. *Stud. Avian Biol.* 6:409–413.
- SHUPE, T. E., F. S. GUTHERY, AND S. L. BEASOM. 1987. Use of helicopters to survey Northern Bobwhite populations on rangeland. *Wildl. Soc. Bull.* 15:458–462.
- SNYDER, N. F. R., J. W. WILEY, AND C. B. KEPLER. 1987. The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. *Western Found. Vert. Zool.*, Los Angeles.
- STOLESON, S. H., AND S. R. BEISSINGER. 1997. Hatching asynchrony in parrots: boon or bane for conservation, p. 157–180. *In* J. R. Clemmons and R. Buchholz [eds.], *Behavioral approaches to con-*

servation in the wild. Cambridge Univ. Press, Cambridge.

STOLESON, S. H., AND S. R. BEISSINGER. In press. Hatching asynchrony, brood reduction and food limitation in a Neotropical parrot. *Ecol. Monogr.* SYSTAT Inc. 1994. SYSTAT for DOS: using SYSTAT, version 6. SYSTAT Inc., Evanston, IL.

TROTH, R. G. 1979. Vegetational types on a ranch in the central Llanos of Venezuela, p. 17-30. *In* J. F. Eisenberg [ed.], *Vertebrate ecology in the northern Neotropics*. Smithsonian. Inst. Press, Washington, DC.

VERNER, J. 1988. Optimizing the duration of point counts for monitoring trends in bird populations. Res. Note PSW-395. Pac. Southwest Forest Range Exp. Sta., U.S. Dept. Ag., Berkeley, CA.

WALTMAN, J. R., AND S. R. BEISSINGER. 1992. Breeding behavior of the Green-rumped Parrotlet. *Wilson Bull.* 104:65-84.

APPENDIX

Here we derive equation (3) for estimating the variance in parrot population estimates from roost surveys. Let

$$r = \frac{1}{n_r} \sum_{i=1}^{n_r} x_i$$

where r = mean number of roosts per night, n_r = number of nights of search, and x_i = the number of roosts on the i_{th} night. And let

$$s = \frac{1}{n_s} \sum_{i=1}^{n_s} y_i$$

where s = mean number of parrotlets in a roost, n_s =

number of roosts counted, and y_i = the number of parrotlets in the i_{th} roost. The population is estimated as

$$N_R = r \cdot s \tag{A1}$$

and

$$\widehat{\text{var}}(N_R) = \widehat{\text{var}}(r \cdot s) \tag{A2}$$

and

$$\widehat{\text{var}}(N_R) = E[(rs)^2] - [E(rs)]^2$$

Since we treated the variables r and s independently

$$\widehat{\text{var}}(N_R) = [E(r^2) \cdot E(s^2)] - [E(r) \cdot E(s)]^2 \tag{A3}$$

and since the variables are discrete

$$E(r^2) = \frac{1}{n_r} \sum_{i=1}^{n_r} x_i^2$$

$$E(s^2) = \frac{1}{n_s} \sum_{i=1}^{n_s} y_i^2$$

$$E(r) = \frac{1}{n_r} \sum_{i=1}^{n_r} x_i$$

$$E(s) = \frac{1}{n_s} \sum_{i=1}^{n_s} y_i$$

Substituting into equation (A3), we get

$$\widehat{\text{var}}(N_R) = \left[\left(\frac{1}{n_r} \sum_{i=1}^{n_r} (x_i^2) \right) \cdot \left(\frac{1}{n_s} \sum_{i=1}^{n_s} (y_i^2) \right) \right] - \left[\left(\frac{1}{n_r} \sum_{i=1}^{n_r} x_i \right)^2 \cdot \left(\frac{1}{n_s} \sum_{i=1}^{n_s} y_i \right)^2 \right]$$