

Seasonal roosts of Red-lored Amazons in Ecuador provide information about population size and structure

Karl S. Berg¹ and Rafael R. Angel

Fundación Pro-Bosque, km 16 via la Costa, Guayaquil, Ecuador

Received 21 June 2005; accepted 13 January 2006

ABSTRACT. Data from roosts of *Amazona* parrots may be useful in creating demographic models, because these birds exhibit high roost fidelity and pairs are conspicuous in flight. However, few investigators have attempted to track changes in the number of pairs using such roosts. We studied Red-lored Amazons (*Amazona autumnalis*) at a communal roost in southwest Ecuador over a 1-yr period to understand better their population structure. Population size was estimated at 214 individuals. Counts revealed seasonal variation in numbers, but the occurrence of pairs and singles was seldom correlated. The number of paired individuals using the roost was lower during the breeding period. In contrast, the number of single birds at the roost nearly doubled during the breeding period. Overall, our data suggest that parental responsibilities during the nesting period explain fluctuations in the number of birds at the roost, and such fluctuations can be used to estimate the reproductive portion of the population. Protection of the small mangrove islands where the parrots roost would likely benefit a population that occupies a much larger area and would, at the same time, provide a useful tool for demographic studies of this poorly known neotropical parrot.

SINOPSIS. Efectos estacionales en un dormitorio de Loro Frentirrojo en el suroeste del Ecuador

Datos colectados desde dormitorios de los loros de *Amazona* podrían ser aptos para modelos demográficos, porque suelen ser fieles a los dormitorios y vuelan en pareja. Apesar de la apreciación general de esto, pocos estudios han atentado documentar los cambios en el número de parejas que visiten los dormitorios a menudo. Realizamos un censo del Loro Frentirrojo (*Amazona autumnalis*) en un dormitorio comunal durante un año en el suroeste del Ecuador para obtener datos sobre la estructura de la población. El tamaño de la población fue estimado en 214 individuos. Los datos indicaron una variación estacional y fuerte, sin embargo, la incidencia de parejas e solitarios no siempre estuvieron correlados. El número de parejas fue mucho más bajo durante el periodo de la anidación. Por otro lado, la cantidad de solitarios fue casi el doble durante la época de anidación. En conjunto, los datos sugieren que las responsabilidades asociadas con la reproducción podrían explicar las fluctuaciones grandes en el dormitorio y así proveer una estimación de la proporción reproductiva. Protección de las islas pequeñas del manglar podría proveer beneficios a una población que ocupan a un área de hábitat mucho más grande y a la vez conservar una herramienta útil para estudios demográficos de un loro neotropical y poco conocido.

Key words: *Amazona autumnalis*, Ecuador, mangrove, psittacidae, reproductive populations, roosting, tropical dry forest

Parrots are among the most threatened groups of birds, and so there is considerable need for monitoring programs based on efficiently collected demographic data. Due to habitat destruction, capture for the pet trade, and life history traits, parrots are more susceptible to extinction than other groups (Casagrande and Beissinger 1997, Collar et al. 1997, Stoleson and Beissinger 1997, Snyder et al. 2000, Owens and Bennett 2000, Wright et al. 2001). The

lowland tropical forests of western Ecuador are famous for high levels of species richness and endemism, but widespread habitat destruction and development threaten numerous species (Dodson and Gentry 1991, Myers et al. 2000), including several species of parrots (Stattersfield and Capper 2000, Ridgely and Greenfield 2001). Inexpensive and rapid techniques are needed to accurately determine the status of threatened species and, in some cases, the impacts of harvesting (Beissinger and Bucher 1992, Casagrande and Beissinger 1997, Wright et al. 2001). Common measures of status include the size and reproductive portion of a population (IUCN 1994), and these have seldom been reported for neotropical parrots

¹Current address: Department of Environmental Science, Policy and Management, University of California, Berkeley, California 94702-3114 USA. Email: kberg@nature.berkeley.edu

(Casagrande and Beissinger 1997, Sandercock et al. 2000). Forest-dwelling parrots are notoriously difficult to study in the wild (Gilardi and Munn 1998). However, where communal roosts are isolated, censusing provides an opportunity to assess critical aspects of population biology (Casagrande and Beissinger 1997, Snyder et al. 2000).

We censused flocks of the poorly known Red-lore Amazon (*Amazona autumnalis*) at a communal roost in southwest Ecuador to understand better their population demographics. *Amazona* parrots make convenient models for demographic studies, because they consistently travel as pairs and singles (Snyder et al. 1987, Wright 1996, Gilardi and Munn 1998). They are also highly gregarious at roosts, and so a large portion of the population can be sampled (Gnam and Burchsted 1991, Snyder et al. 2000, Coughill and Marsden 2004). Given the reproductive activities of breeding pairs, one can make predictions about how the composition of roosting aggregations should change between the breeding and nonbreeding periods. If the number of pairs is predictable based on breeding patterns, this information could then be used to estimate the reproductive portion of the population. Because roost data can be gathered with a fraction of the effort needed to directly monitor nest attempts in an entire population, such roost counts may thus provide a viable method for monitoring wild parrot populations.

The idea of using roost counts to estimate parrot population parameters is not new. Gnam and Burchsted (1991) used roost counts during the nonbreeding season to estimate the population size of the Cuban Amazon (*Amazona leucocephala*). Using a marked population, Casagrande and Beissinger (1997) estimated the population size of Green-rumped Parrotlets (*Forpus passerinus*) using roost counts, and found higher numbers outside the breeding period, despite unpredictability in the location of roosts. Coughill and Marsden (2004) estimated the population size of Red-tailed Amazons (*Amazona brasiliensis*) based on roost counts, and found a sharp decline in numbers as the breeding period approached. At our study site, Kunz (1995) estimated population size using roost counts of Red-lore Amazons and found that numbers increased during the months after breeding was completed.

Fewer attempts have been made to compare the size of roosts during the breeding and nonbreeding periods, because counts would have to be conducted over a period of at least 1 yr. Snyder et al. (1987) found flock sizes to be significantly larger during the nonbreeding season for Hispaniolan Amazons (*Amazona ventralis*). Enkerlin-Hoeflich (1995) also found that roost counts of Red-lore Amazons were higher during the nonbreeding season. At least for *Amazona* parrots, roost counts can thus be used to estimate population sizes; and data collected throughout the year are affected by the portion of the population that abandons the communal roost to nest.

Although no quantitative attempts have been made to link the reproductive portion of the population with changes in roost counts, this may be especially feasible for *Amazona* parrots, because the pair is the principal social unit in all species studied to date. Within flocks, individuals consistently travel in pairs (Snyder et al. 1987, Gilardi and Munn 1998, Ridgely and Greenfield 2001, K. S. Berg, pers. obs.), reflecting the monogamous social system and especially strong pair bonds in several *Amazona* parrots (Wright 1996, Bradbury et al. 2001, Bradbury 2003). Because most parrots are sexually monomorphic, all pairs in flight cannot be assumed to be male–female pairs. Male–male pairs and siblings may also occasionally fly in pairs (Snyder et al. 1987, Enkerlin-Hoeflich 1995, Beissinger et al. 1998). However, the incidence of male–male pairs in a given population is likely small and of a temporary nature, even where adult populations are strongly male-biased (Sandercock et al. 2000, K. S. Berg, pers. obs.). Our study focuses on the number of pairs roosting. We assumed that these were primarily male–female pairs, but acknowledge that our methods did not allow us to determine the extent to which pairs consisted of male–male pairs and siblings.

Red-lore Amazons occur from Mexico south through to western Ecuador and Brazil (Forshaw 1977, Juniper and Parr 1998). In Mexico, they are better known (Enkerlin-Hoeflich 1995) and clutches range in size from 1 to 4 eggs. The incubation period begins with the laying of the first egg and lasts 28 d. Females cease brooding nestlings about 28 d posthatching, and fledging occurs asynchronously beginning at about 55 d posthatching. In most psittacids studied to date,

only females incubate and they begin to roost in the nest cavity prior to egg-laying, causing the number of pairs at communal roosts to decline (Snyder et al. 1987, Waltman and Beissinger 1992, Enkerlin-Hoeflich 1995). However, the duration of the overnight brooding period appears to differ across *Amazona* species (Snyder et al. 1987, Enkerlin-Hoeflich 1995, Renton and Salinas-Melgoza 1999), and it is not clear when, after the breeding hiatus, parents resume attendance at communal roosts. Thus, females must abandon the communal roost if they attempt to breed, causing a decline in the number of pairs at the roost during the breeding season.

Seasonal fluctuation in the number of singles at roosts is more difficult to predict, but may also provide information about breeding. During the nonbreeding period, birds not flying in pairs should consist of fledglings and unmated adults. If we are correct, then the number of singles during the nonbreeding period should decline due to fledgling mortality and successful pairing. Our data did not, however, allow us to distinguish between these two possibilities. During breeding, male parents attend the nest during the day, but sleep at communal roosts (Waltman and Beissinger 1992, Enkerlin-Hoeflich 1995, K. S. Berg, pers. obs.). Thus, if male parents roost communally during breeding, there should be an increase in the number of singles roosting at this time. We thus predicted that the number of singles roosting should increase at the onset of breeding. Although immigration and emigration could affect the number of singles and pairs any time during the year, we had no way to quantify this. We suspect, however, that potential effects are likely small, given the highly philopatric nature of parrots (Enkerlin-Hoeflich 1995, Sandercock et al. 2000, Bradbury et al. 2001). The geographic isolation of the population studied (Ridgely and Greenfield 2001, K. S. Berg, pers. obs.) further argues against permanent, significant migratory effects. Finally, we expected the number of singles to increase at the end of the breeding season, reflecting the number of fledglings recruited into the population.

METHODS

Study area. Our study was conducted at Puerto Hondo (2°11'47"S, 79°59'58"W), Province of Guayas, Ecuador. The area included

a fishing village located between a mangrove forest and a series of hills known as the Cordillera de Chongón. The latter was mainly covered in 40- to 80-yr-old Tropical Dry Forest and cattle pastures extending from near sea level to approximately 400 m elevation (Foster 1992). The roost site was on a mangrove island 0.7 km from where we conducted counts and is the only known roost for several hundred kilometers (Ridgely and Greenfield 2001, K. S. Berg, pers. obs.). The island was located on a tributary of the Estero Salado that converges with the Río Guayas and empties into the Gulf of Guayaquil and the Pacific Ocean about 75 km to the west. Red-lore Amazons forage and nest several kilometers to the north in the forested hills of the Cordillera Chongon. This is the only suitable habitat for Red-lore Amazons for many kilometers, with a city of 3 million people to the east, a large extension of mangroves to the south, and dry tropical scrub and agricultural holdings to the west. This combination of factors made the flight path to and from the mangroves predictable. Rainfall in the region is highly seasonal. A weather station located 15 km east of the study site recorded a median of 1050 mm of rain, with 99% concentrated between December and May. The median temperature was 22°C, ranging from a maximum of 34.4°C to a minimum of 18.0°C ($N = 10$ yr; INAMHI 1994).

Breeding. At our study site, Red-lore Amazons breed between late December and early April (Kunz 1995, Juniper and Parr 1998, K. S. Berg, pers. obs.). Kunz (1995) documented two nesting attempts (range = 8 January–19 March 1994) and juveniles were seen begging from parents until early May, presumably more than a month after fledging. To establish the nesting period during our study, we monitored one successful nest that was active between late December 1999 and late March 2000. This breeding period was consistent with the breeding period in 1994 (Kunz 1995). The nest tree was located about 3 km from the roost site inside the Bosque Protector Cerro Blanco (2°12'0"S, 80°0'0"W), a privately owned and managed reserve protecting 6000 ha of Tropical Dry Forest in the Cordillera del Chongón. We observed the nest for a total of 175 h from a blind at a distance of 35 m.

Roosting. Red-lore Amazons were counted from a fixed point along a known

flyway, on average, every 1.4 d from 15 June 1999 to 7 June 2000 ($N = 504$ h). We alternated counts between dusk arrivals and dawn departures. Dawn counts began at 05:50 (± 10 min) and continued until 07:50 (± 10 min; depending upon local sunrise). Dusk counts were conducted between 17:10 (± 10 min) and 19:10 (± 10 min). Numbers of pairs and single individuals were recorded. Although not quantified, flock size typically varied from 10 to 30 individuals and, within these flocks, pairs were usually clearly distinguishable; birds not clearly flying as pairs were treated as singles. Cloud cover was categorized during each count as cloudy, partly cloudy, or clear. Counts were canceled if it rained.

Preliminary analysis indicated significant differences between the dawn and dusk counts. Pooling counts of singles and pairs, the dawn and dusk counts conducted on the same day were highly correlated throughout the year ($N = 112$, $r = 0.64$, $P < 0.0001$). However, counts conducted at dawn ($N = 130$) were significantly higher ($t = 3.12$, $P = 0.002$) than those at dusk ($N = 123$), with mean counts of 117 at dawn and 98 at dusk. Dawn numbers were more stable, but the difference was not significant (two-sample test of variance, $F_{122,129} = 1.33$, $P = 0.11$). Dawn counts were probably more accurate than those at dusk, because the census was conducted only 0.7 km from the roost site. Thus, in the morning, birds left the roost at ca. 10 m above the ground on the same small island much closer to the observer than in the evening, when they arrived from a considerable distance (2–7 km) and height (50–500 m). Dawn counts were also found to be more precise in estimating the number of Red-tailed Amazons at roosts (Cougill and Marsden 2004). Based on our results, we included only dawn counts in the main analysis. Cloud cover was unrelated to the number of birds departing from the roost each morning ($F_{2,120} = 0.96$, $P = 0.39$) and was ignored for subsequent analyses.

Statistical analyses. Statistical analyses were conducted using the Statistical Analysis System (SAS Institute 2002). General linear models (GLM) were used for ANOVA. Analysis of residuals and normality tests initially suggested that roost counts deviated from a normal distribution. The mean and the variance were strongly correlated ($r = 0.66$), suggesting that

the data were best represented by a Poisson distribution. We used the GENMOD Procedure to construct an appropriate probability distribution against which the data were tested. However, because of the large number of roost counts, the results did not differ significantly from models analyzed under normal assumptions, and we thus present only the results of GLM. The GLM was used to test whether breeding period and month were related to the number of pairs and singles at the roost. We fit the data on pairs to a second-order polynomial, using the Julian date and date interaction. Because parrot movements may be influenced by rainfall, we also included season (wet vs. dry) in the model. However, because breeding occurred entirely during the wet season, when used as categorical predictors, season and breeding are confounded; and if combined in the same model, would violate assumptions regarding independence. We thus analyzed each of the factors in separate models. We used GLM to test whether Julian date predicted a decline in singles, using only dawn counts during the nonbreeding season. To control for seasonal variations in roost size, we calculated the proportion of pairs to total counts each day. We arcsine-transformed proportions and used GLM to test for effects of breeding period, date, and date interaction. Because we believed breeding was the biological cause of the quadratic fit of the data, and not an independent source of variation, we used Type I Sum of Squares to analyze effects sequentially.

Given the high degree of variability in counts and the lack of more direct observations of breeding, estimating the breeding proportion or fledgling output is not an easy task. As such, we compare several methods for estimating the reproductive portion of the population, differences between mean counts and mean proportions in each season, and differences between the mean of the five highest counts (or proportions) in each season. To estimate fledgling success per pair, we calculated the mean of the five highest counts of singles during 2 mo postbreeding and corrected this number by the mean ($+1$ SD) of counts of singles 1 mo prior to breeding (i.e., unpaired adults prior to breeding).

RESULTS

Breeding. Red-lore Amazons nested in dry tropical forest dominated by *Ceiba*

trichistandra (Bombacaceae). The nest was in a natural cavity in the trunk of a living *C. trichistandra* tree. On 9 December 1999, a pair was first observed occupying the cavity and, by 19 December, the birds occupied the cavity throughout the day and were assumed to have begun incubation. A chick was first seen at the entrance on 7 February 2000, and both parents were observed regurgitating food to the young on 12 February. On 10 March, two chicks were observed begging at the cavity entrance and likely fledged by 25 March, because they were not seen at the nest thereafter. On one occasion, the male (judging by this individual's reduced role in nest care and larger size) was observed flying in the direction of the communal roost site just after sundown. At least one focal adult, presumably the incubating female, was typically present at the nest in the morning before the exodus from the communal roost began. Thus, the breeding period was between 19 December and 25 March (96 d) and, during this period, the female roosted in the nest and the male appeared to return to the communal roost.

Roosting. A large roost of Red-lore Amazons was censused throughout 1 yr ($N = 123$ dawn point counts). The mean (\pm SD) number of birds leaving the roost each morning was 116 (± 43), and ranged from 31 on 10 May 2000 to 229 on 18 September 1999. The highest count occurred on the evening of 18 September (248 birds). We estimate the population size at 214 individuals, based on the mean of the five highest counts during the nonbreeding season.

Pairs comprised 91% ($\pm 7\%$) of all roosting observations. Counts of pairs and singles differed significantly between breeding and nonbreeding periods (Table 1), but were only marginally correlated (Pearson Correlation Coefficient $N = 123$, $r = 0.16$, $P = 0.08$). Counts of pairs (Y) provided a good fit to a second-order polynomial with date (X) and date-squared (X^2) ($Y = 47 (\pm 10 \text{ SE}) + 0.93 (\pm 0.12) X - 0.002 (\pm 0.0003)$

X^2 , $F_{2,120} = 29$, $r^2 = 0.33$, $P < 0.0001$; Fig. 1A). Solving this equation for a zero slope, the highest expected counts of pairs occurred on 6 June 1999, about 5 mo before nesting began. Breeding period, season, and month, all affected the numbers of pairs and singles roosting, but counts of pairs and singles responded differently (Table 2). For pairs, breeding period had a stronger effect than season, but the situation was reversed for singles. Month had the strongest effect on both pairs and singles. On average, there were 17 fewer pairs in the breeding period (Table 1). In contrast, the average number of singles increased by five during the breeding period (Table 1). During the nonbreeding period, the number of singles was strongly and inversely related to Julian date ($F_{1,93} = 93.9$, $P < 0.0001$, $r^2 = 0.50$; Fig. 1), but no such pattern was evident during the breeding period ($F_{1,26} = 0.81$, $P = 0.38$, $r^2 = 0.03$; Fig. 1).

If differences in counts of pairs during the breeding and nonbreeding seasons are the result of breeding females roosting at nests, and not simply a reflection of seasonal movements, then the ratio of pairs to singles at the communal roost should also decline during breeding. The proportion of pairs roosting had a similar, yet stronger quadratic fit with date and date-squared than when based on actual numbers of pairs (Fig. 1C; Table 3), and a significantly lower percentage of pairs roosting communally during the breeding season (Fig. 1C). These results reinforce our earlier conclusion that the dissolution of pairs during breeding is the biological cause of the observed reduction in pairs roosting during this time.

Because our hypothetical model of roosting fit well with a series of empirical tests, we felt justified in estimating the reproductive portion based on roost counts. Table 4 provides four methods for estimating the reproductive portion of the population based on roost counts. The most conservative estimates of the breeding portion (7%) were based on proportions; the

Table 1. Summary statistics for counts of paired and single Red-lore Amazons at a communal roost in southwest Ecuador during the breeding and nonbreeding seasons.

	Paired					Singles				
	Mean	SE	Min	Max	<i>N</i>	Mean	SE	Min	Max	<i>N</i>
Breeding	82	4	36	122	95	13	1	4	19	28
Nonbreeding	115	5	14	222	28	8	1	0	24	95

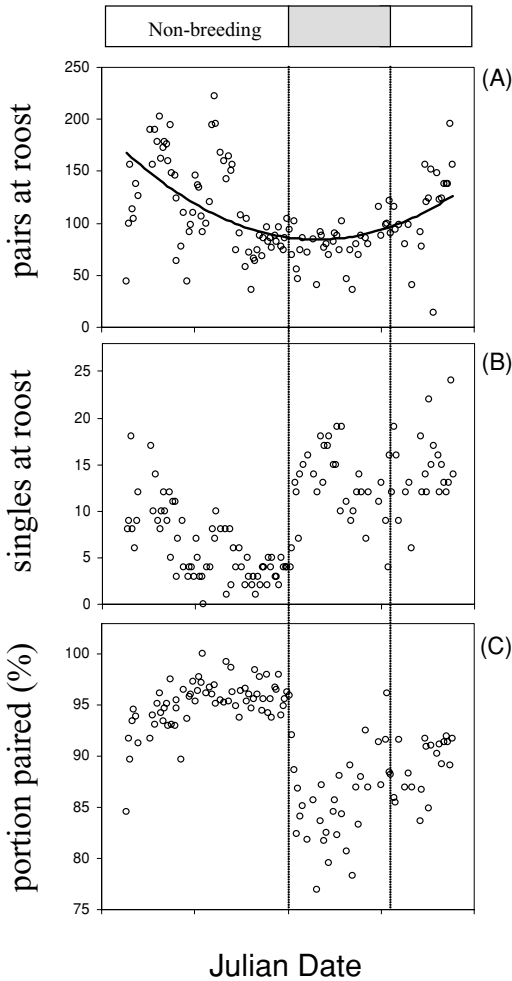


Fig. 1. Seasonal variation in counts of Red-lore Amazons at a communal roost in Guayas Province, Ecuador. (A) The number of paired individuals at the roost by Julian date fit to a second-order polynomial ($r^2 = 0.33$, $P < 0.0001$). There were significantly fewer pairs at the roost during the breeding period. (B) The number of single parrots at the roost by Julian date. The number of single parrots declined continuously during the nonbreeding period ($r^2 = 0.50$, $P < 0.0001$) and was, on an average, higher during the breeding period. (C) Proportion of total roosting birds that were paired by Julian date. The proportion of pairs was higher during the nonbreeding period and declined at the start of the breeding period, as indicated by vertical hashed-lines. Horizontal axis is Julian serial date (16 June 1999–31 May 2000).

mean, or the mean based on the five counts with the highest proportion of pairs, yielded nearly identical results. At the other extreme, the differences between the five highest counts

in the breeding and nonbreeding periods suggest that as much as 43% of the population may have attempted to breed.

Obtaining an estimate of fledgling output is not as straightforward, given that unpaired adults and fledglings are likely included in counts of singles in the nonbreeding period. Because the number of single individuals declined consistently throughout the nonbreeding period, we calculated the average number of singles for the month prior to breeding ($5.5 + 1 \text{ SD } (3.4)$), to arrive at an estimate of 8.9 or 9 individuals unpaired at the onset of breeding. Our highest count of singles was 36 individuals on 6 June, a little more than 2 mo after the end of the breeding period. More conservatively, the highest five counts of singles during the 2-mo period after the end of breeding averaged 26 individuals. Thus, an estimate of 26 singles after breeding might involve ca. 17 fledglings recruited into the roost population. Returning to Table 4, this suggests, according to our methods, a range of 0.36–2.36 fledglings per nest attempt.

DISCUSSION

Our estimate of the population size (214) was based on the five highest counts, all of which occurred during the nonbreeding season. This increases earlier estimates of this roosting population by nearly 100 birds (Kunz 1995). This estimate also represents a substantial portion of the 400–600 individuals estimated for the entire *lilacina* race of Red-lore Amazon (Juniper and Parr 1998), and supports the long-held notion that population estimates based on parrot roosts should exclude counts made during the breeding period.

Roost counts showed marked seasonal fluctuations in both the number of pairs and singles, but season affected these in different ways. As predicted, the number of pairs during the breeding season was significantly lower than during the nonbreeding season, supporting the hypothesis that the breeding portion of the population abandoned the communal roost to nest. For singles, the situation was essentially reversed; more singles were observed during the breeding period. This supports the idea that breeding males continue to roost communally during breeding. However, because breeding occurred entirely during the wet season, these results by themselves do not allow us to rule-out possible effects due to seasonal movements

Table 2. Effects of breeding period (breeding vs. nonbreeding), season (wet vs. dry), and month on the number of paired and single Red-lored Amazons at a communal roost in southwest Ecuador (June 1999–May 2000).

Independent variables	df	Dependent variable					
		Pairs			Singles		
		<i>F</i>	<i>P</i>	<i>r</i> ²	<i>F</i>	<i>P</i>	<i>r</i> ²
Breeding period	1,121	15.5	<0.0001	0.11	24.4	<0.0001	0.17
Season	1,121	8.4	0.0046	0.06	110.0	<0.0001	0.48
Month	11,111	11.4	<0.0001	0.53	17.8	<0.0001	0.64

of the population that may be independent of breeding activity (i.e., food scarcity; see Renton 2001).

On the other hand, the breeding period appears evolutionarily labile in sympatric psittacines, and food availability may be related to this lability (Brightsmith 2005). Even within species, the breeding period appears highly plastic. Red-lored Amazons in Ecuador breed 4 mo earlier than in Mexico (Enkerlin-Hoeflich 1995, Kunz 1995, our study). Our finding that temporal changes in the proportion of pairs predicted better a decline during the breeding season essentially controls for possible changes related to season (or food), because it considers both singles and pairs simultaneously. The seasonal movement hypothesis, on the other hand, does not make clear predictions about proportional changes in roost composition. Furthermore, if the prolonged decline in pairs from mid-December through March reflects seasonal displacement in our study, this would contradict patterns observed in other psittacine populations, because these were wet months when plant energy production is likely higher (Renton and Salinas-Melgoza 1999, Renton 2002). Taken together, these results provide strong support for the hypothesis that roost counts provide information concerning the reproductive portion of the population.

Most of our roosting population consisted of pairs. Similarly, Gilardi and Munn (1998) found that *Amazona* parrots traveled mainly in pairs. Higher reproductive rates should be associated with a higher proportion of single birds during the nonbreeding season, even after controlling for dispersal. The consistently high proportion of pairs in our study during the nonbreeding season suggests the same low reproductive rate reported for numerous parrot species (Stoleson and Beissinger 1997, Wright et al. 2001).

We observed a marked decline in the number of single parrots using the roost during the nonbreeding period. This decline is likely explained by fledgling mortality, known to be high in first-year parrots (Stoleson and Beissinger 1997, Wright et al. 2001). Some of this decline could also be explained either by successful pairing of adults or by dispersal, but our results do not allow us to distinguish between these alternative explanations.

Although our model generally responded well to empirical tests, the variability in daily counts and our limited knowledge of the breeding behavior of Red-lored Amazons make estimating the reproductive portion of the population and fledgling output difficult. As such, we present four possible methods for estimating the reproductive portion of the population (Table 4). These estimates range from 7% to 43% of the population. Calculating the differences in means (Method 1) is not very realistic, because it caps the population at 114, and the total population size far exceeded this (214). However, this method might provide a more realistic estimate of the proportion of successful breeders. The estimates of 7% that come from comparing how proportions change (Methods 3 and 4) seem, on the other hand, too conservative, and

Table 3. Results of a general linear model comparing the effects of breeding season, date, and date-squared on the proportion (%) of paired Red-lored Amazons at a communal roost. Proportions were arcsine-transformed prior to analysis.

	df	<i>F</i>	<i>P</i>	<i>r</i> ²
Model	3119	28.88	<0.0001	0.42
Breeding	1	57.34	<0.0001	
Date	1	21.44	<0.0001	
Date-squared	1	7.86	0.006	

Table 4. Comparison of four methods of estimating the reproductive portion and fledgling output of Red-
lored Amazons based on roost counts. All numbers are given based on individuals. Output is given in fledglings
per breeding female and based on an estimate of 17 fledglings recruited into the population after breeding,
and corrected for the average number of single individuals observed 1 mo prior to breeding (± 1 SD).

Method	Roosting		Breeding estimate		
	Nonbreeding	Breeding	Individuals	Portion	Fledglings
	(NB)	(B)	(NB - B)	$((NB - B)/NB)$	$(17/((NB - B)/2))$
(1) Mean number of paired individuals	114	82	32	28.1%	1.06
(2) Mean of 5 highest counts (pairs)	214	121	93	43.5%	0.36
(3) Mean proportion of pairs	93%	85%	$((NB - B)/NB) \times 214$		
(4) Mean of 5 highest proportions	99%	92%	16	7.5%	2.13
			14	6.7%	2.36

yielded a high rate of fledgling output (2.1–2.6 per attempt). Enkerlin-Hoeflich (1995) estimated 0.97 fledglings per nest attempt, which is closer to our estimate using Method 1 (1.06 per attempt).

This leaves the comparison of the highest counts between periods (Method 2) that we feel comes closest to estimating the real reproductive portion. Few direct estimates of the reproductive portion of parrot populations have been made, because such estimates require an intensive marked-resighting effort and exhaustive monitoring of all nests in a population. Sandercock et al. (2000) reported a breeding portion of 77% and 49% in female and male Green-rumped Parrotlets, respectively, based on 1334 adults studied over a 10-yr period. Thus, our best estimate of the reproductive proportion (43%) of our population of Red-lored Amazons is close to that reported for male parrotlets. The estimate determined by using Method 2 corresponds to 0.37 fledglings per attempt, which is lower than that reported for Red-lored Amazons in Mexico and less than half of the minimum of several congeners (reviewed by Enkerlin-Hoeflich 1995). However, this could be due to problems with our estimate of 17 fledglings, and not reproductive portion per se. Both estimates of the reproductive portion and fledgling output should be viewed with caution and data for successive years are needed to confirm whether the patterns described above are repeatable.

Currently, Red-lored Amazons do not have global protected status (Stattersfield and Capper 2000). However, the *lilacina* race is endemic to western Ecuador, where it was recently classi-

fied as near-threatened (Ridgely and Greenfield 2001). The roost used by Red-lored Amazons in our study was the closest patch of mangrove to an important extension of dry tropical forest in the Cordillera de Chongon-Colonche (50,000 ha). Bosque Protector Cerro Blanco (6000 ha) undoubtedly protects critical habitat for breeding and foraging. However, the roost site is only 15 km from a city of 3 million people and poaching at the roost persists (R. R. Angel, pers. obs.). Our finding that as much as half of the estimated total population of *A.a.lilacina* uses one, vulnerable roost, when considered with their potentially low reproductive rate, supports the recommendation by Ridgely and Greenfield (2001) that threatened status is warranted in Ecuador. Increasing the level of protection for the small island used as a roost site by Red-lored Amazons in our study would help protect a population that ranges over a much larger area and, at the same time, preserve a potentially useful tool for demographic studies of a poorly known neotropical parrot.

ACKNOWLEDGMENTS

This study was supported by the Loro Parque Fundacion and Fundacion Pro-Bosque. We thank the community of Puerto Hondo for allowing us to census the parrots, and to the Club Ecológica de Puerto Hondo for use of canoes. Holcim Ecuador permitted access to the nest site in the Bosque Protector Cerro Blanco. The Ecuadorian Ministerio de Ambiente provided the necessary permits. E. Horstman provided logistical support. We are especially grateful to V. Apanius for help with statistical analysis, and C. Canaday, S. R. Beissinger, and Z. Peery for additional insights. D. Brightsmith and two anonymous reviewers provided valuable comments on earlier manuscripts.

LITERATURE CITED

- BEISSINGER, S. R., AND E. H. BUCHER. 1992. Can parrots be conserved through sustainable harvesting? *BioScience* 42: 164–173.
- , S. TYGIELSKI, AND B. ELDERD. 1998. Social constraints on the onset of incubation in a neotropical parrot: a nest box addition experiment. *Animal Behaviour* 55: 21–32.
- BRADBURY, J. W., K. A. CORTOPASSI, AND J. R. CLEMMONS. 2001. Geographical variation in the contact calls of Orange-fronted Parakeets. *Auk* 118: 958–972.
- . 2003. Vocal communication in wild parrots. In: *Animal social complexity: intelligence, culture and individualized societies* (F. B. M. de Waal, and P. L. Tyack, eds.), pp. 293–316. Harvard University Press, Cambridge, MA.
- BRIGHTSMITH, D. J. 2005. Parrot nesting in southeastern Peru: seasonal patterns and keystone trees. *Wilson Bulletin* 117: 296–305.
- CASAGRANDE, D. G., AND S. R. BEISSINGER. 1997. Evaluation of four methods for estimating parrot population size. *Condor* 99: 445–457.
- COLLAR, N. J., D. C. WEGE, AND A. J. LONG. 1997. Patterns and causes of endangerment in the New World avifauna. In: *Studies of neotropical ornithology honoring Ted Parker* (J. V. Remsen, Jr., ed.). Ornithological Monographs No. 48, American Ornithologists' Union, Washington, D.C.
- COUGILL, S., AND S. J. MARSDEN. 2004. Variability in roost size in an *Amazona* parrot: implications for roost monitoring. *Journal of Field Ornithology* 75: 67–73.
- DODSON, C. H., AND A. H. GENTRY. 1991. Biological extinction in western Ecuador. *Annals of the Missouri Botanical Garden* 78: 273–295.
- ENKERLIN-HOEFLICH, E. C. 1995. Comparative ecology and reproductive biology of three species of *Amazona* parrots in northeastern Mexico. Ph.D. dissertation, Texas A&M University, College Station, TX.
- FORSHAW, J. M. 1977. *Parrots of the world*. T.F.H. Publications, Inc., Neptune, NJ.
- FOSTER, R. B. 1992. Cerro Blanco (moist limestone forest): site description and vegetation. In: *Status of forest remnants in the Cordillera de la Costa and adjacent areas of southwestern Ecuador* (T. A. Parker, III, and J. L. Carr, eds.), pp. 42–43. RAP Working Papers No. 2, Conservation International, Washington, D.C.
- GILARDI, J. D., AND C. A. MUNN. 1998. Patterns of activity, flocking and habitat use in parrots of the Peruvian Amazon. *Condor* 100: 641–653.
- GNAM, R., AND A. BURCHSTED. 1991. Population estimates for the Bahama Parrot on the Abaco Island, Bahamas. *Journal of Field Ornithology* 62: 139–146.
- INAMHI. 1994. *Anuario meteorológico*. Instituto Nacional de Meteorología e Hidrología. Quito, Ecuador.
- IUCN. 1994. *Categorías de las listas rojas de la UICN*. Union Internacional para la Conservación de la Naturaleza, Gland, Switzerland.
- JUNIPER, T., AND M. PARR. 1998. *A guide to parrots of the world*. Pica Press, Sussex, UK.
- KUNZ, B. 1995. Autecology and distribution pattern of the Lilacine Amazon (*Amazona autumnalis lilacina*, Psittacidae) and its population dynamics under direct and indirect human influences. M.S. thesis, Ruhr-Universität, Bochum, Germany.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. DE FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- OWENS, I. P. F., AND P. M. BENNETT. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences* 97: 12144–12148.
- RENTON, K. 2001. Lilac-crowned Parrot diet and food resource availability: resource tracking by a parrot seed predator. *Condor* 103: 62–69.
- . 2002. Seasonal variation in occurrence of macaws along a rainforest river. *Journal of Field Ornithology* 73: 15–19.
- , AND A. SALINAS-MELGOZA. 1999. Nesting behavior of the Lilac-crowned Parrot. *Wilson Bulletin* 111: 488–493.
- RIDGELY, R. S., AND P. GREENFIELD. 2001. *The birds of Ecuador*. Cornell University Press, Ithaca, NY.
- SANDERCOCK, B. K., S. R. BEISSINGER, S. H. STOLESON, R. R. MELLAND, AND C. R. HUGHES. 2000. Survival rates of a neotropical parrot: implications for latitudinal comparisons in avian demography. *Ecology* 81: 1351–1370.
- SAS INSTITUTE. 2002. SAS OnlineDoc Version 9.1.3. Cary, NC.
- 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 Foundation of Vertebrate Zoology, Los Angeles, CA.
- , P. MCGOWAN, J. GILARDI, AND A. GRAJAL, Eds. 2000. *Parrots: status survey and conservation action plan 2000–2004*. IUCN, Gland, Switzerland.
- STATTERSFIELD, A. J., AND D. R. CAPPER. 2000. *Threatened birds of the world*. Birdlife Internacional, Cambridge, UK, and Lynx Edicions, Barcelona, Spain.
- STOLESON, S. H., AND S. R. BEISSINGER. 1997. Hatching asynchrony, brood reduction, and food limitation in a neotropical parrot. *Ecological Monographs* 67: 131–154.
- WALTMAN, J. R., AND S. R. BEISSINGER. 1992. Breeding behavior of the Green-rumped Parrotlet. *Wilson Bulletin* 104: 65–84.
- WRIGHT, T. F. 1996. Regional dialects in the contact call of a parrot. *Proceedings of the Royal Society of London B* 263: 867–872.
- , C. A. TOFT, E. ENKERLIN-HOEFLICH, J. G. GONZALEZ-ELIZONDO, M. ALBORNOZ, A. RODRIGUEZ-FERRARO, F. ROJAS-SUAREZ, V. SANZ, A. TRUJILLO, S. R. BEISSINGER, V. BEROVIDES A, X. GALVEZ A, A. T. BRICE, K. JOYNER, J. EBERHARD, J. GILARDI, S. E. KOENIG, S. STOLESON, P. MARTUSCHELLI, J. M. MEYERS, K. RENTON, A. M. RODRIGUEZ, A. C. SOSA-ASANZA, F. J. VILELLA, AND J. W. WILEY. 2001. Nest poaching in neotropical parrots. *Conservation Biology* 15: 710–720.