# The Influence of Habitat, Season, and Detectability on Abundance Estimates across an Amazonian Parrot Assemblage

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## ABSTRACT

The Amazon basin holds very high parrot species richness but almost nothing is known of parrot population densities in the region or how these vary between species, habitats, sites, and seasons. Such data are becoming important as humans impact on increasing areas of the region. Seventeen parrot species were surveyed using a line transect distance sampling method over 3 yr in floodplain and *terra firme* forests at two sites in the Tambopata region of southeast Peru. Density estimates for most species were in the range of 3.3–7.8/km², with *Brotogeris cyanoptera* and *Amazona farinosa* reaching densities of 22 and 23/km² in floodplain forest during the dry season. Parrot densities were higher in floodplain forest than in *terra firme* forest at both sites. The parrot communities of *terra firme* forests were similar across sites and seasons, but those in floodplain forests differed widely across sites and across seasons. Upper canopy birds are notoriously difficult to survey. We introduce a procedure to correct for the likely violation of the assumption that all birds on the transect line are detected (distance sampling assumption g(0) = 1). We correct g(0) based on calling rates of birds using a cue-counting technique. Multipliers for g(0) differ across species and site, but not season. This method yielded density estimates on average 22 percent higher (6–40% higher in individual species) than those from the standard method.

Abstract in Spanish is available in the online version of this article.

*Key words*:  Amazon; bird survey; distance sampling; Peru; Psittacidae; Tambopata.

THE AMAZON BASIN HOLDS A HUGELY RICH AVIFAUNA (Haffer 1990). Up to 20 species of parrots (Psittacidae) are known from individual sites (Terborgh *et al.* 1984), and they are an important attraction, especially when gathered at riverside claylicks, for tourists (Lee *et al.* 2010). Over one-third of South American parrot species are considered threatened (IUCN 2008), yet little information exist on abundance or how this differs across habitats or sites (Lloyd 2004). This lack of quantitative data is acute for Amazonian parrots, for which there are density estimates for just – a few species (Lloyd 2004, Haugaasen & Peres 2008). Although they are not currently among the continent's most threatened psittacids, mainly on account of their large ranges, species belonging to the rich Amazonian parrot communities may be patchily distributed, occur at low densities, and respond poorly to habitat change and hunting (Lees & Peres 2006).

Distance sampling is a widely used technique for estimating abundance of wild animal populations (Buckland & Anderson 2004), and the method is commonplace among studies of parrot and other bird abundances where actual animal density (number of individuals per unit area) is presented (Marsden 1999, Kinnaird *et al.* 2003, Marsden & Pilgrim 2003). The most important assumption for standard distance sampling is that objects on or near the transect line or observation point need to be detected with certainty, *i.e.*, g(0) = 1. Failure to do so will underestimate animal density (Buckland *et al.* 2008). The assumption that g(0) = 1 is rarely tested (Bächler & Liechti 2007) but violation is likely in tall and structurally complex tropical forests where many birds spend large amounts of time perched quietly (Gale *et al.* 2009). The probability that a bird is available to be detected (usually through singing or calling during the survey interval) can be as low as 0.1, and unadjusted distance sampling may underestimate density by as much as a factor of four (Diefenbach *et al.* 2007).

The primary aim of this study was to compare density estimates for a range of parrot species across floodplain and *terra firme* forests taking into consideration the limitations of detecting quiet birds in tall and complex forests. No regional density estimates exist for the parrot assemblage in southeast Peru (but see Lloyd 2004 and Terborgh *et al.* 1990), an area of high conservation importance (Stattersfield *et al.* 1998). Seasonal change in relative abundance has been documented for one site in the region (Brightsmith 2006), but if these are related to seasonal changes in detectability, differences in phenology, or the presence of a large riverside claylick is not known. We examine seasonal changes in abundance in habitat types at two sites in southeast Peru. Then, we describe a call-counting component that can be integrated into the standard distance sampling transect method that will yield more accurate density estimates for parrots in tall and complex forests. This method is based on species-specific corrections to estimates of g(0) that helps account for those individuals at the transect line that are missed.

## METHODS

STUDY SITES.—Surveys of the parrot species listed in Table 1 were conducted at Posada (12°48′ 6″ S, 69°18′ 1″ W) and Refugio

TABLE 1. *Encounter rates (individuals/km walked ± SE) and the total number of perched groups encountered during the survey (n) for sixteen parrot species across three sites in the Tambopata region. Body size was taken from Forshaw (2006). Density estimates (individuals/km$^2$; lower 95% confidence interval – upper 95% confidence interval) based on standard distance sampling (Density) and distance sampling using multipliers from Table S2 (Corrected density) are presented. Aratinga spp. density based on common detection function, stratified by species. Primolius couloni and Ara severus density based on common detection function, post-stratified by species. Orthopsittaca manilata density based on A. severus detection function. GOF CvM (cos) are cosine-weighted Cramer-von-Mises goodness-of-fit scores for corrected density estimates.*

| Species | Body size (cm) | Encounter rate | n | Density | Corrected density | GOF CvM (cos) |
|---|---|---|---|---|---|---|
| Blue-and-yellow Macaw *Ara ararauna* | 86 | 0.05 ± 0.01 | 58 | 0.33; 0.16–0.67 | – | |
| Scarlet Macaw *Ara macao* | 85 | 0.23 ± 0.03 | 229 | 1.47; 1.21–1.79 | 1.69; 1.38–2.08 | 0.6 |
| Red-and-green Macaw *Ara chloropterus* | 90 | 0.28 ± 0.02 | 369 | 1.78; 1.58–1.99 | 2.04; 1.79–2.33 | 0.8 |
| Chestnut-fronted Macaw *Ara severus* | 46 | 0.03 ± 0.01 | 23 | 0.26; 0.10–0.63 | 0.18; 0.09–0.33 | 0.3 |
| Red-bellied Macaw *Orthopsittaca manilata* | 46 | 0.04 ± 0.02 | 12 | 0.73; 0.15–3.62 | – | |
| Blue-headed Macaw *Primolius couloni* | 41 | 0.01 ± 0.007 | 7 | 0.09; 0.04–0.23 | – | |
| White-eyed Parakeet *Aratinga leucophthalma* | 32 | 0.13 ± 0.03 | 46 | 0.88; 0.47–1.63 | – | |
| Dusky-headed Parakeet *Aratinga weddellii* | 28 | 0.09 ± 0.69 | 26 | 0.59; 0.27–1.26 | – | |
| Black-capped Parakeet *Pyrrhura rupicola* | 25 | 0.60 ± 0.04 | 331 | 7.30; 5.57–9.26 | 9.02; 7.01–11.59 | 0.6 |
| Cobalt-winged Parakeet *Brotogeris cyanoptera* | 18 | 1.37 ± 0.13 | 383 | 10.3; 7.0–15.33 | 14.17; 9.51–21.10 | 0.7 |
| Amazonian Parrotlet *Nannopsittaca dachilleae* | 12 | 0.007 ± 0.00 | 1 | – | – | |
| Dusky-billed parrotlet *Forpus modestus* | 12 | 0.01 ± 0.005 | 3 | – | – | |
| White-bellied Parrot *Pionites leucogaster* | 23 | 1.02 ± 0.05 | 649 | 10.16; 9.4–10.97 | 10.79; 9.06–12.85 | 0.8 |
| Orange-cheeked Parrot *Pyrilia barrabandi* | 25 | 0.09 ± 0.02 | 73 | 0.79; 0.54–1.18 | – | |
| Blue-headed Parrot *Pionus menstruus* | 28 | 0.25 ± 0.02 | 244 | 2.17; 1.68–2.80 | 2.73; 2.11–3.53 | 0.9 |
| Yellow-crowned Amazon *Amazona ochrocephala* | 38 | 0.09 ± 0.01 | 112 | 0.72; 0.53–0.99 | 1.01; 0.68–1.51 | 0.2 |
| Mealy Amazon *Amazona farinosa* | 38 | 1.91 ± 0.15 | 1587 | 10.89; 8.3–14.2 | 13.59; 10.34–17.85 | 0.7 |

(12°52′ 27″ S, 69°24′ 38″ W; Fig. S1), two study sites 14 km apart, within the Tambopata National Reserve (TNR) and associated buffer zone (BZ) (274,690 ha and 186,450 ha respectively), in lowland Amazon rain forest of southeast Peru. These study sites are located in the department of Madre de Dios, which was considered one of the best protected areas of Amazon forest as accessibility has been restricted until the recent completion of the Interoceanic highway (Salmón *et al.* 2003). The predominant forest types are floodplain (TNR: 32.7%, BZ: 15.4%) and *terra firme* (TNR: 62.6%, BZ: 83.2%; Salmón *et al.* 2003). *Terra firme* includes previously flooded terraces of ancient Holocene and Pleistocene alluvial terraces (Räsänen 1993). Floodplain forests were associated with the Tambopata River. The altitudinal range was between 350 and 195 m asl. Annual rainfall ranges between 1600 and 2400 mm and temperature between 10°C and 38°C (Räsänen 1993). To improve global density estimates for rare species, a small amount of additional sampling was conducted at the Tambopata Research Centre (TRC). All transects at Posada were within five km of known parrot claylicks. All sampling at Refugio was conducted 5–10 km from any known macaw claylick.

Parrot surveys.—From December 2005 to December 2008, a variable-width line transect method was used to estimate parrot densities (following Bibby *et al.* 1998). Surveys were carried out throughout the year by three main observers (AL and two full-time field assistants). Supplementary observations were taken by part-time field assistants, who undertook rigorous training and testing in species identification and field methods onsite for a

minimum period of 6 wk. A specific focus of training was distance measurement and identification of parrot vocalizations. Any observer whose detection rate was significantly different from the principal observers was rejected – for a full review of accounting for observer impact see Lee (2010). No surveys were conducted on rainy days. Surveys were conducted from daybreak (0500–0545 h) up to 1100 h and from 1515 to 1730 h. The 15 transects at the three sites ranged from 2 to 5 km in length, for a total of 49 kms. Random 2-km portions of transects were completed during the shorter afternoon survey periods. Sampling was conducted in both directions along the transects twice per month. Detections from the repeat visits for each line were pooled and the line length treated as the sum of all sampling effort for each transect to avoid pseudoreplication and underestimation of variance (Buckland *et al.* 2008). For season stratification the relevant subsets of each transect were extracted for analysis. In all, 1235 km of transect was walked at Posada, 1116 km at Refugio and 61 km at TRC.

Transects were surveyed at 1 km/h, with any parrot recorded less than 100 m in front of the walker being recorded. Detection cue and activity (perched, flying, perched-then-flying or flying-and-then-perched) were recorded. For each encounter, perpendicular distance (to the nearest meter) from the line to the bird contact was measured with laser rangefinders when vegetation allowed (> 50% of occasions). For groups of birds, the distance to the 'centre of gravity' of the group was estimated, usually by measuring the distance to the stem of the main tree in which a group was perched, or in the case of aural contacts,

believed to be perched. The number of individuals in each encounter was recorded, if known. For contacts where birds were heard only, it was usually not possible to assess the size of the group involved. In those cases mean group size for that species was substituted for the missing group size values. Mean group size was calculated from accurate group counts from towers for 3 mo intervals (Table S1).

DENSITY CALCULATIONS.—Density estimates were produced using the DISTANCE 6.0 program (Thomas *et al.* 2010). For software settings, we followed the recommendations of Buckland *et al.* (2001) and those used by others for estimating the densities of large birds from similar rain forest environments (*e.g.*, Anggraini *et al.* 2000). All transects were cut for the purpose of the survey. Two transects were laid out leading away from claylicks at Posada, but were otherwise placed as randomly as possible (they were not straight but did not cross one another or contain any bends > 90⁰). Sampling design impacts the choice of appropriate variance estimator; a systematic design can provide estimators for encounter rates with greater precision than those obtained under a random design in the event of a trend in object density throughout the survey region (Fewster *et al.* 2009). Consequently, the variance estimator S2 that accounted for non-random placement of transect lines was used. For all species, birds were entered as clusters in ungrouped format. It was generally found that truncating the greatest 5–10 percent of distances for observations gave the best model fits. Flying and flying-then-perched groups were not included following Marsden (1999). Perched and perched-then-flying groups are hereon referred to as perched birds except where the difference is important. A sequential testing of the key functions and series expansions were examined to fit detection functions to the data as suggested by Buckland *et al.* (2001). Models were fitted in the DISTANCE 6.0 program using the automated sequential selection and the Akaike's Information Criteria (AIC) stopping rule. Model goodness-of-fit was tested using the cosine-weighted version of the Cramer-von Mises test, a goodness-of-fit test available in DISTANCE and designed to emphasize departures in model fit closest to the transect line, where such deviations are most important. Densities for each species with > 70 detections were stratified by site, season, and habitat using the global detection function where the combined AIC for sub-sets was greater than the AIC for the global AIC model.

To quantify density changes by habitat, site and season, records for the entire parrot assemblage were used to calculate densities based on the sum of species density estimates by stratification with detection function and group sizes calculated for each stratum. As this produces a final value without standard error, the density range as determined by 95% confidence intervals is provided. Differences in density across seasons for individual species were tested in four habitat/sites (floodplain at Posada, *terra firme* at Posada, floodplain at Refugio and *terra firme* at Refugio) using Wilcoxon signed ranks tests in PASW v.18.0 (SPSS, Inc., Chicago, Illinois, U.S.A).

CORRECTING FOR UNCERTAIN DETECTION AT THE TRANSECT LINE.— Observers recorded parrots using a 'look forward only' method

(*i.e.*, only parrots less than 100 m in front of the fieldworker were recorded). This means that at a sampling speed of 1 km/h, each parrot group was 'available for counting' for a period of 6 min (the amount of time it took to walk 100 m).

If groups call less frequently than once per 6 min, then there is a strong probability that they will go undetected (only 4% of 2681 parrot encounters within 30 m of the transect line were of silent 'seen only' groups). The greater the proportion of birds that do not call within 6 min, then the lower will be $g(0)$. We recorded the calling rates of a range of parrot species to determine the probability of perched parrots calling during the 6 min recording window. We then estimated the proportion of groups of each species that might be missed, and used this as a correction for $g(0)$ in transects where calling birds only are recorded (a cue-counting method but with each group recorded only once).

Calling rates of visible perched birds were monitored from four vantage points: two 30+ m towers and two 20+ m riverbank viewpoints, from December 2005 to December 2007. The following information was recorded for each encounter: time of onset of encounter when the bird/s flew into view or was detected; species; group size; number of vocalizations (classified as a discrete note or joined notes of up to 3 sec in length); and the end of the encounter (time when birds were lost from view or flew off). A total of 626 observation sessions (2198 h) of vocalizing birds were conducted.

The proportion of all occasions in which birds called more frequently than once every 6 min was calculated for each species. A logistic regression (a GLM with binomial error structure and logit link function) was undertaken in R (R DEVELOPMENT CORE TEAM 2009) to determine influences on the calling rates (whether or not they called within 6 min) of perched parrots. Each parrot group ($N = 872$) monitored from the four vantage points was coded according to whether or not individuals within it vocalized (= 1) or not (= 0) more than once per 6 min. Parrot species with fewer than 15 records of duration greater than 6 min were excluded (the analysis included only species in Table 2). Species, study site (Posada or Refugio), time period (0500–0800 h; 0801–1100 h; 1500–1800 h), and season (Feb–April; May–July; Aug–Oct; Nov–Jan) were entered as categorical variables and group size entered as a continuous variable. The minimum adequate model was chosen based on Akaike Information Criterion (AIC) minimization.

An additional issue is that fieldworkers walking transects often flush perched parrots from close to the transect line. Since they call in response to recorder presence, their call rate is unnaturally high and so we exclude them from the correction calculations – in effect we assume that $g(0)$ for flushed birds is certain. So we use the following correction equation:

Multiplier for $g(0) = ((P * V_p) + PF)/(P + PF)$

where P is the number of vocal records of perched birds that do not flush in response to the fieldworker, PF is the number of birds (both seen and heard) that flush in response to the

TABLE 2. *Density estimates (individuals/km², 95% confidence interval) for parrots in the wet and dry seasons in floodplain and terra firme forest at two sites in the Peruvian Amazon. Also shown is survey effort (km) of transect surveyed. Overall densities are density estimates by stratification for the entire parrot assemblage and presented.*

| | Posada | | | | Refugio | | | |
|---|---|---|---|---|---|---|---|---|
| | Floodplain | | *Terra firme* | | Floodplain | | *Terra firme* | |
| | Dry Km = 344 | Wet Km = 317 | Dry Km = 258 | Wet Km = 316 | Dry Km = 377 | Wet Km = 286 | Dry Km = 265 | Wet Km = 188 |
| *Ara macao* | 0.6; 0.2–1.4 | 0.6; 0.2–1.6 | 0.7; 0.4–1.2 | 0.8; 0.4–1.4 | 2.2; 1.6–3.1 | 1.2; 0.8–1.8 | 1.6; 1.0–2.5 | 1.3; 0.5–3.7 |
| *Ara chloropterus* | 2.7; 0.5–15.0 | 2.8; 1.8–4.3 | 1.5; 0.9–2.5 | 1.3; 0.06–27 | 1.2; 0.8–1.8 | 0.9; 0.5–1.8 | 0.8; 0.6–1.1 | 1.2; 0.5–2.9 |
| *Pyrrhura rupicola* | 8.2; 6.5–10.2 | 7.4; 4.4–12.2 | 5.8; 2.4–13 | 3.7; 1–13.3 | 4.8; 3.4–6.8 | 3.5; 2.1–5.7 | 1.3; 0.4–3.9 | 1.8; 0.8–3.6 |
| *Brot. cyanoptera* | 22; 16–28 | 13; 6.5–27 | 8.2; 5.3–12.8 | 7.7; 5.1–11.4 | 16; 11–23 | 9.4; 3.1–28 | 1.8; 0.2–15 | — (n = 1) |
| *Pyrilia barrabandi* | 0.3; 0.2–0.6 | 0.9; 0.5–1.5 | 0.3; 0.2–0.5 | 0.4; 0.1–1.0 | 0.7; 0.3–1.5 | 1.7; 0.3–8.6 | 0.6; 0.2–2.3 | 2.5; 0.5–11 |
| *Pionites leucogaster* | 9.8; 4.4–22.1 | 6.7; 5.1–8.9 | 8.9; 3.6–21 | 10.8; 8.9–13 | 11.8; 10–14 | 11.1; 9.3–13 | 8.4; 5.6–12.6 | 7.5; 5.7–9.9 |
| *Pionus menstruus* | 2.9; 1.8–4.8 | 1.9; 1.2–3 | 2.8; 1.5–5.6 | 1.3; 0.9–2 | 2.1; 1.5–2.8 | 1.3; 0.7–2.5 | 0.3; 0.1–1.3 | 0.4; 0.1–1.7 |
| *Amaz. ochrocephala* | 2.6; 1.8–3.5 | 0.9; 0.3–2.3 | 0.1; 0.04–0.3 | 0.2; 0.1–0.6 | 0.5; 0.2–1 | 0.1; 0.03–0.7 | 0.2; 0.1–0.7 | 0.3; 0.1–1.1 |
| *Amazona farinosa* | 23; 12–42 | 14; 10–21 | 5.3; 1.1–2.7 | 5.7; 4.5–7.1 | 10.5; 8.8–13 | 8.1; 5.6–11.5 | 6.3; 4–9.8 | 3.8; 3.1–4.8 |
| Overall densities | 90; 78–106 | 56; 44–71 | 39; 29–51 | 36; 29–44 | 60; 45–79 | 83; 21–318 | 24; 18–31 | 36; 29–44 |

fieldworker, and Vp is the proportion of parrot individuals (from the call rate study) that called at least once per 6 min. A variance estimate (SE) for the multiplier was calculated from 1000 bootstrap samples in PASW v.18.0.

The multiplier was used to calculate revised density estimates by including it as a generic multiplier field and using the '/' operator. We excluded encounters with perched birds that had been detected visually (even if they subsequently vocalized), unlike standard distance sampling, which should use all incidents of perched birds however detected. The DISTANCE program cannot currently incorporate stratum-specific multipliers thus making the inclusion of multipliers for site impossible, so multipliers were based on all available data

## RESULTS

DENSITY ESTIMATES BY SITE, SEASON AND HABITAT.—Table 1 shows regional density estimates and encounter rates (birds/km walked) for the entire parrot assemblage recorded along transects. Summing the g(0) corrected densities (see later) of all sixteen parrot species in our study yields total parrot densities ranging from around 24–39 parrots/km² in *terra firme* forest to 56–90/km² in floodplain forest. Sufficient encounters (> 70) were obtained to calculate reasonably reliable density estimates by site, habitat and season for 9 of 17 parrot species encountered on transects (Table 1). The goodness-of-fit statistics from the cosine-weighted version of the Cramer-von Mises test were poor (closer to 0) for species with low encounter rates and better (closer to 1) for species with high encounter rates. For the rarer species this treatment was not realistic but it is still useful to gauge their likely abundance across the region as a whole, especially as these species are likely to include the particularly rare or patchily distributed species. Density estimates for all these species were, or are expected to be, less than one individual/km². In some species,

such as the tiny *Forpus* and *Nannopsittaca* encounter rates were extremely low, with the latter being detected at a rate of one individual per 140 km of walking.

Table 2 shows density estimates by site, habitat, and season for the more frequently recorded species. The interquartile range for density estimates across habitats was 3.3–7.8 individuals/km². Three of the four species with the overall highest densities were all recorded at their highest densities in the floodplain forest of Posada during the dry season (*Brotogeris cyanoptera* 22, 16–28; *Amazona farinosa* 23, 12–42; and *Pyrrhura rupicola* 8.2, 6.5–10.2 birds/km², Table 2). These three species were found at their lowest densities at Refugio in *terra firme* forest in the wet season (*B. cyanoptera* almost absent; *A. farinosa* 3.8, 3.1–4.8; *P. rupicola* 1.8, 0.8–3.6 birds/km²). Conversely, the consistently rare *Pyrilia barrabandi* reached its highest densities in Refugio *terra firme* forest during the wet season, with 2.5, 0.5–11 individuals/km². The species with the third highest overall density, *Pionites leucogaster*, displayed little variation in density between site, habitat, and season (Table 2).

There was no difference in density estimates between wet and dry seasons in *terra firme* at either Posada ($z = 0.30$, $P = 0.77$) or Refugio ($z = 0.94$, $P = 0.34$), but densities were significantly lower during the wet season in floodplain forest at both sites (Posada; $z = 2.1$, $P = 0.04$, Refugio; $z = 2.2$, $P = 0.03$). Similarly, parrot densities were significantly higher in floodplain forest than in *terra firme* at both sites (Posada; $z = 2.4$, $P = 0.02$, Refugio; $z = 2.7$, $P = 0.008$) during the dry season, but there were no significant differences between habitats in the wet season (Posada; $z = 1.7$, $P = 0.09$, Refugio; $z = 1.4$, $P = 0.17$).

The parrot communities of the different sites, habitats, and seasons do not separate out neatly or simply (Fig. 1). There was generally good separation between communities of *terra firme* forests, which were similar to each other, and floodplain forests which were more varied. *Terra firme* forest at both sites had similar
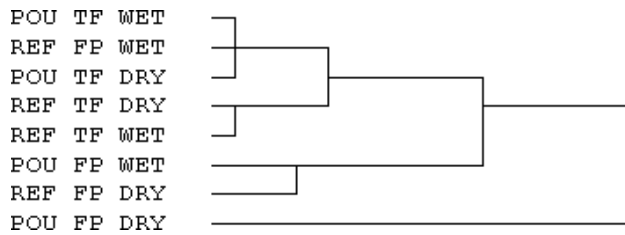
FIGURE 1. Dendrogram from hierarchical cluster analysis (between-groups linkage using squared Euclidean distances) of unstandardized estimates of density for nine parrot species across two sites (POSADA and REFUGIO), *terra firme* (TF) and floodplain (FP) forests in the wet and dry seasons.

parrot communities in both seasons. This was not, however, a pattern shared with floodplain forests which had very different communities across season at both sites. The seasonal differences in floodplain forest were driven by differences in abundance of *Brotogeris cyanoptera* and *Amazona* spp.

CORRECTING g(0) FOR UNDETECTED BIRDS.—A total of 626 observation sessions of vocalizing birds were conducted. A total of 825 perched parrot groups were monitored over periods exceeding 6 min. The logistic model that minimized AIC included significant terms for Lodge ($z = 3.32$, $P < 0.001$), species (*B. cyanoptera* $p = 0.05$; *Ara chloropterus* $P = 0.005$; *Ara macao* $p = 0.04$; *Pionites leucogaster* $P = 0.001$), group size ($\beta = +0.15$, $z = 3.68$, $P < 0.001$), and survey period, with late morning survey periods being associated with infrequent calling ($\beta = -0.71$, $z = 3.13$, $P = 0.002$). Multipliers for g(0) ranged from 0.65 in *Pionus menstruus* to 0.92 for *Pionites leucogaster* (Table S2).

## DISCUSSION

ABUNDANCE OF AMAZONIAN PARROTS.—Amazonian parrot communities may be the richest in the world, but are parrots as a group commoner in Amazonia than in other parts of the world? Comparisons between these overall parrot densities and those from other regions are confounded by difference in methodology, habitat etc., but might still be useful in broad terms. Marsden *et al.* (2000) found overall parrot densities of around $130/km^2$ in a large Atlantic forest reserve holding around 12 parrot species. In a New Guinean parrot community, combined density of the 15 parrot species was $> 250$ individuals/$km^2$ (Marsden & Symes 2008). On less speciose Indonesian islands, parrot density has been reported as variable, but generally lower; Sumba (five species) $84/km^2$; Seram (nine species) $157/km^2$; Buru (eight species) probably $< 100/km^2$ (Marsden 1999); Sulawesi (five species) $64/km^2$ (Walker 2006). The above suggest that parrots at the Amazonian sites are no commoner as a group than in other parts of the world, presumably due to low population densities for individual species.

Our density estimates for species such as *Ara macao*, *Ara chloropterus*, *Pyrrhura rupicola*, *Pyrilia barrabandi,* and *Pionites leucogaster* were similar to those from nearby Manu (Terborgh *et al.* 1990) and standard density estimates for *Ara macao* and *Ara chloropterus*

similar to results from two other western Amazon studies (Lloyd 2004, Haugaasen & Peres 2008). Our density estimates for *Primolius couloni* are within the range predicted by Tobias and Brightsmith (2007) of 0.020.1 birds/$km^2$. Evidence is building that most parrots species in the Amazon are relatively rare, and although some may have ranges of 5+ million $km^2$ (BirdLife International 2009), we emphasize that only four of sixteen species have density estimates in any habitat greater than 5 birds/$km^2$.

VARIABILITY IN PARROT ABUNDANCE ACROSS SITES, HABITATS AND SEASONS.—No study of parrot densities from the western Amazon has considered seasonal population changes although movements do occur at least at a regional level (Renton 2002, Karubian *et al.* 2005). Population densities were stable throughout the year in *terra firme* and dynamic in floodplain forest. Such seasonality has recently been identified in understory birds associated with várzea and floodplain bird species (Beja *et al.* 2010). The floodplain forests of southeast Peru represent the most threatened forest types of the region (Phillips *et al.* 1994). Important nesting resources for parrots are found predominantly in this habitat type (Brightsmith 2005), and a larger proportion of floodplain is in close proximity to claylicks (Lee *et al.* 2010). Also linked to the seasonal differences in parrot abundance is the presence at certain times of year of important sources of food such as abundantly flowering *Ochroma pyramidale* and *Cecropia* spp. (Cowen 2008). *Mauritia* palm swamps are associated with floodplain forest and account for approximately five percent of the protected area system. A degree of wet season changes in abundance may be due to the phenological patterns in this habitat as the *Mauritia* palm fruits from September to April (Manzi & Coomes 2009). This palm is an important food resource for large macaws and parrots (Brightsmith & Bravo 2006).

Most publications on bird abundance in the Peruvian Amazon have focused on floodplain forests (Robinson & Terborgh 1997, Lloyd 2004), whereas *terra firme* forest is a more extensive forest type, accounting for 80 percent of Peruvian Amazon (Salo *et al.* 1986) that will come under threat as the network of roads grows across the region. Lloyd (2004) encountered no *Ara macao* in the *terra firme* forest type sampled in the general area of this study, although known important foods for this species occur in this habitat type (Trivedi *et al.* 2004, Haugaasen 2008). *Terra firme* represents a considerably larger proportion of the landscape so statistical analysis (sensitive to large variation) may not have been sufficient to show any between habitat movements, meaning we are unable to rule out larger scale movements which may account for changes in abundance. Large-scale movements have been observed in other studies of Neotropical parrot species (Bjork 2004), including *Ara* species (Myers & Vaughan 2004).

The protected area associated with the study sites was first established in 2000. Prior to this, the area was undoubtedly subjected to selective logging and small-scale direct exploitation of animals, most often not only subsistence hunting but also some limited commercial extraction. These activities are known to especially influence larger parrot species (Snyder *et al.* 2000). *Ara* spp.

densities, however, are almost equivalent to those from nearby Manu National Park (Terborgh *et al.* 1990), established in 1973. Posada is the closest of the study sites to centers of human population. Nevertheless, parrot densities were higher at this site compared to those at Refugio. Together, this suggests that these density estimates are not far-off of what would be expected from an area with limited anthropogenic disturbances. Instead Posada was the site located closest to a claylick. Although this claylick is small by standards of the area (< 15 m high, Lee *et al.* 2010) the presence of the claylick may contribute to the seasonal fluctuations in density observed in floodplain forest at this site. We were unable to quantify seasonal changes in abundance, however, for the species that use the claylick most as a proportion of their abundance – the successional species *Aratinga weddellii, Aratinga leucophthalma* and *Amazona ochrocephala* (Lee 2010). Instead, most seasonal changes in abundance was due to the presence of species not strictly associated with successional forest (*B. cyanoptera, Amazona farinosa, Pyrrhura rupicola*), suggesting that seasonal changes in floodplain forest type are instead mediated by phenological patterns in this habitat type (Lee 2010).

Implications for bird surveys in tall rain forests.—This study, as with most Distance sampling studies of fauna in forest environments, faced a level of uncertainty with regards the inputs for the program Distance. That parrots appeared to have different calling rates at the two study sites indicates that multipliers may, ideally, need to be site-specific to reflect local calling rates. Probability of calling increases as a function of group size and we assume mean group size of perched groups encountered along the trails is the same as those as group sizes for which the correction factors were calculated, given that the study and transects were concurrent in time and location and that mean group sizes from tower counts were used for group encounters along transects where group size was unknown. The use of the mean group size by season to account for group size in all likelihood reduces variation in subsequent density outputs. Although the substitution of the mean for unobserved group sizes is suggested (Bibby *et al.* 1998) and can be automatically implemented by the DISTANCE software, counting canopy birds from the forest floor is notoriously difficult and our observations showed that even mean group size for counts recorded as accurate along transects were lower than group counts of perched birds conducted from towers where visibility of the birds was less impeded.

In Amazonian forests, the height and density of the canopy means that the distance sampling assumption that certain detection on the transect line (g(0) = 1) cannot be considered valid. Using a multiplier based on detection cue increased density estimates by 6–40 percent in individual species. If g(0) < 1, which we suggest it is, and if absolute parrot densities are required (*e.g.,* for assessments of harvest, IUCN Red List assessments) then fieldworkers must build multipliers into their density calculations. Multipliers that account for the proportion of a population available for counting have been used previously, but can reduce precision (Hounsome *et al.* 2005). Multipliers as calculated in this study are likely to differ across species and also across sites, but

we cautiously suggest the inclusion of a correction based on that of a similar species. The average of 22 percent could also improve density estimates for transects conducted at 1 km/h. As the correction factors are pace dependent transects conducted at a faster pace will potentially miss more birds and need a higher correction factor.

Despite thousands of kilometers of distance sampling line transects, accumulated data were inadequate for quantifying abundance for the three species of parrotlet that occur in the region. It is unlikely that point transects would be an adequate alternative for focusing on these species, since variable circular plots used in Atlantic rain forest also failed to quantify density for the parrotlet species there (Marsden *et al.* 2000). Although distance sampling has been used to calculate densities for Green-rumped Parrotlet *Forpus passerinus* (Casagrande & Beissinger 1997), this species was common and occurs in open habitats. Alternate sampling techniques (*e.g.,* spot mapping, look-down surveys or roost counts) may be better for monitoring parrotlet populations in rain forest environments. Similarly, the *Mauritia* palm swamp specialists *Ara ararauna* and *O. manilata* would be best surveyed using roost counts in their preferred habitats.

Determining cue-rates is relatively straightforward compared to double observer and mark-recapture distance sampling techniques; can be achieved by single observers; and are relatively easy to implement as multipliers in either conventional distance sampling or multiple covariate distance sampling analysis. If there are concerns regarding measuring or detecting objects at increased distances from the transect line, then the detection range could be reduced *e.g.,* to 50 m. Doing so would also effectively reduce by 50 percent the amount of time that birds are available for counting, reducing the multipliers as calculated here. Researchers should determine the tradeoff between accurate distance measurements and vocalization rates for their own target species and habitat. Although an extensive period was dedicated to collecting information on cue-rate in this study, the results suggest that since cue-rate was not impacted by season, a relatively short and focused study should allow researchers to obtain correction factors fairly quickly for common species. Conducting multiple covariate distance sampling may allow further investigation of possible interactions between species and site. The precision of variance estimates associated with rarer species may be improved by including species as a covariate in an analysis of this type. Its application is by no means restricted to parrots, and the cue-counting corrections used here in would be useful in surveys of pigeons, toucans, and a host of other bird species.

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