

EFFECT OF SAMPLE SIZE, PLOT SIZE, AND COUNTING TIME ON ESTIMATES OF AVIAN DIVERSITY AND ABUNDANCE IN A CHILEAN RAINFOREST

JAIME E. JIMÉNEZ¹

*Department of Fisheries and Wildlife, and Berryman Institute
Utah State University, Logan, Utah 84322 USA*

Abstract.—The bird assemblage of a southern temperate rainforest on Chiloé Island, southern Chile, was studied during the breeding season of 1993–1994. The modified variable-circular plot method was used to examine the effects on the estimated overall density and species richness of birds when the size of the plot, duration at the plot, and number of plots were varied, one variable at a time. A total of 459 individuals of 24 species was recorded on 18 plots sampled for a maximum of 10 min with unlimited distance. When increasing either the plot size, sampling length, or number of plots, the number of species detected increased at a decreasing rate, but without reaching an asymptote. The estimated density decreased with increasing plot size, increased with sampling length, and did not change with increasing plot number. However, the precision substantially improved. Plots of 40-m radius counted for 10 min detected 78% of the species found in larger plots and rendered an overall bird density of 34 individuals/ha, almost twice as many as the only comparable study found. On average, more than 75% of all species detected were within 40 m of the observers, using a 4-min sampling period at five plots. The migrant omnivorous flycatcher *Elaenia albiceps* was the most abundant species (22% of total counts), followed by the hummingbird *Sephanoides galeritus*, the tapaculo *Scelorchilus rubecola*, the treecreeper *Aphrastura spinicauda*, and the parakeet *Enicognathus ferrugineus*. These species, which were the most common in other studies conducted in similar temperate South American forests, showed species-specific responses to changes in the sampling variables.

EFFECTO DEL TAMAÑO MUESTRAL, TAMAÑO DE LA PARCELA Y TIEMPO DE CONTEO EN LA ESTIMACIÓN DE LA DIVERSIDAD Y ABUNDANCIA DE AVES EN UN BOSQUE LLUVIOSO CHILENO

Sinopsis.—Durante la estación reproductiva de 1993–1994 se estudió el ensamble de aves de un bosque lluvioso temperado prístino en la Isla de Chiloé, en el sur de Chile. Se usó el método de estaciones de radio variable modificado para examinar el efecto de la variación del tamaño de la parcela, la duración en la estación y el número de estaciones sobre la densidad total y la riqueza de especies de aves estimadas. En total se registraron 459 individuos de 24 especies en las 18 estaciones, las que fueron muestreadas durante 10 min con distancia ilimitada. Al aumentar tanto el tamaño de la parcela, como la duración en la estación o el número de estaciones, el número de especies detectadas aumentaba a una tasa decreciente, pero sin alcanzar una asíntota. La densidad estimada decrecía al aumentar el tamaño de la parcela, aumentaba con la duración en la estación, pero no variaba al aumentar el número de estaciones. Sin embargo, la precisión aumentaba sustancialmente. Parcelas con un radio de 40 m, muestreadas durante 10 min, detectaban el 78% de las especies encontradas en parcelas más grandes y produjeron una densidad total estimada de 34 individuos/ha, casi el doble que en el único estudio comparable. En promedio, más del 75% de todas las especies detectadas se encontraban a menos de 40 m de los observadores, dentro de los primeros 4 min del conteo y en sólo cinco parcelas. El cazamoscas migrante omnívoro *Elaenia albiceps* fue la especie más abundante (22% de todos los individuos), seguido por el colibrí *Sephanoides galeritus*, el tapaculo *Scelorchilus rubecula*, el trepador *Aphrastura spinicauda* y la cotorra *Enicognathus ferrugineus*. Estas especies, que también fueron las más abundantes en otros estudios conducidos en bosques neotropicales similares, mostraron respuestas especie-específicas a las variables de muestreo.

¹ *Current address: Laboratorio de Ecología, Universidad de Los Lagos, Casilla 933, Osorno, Chile*

Questions related to abundance and distribution of organisms are central to ecological research (Krebs 1994). Therefore, understanding how many individuals and what species are present at a given site is crucial when studying biological systems. Bird studies have provided much of our current knowledge in population and community ecology (Wiens 1989). However, sampling techniques to assess bird abundance and species richness have not been fully standardized and need continual refinement (Ralph and Scott 1981, Ralph et al. 1995).

The most common techniques in current use for estimating bird densities and species compositions are (Ralph and Scott 1981, Verner 1985, Bibby et al. 1993): (1) the mapping of territories, based on determining the territorial boundaries of pairs during the breeding season; (2) sampling with transects, where an observer moves at constant speed and records the birds detected and their perpendicular distances to the transect; and (3) sampling with point counts, of more recent development (Blondel et al. 1970, Järvinen 1978, Reynolds et al. 1980, Buckland et al. 1993). During point counts, the observer records the birds detected from spatially replicated stations or plots (Ramsey and Scott 1979, Blondel et al. 1981). On each plot, for a given period of time, all birds seen or heard from a single point are recorded.

Point counts provide several advantages when compared with the first two techniques, including being the most cost-efficient for censusing birds in structurally complex habitats such as forests (Reynolds et al. 1980). Edwards et al. (1981) offer an empirical comparison of these three methods.

Many variables affect the estimates derived from point counts, especially those related to detectability of individual species (Järvinen 1978, Ramsey and Scott 1979, Reynolds et al. 1980). These variables include: season of the year, time of day, behavior (e.g., mobility, aggregation, song) and conspicuousness (e.g., size, color) of the species, climatic conditions, habitat type, observer skill, detection distance, duration of sampling, and number of replicates (Ramsey and Scott 1979, Ralph and Scott 1981, Fuller and Langslow 1984, Verner 1985, Bibby et al. 1993, Ralph et al. 1995).

In this study I examined the effect of: (1) the sampling radius or area covered by each station; (2) the duration of sampling at each station; and (3) the number of stations in estimating (a) the number of species and (b) the densities of birds present in a forest environment. As a model system, I studied a little-known bird assemblage in a temperate rainforest on Chiloé Island, in southern Chile.

To my knowledge, no study has attempted to use variable-circular plots to examine the effects of these variables when quantifying species richness or abundances of forest birds in the Neotropics (see reviews by Lazo and Silva 1993 and Jaksić 1997 for Chilean birds). The importance of understanding the performance of this technique should be emphasized in light of the uniqueness of this south-temperate bird assemblage (Vuilleumier 1985, Rozzi et al. 1996a) and its habitat, the southern temperate

rainforests (Armesto et al. 1996). Both, these birds and these forests are virtually unknown and are facing increasing human impacts in different forms (Fuentes 1994, Willson et al. 1994, Lara et al. 1996).

STUDY SITE

I sampled birds in a broad-leaved evergreen rainforest at Piruquina (42°23'S, 73°53'W), on Chiloé Island in southern Chile. The study area is located on the eastern slope of Cordillera del Piuché at 200–500 m elevation. Climate is wet-temperate with annual precipitation higher than 3500 mm and concentrated during the winter (Smith-Ramírez 1993, Smith-Ramírez and Armesto 1994). Temperatures average 2–5 C during winters and 5–20 C during summers. The vegetation is a multi-stratified, old-growth, Valdivian-type forest with abundant lianas, mosses, and ferns (Donoso 1994) that resembles a tropical forest in structure (Vuilleumier 1985). The forest is pristine with a few natural and man-made gaps. The canopy is dominated by fruit-bearing trees of the family Myrtaceae, which reach 15–25 m in height with frequent emergent *Eucryphia cordifolia*, *Laureliopsis philipiana*, and *Weinmannia trichosperma* trees (see Smith-Ramírez 1993 and Smith-Ramírez and Armesto 1994 for more details). Bird nomenclature follows Araya and Millie (1979).

METHODS

Bird sampling.—During the first week of January 1994 (mid-Austral summer), I sampled birds using the modified variable-circular plot technique (Reynolds et al. 1980) on 18 plots. Plots were separated by 400 m along a transect. Plots were at least 400 m from any forest edge. Counts were done between 0620 and 0930 h on calm, cloudless days (i.e., wind speed <10 km/h; Ralph et al. 1995) simultaneously on each plot by two observers familiar with the forest and the birds (Verner and Milne 1989). Using two observers improves the number of birds detected (Preston 1979, Scott and Ramsey 1981a). At each plot, we began recording birds as soon as we arrived at the spot (Ralph et al. 1995). The species and the number of individuals detected through direct observation or by their songs were tallied in 2-min intervals for a total of 10 min per plot. Each plot was sampled once. We estimated the horizontal distances to the birds when first detected (i.e., the radius) in 10-m intervals. Our ability to estimate distances, as gauged with an optical range finder, was ± 8 –12% at about 60 m and improved at shorter distances (see also Reynolds et al. 1980, Scott et al. 1981).

Data analyses.—I compared the cumulative species richness and total densities for the different radii of the plots, the duration of counts on plots, and the number of sampled plots. I kept two of the three variables constant in each analysis. To maintain the randomness for the number of plots sampled, I generated bootstrap estimators for each sample size (i.e., 1–18) with 500 random iterations (Lanyon 1987), from the 18-plot sample. This method, compared with the one used by Morrison et al. (1981) presents advantages such as the flexibility to construct confidence

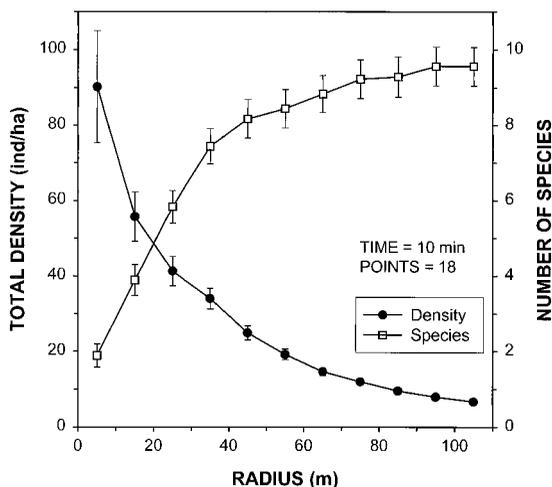


FIGURE 1. Changes in the estimated number of species and density of the entire bird assemblage with radius. Shown are means and 1 standard error.

intervals. Separately, I analyzed the effects of these same three variables on the densities of the five most abundant bird species. I computed mean estimates of all variables and confidence intervals. I equated the radius with Ramsey and Scott's (1979:160) basal radius and computed the density estimator accordingly.

Statistical comparisons were performed using SAS system release 6.12 (SAS Institute Inc. 1996). Given the dependent nature of the cumulative data, I used paired *t*-tests (SAS Institute Inc. 1988: 946; Ott 1988: 194) for differences between means (i.e., densities and species richness) as time spent on the plot progressed or as the radius of the plot increased. Significance levels were corrected by the Bonferroni method (Sokal and Rohlf 1995: 240) to control for the experimentwise type I error rate due to the multiple pairwise comparisons (Ott 1988: 440).

RESULTS

In total (i.e., unlimited radius, 10 min per plot, and 18 plots), we detected the presence of 24 species and 459 individual birds in the forest at Piruquina (Appendix). The number of species and individual birds per plot ranged from 7 to 14 ($n = 18$; mean = 9.67 ± 2.22 SD) and from 16 to 43 ($n = 18$; mean = 25.50 ± 7.50 SD), respectively.

Size of the plot.—As the size of the plot increased from a radius of 10 m to over 100 m (a plot of 40 m radius has a surface area of about 0.5 ha), the number of species detected increased asymptotically from an average of 1.89 to 9.56 species (Fig. 1). The rate of species detection resembles a diminishing return curve. The variance of the estimate remained relatively constant and independent of the plot size (Fig. 1). The number of species detected did not increase significantly for plots differ-

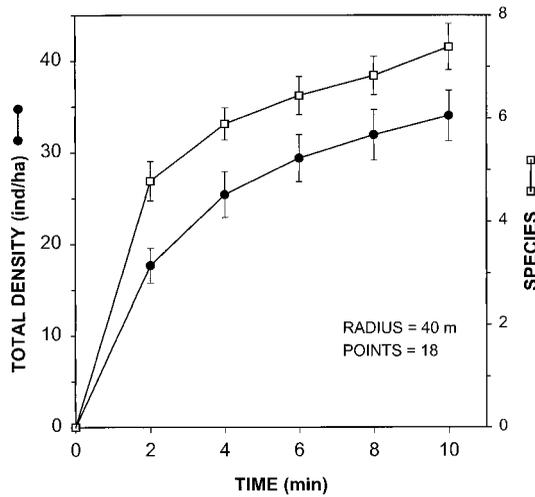


FIGURE 2. Changes in the estimated number of species and density of the entire bird assemblage with time at the point. Birds were counted on 18 points with radius held constant (radius = 40 m). Plotted values are means and 1 standard error.

ing in 10 m increments of radii beyond a radius of 50 m (all ten paired t -tests, $t_{17} \leq 1.76$, $P \geq 0.87$). At this point, 77.82% of all the species recorded could be detected.

In contrast, the density estimate for all species combined showed the opposite pattern. The density of all birds fell sharply from a high of 90.19 individuals/ha with the smallest plot size and stabilized slowly as the plot size increased (Fig. 1). It reached a low of 6.71 individuals/ha at a radius of 110 m, but the slope did not stabilize (e.g., the means differed between adjacent distances, all ten paired t -tests, $t_{17} > 3.49$, $P < 0.03$). The variance estimator of the density also decreased inversely with the plot radius, from a SE of 14.84 to 0.46.

Duration of the counts.—The number of bird species detected increased as the observation time at the plots increased (note that plot radius was held constant at 40 m), from a low of 4.78 species within 2 min to 7.39 species within 10 min (Fig. 2). However, the rate of detection of new species did not level off during the 10-min count period (all four paired t -tests, $t_{17} \geq 3.01$, $P \leq 0.03$). The variability remained relatively unchanged as observation time increased. Similarly, the density estimates followed the same trend with time at the plot, increasing from 17.68 to 34.03 individuals/ha, between 2 and 10 min, respectively. The variability, however, increased slightly as observation time progressed. Again, the density estimate did not level off within the 10 min observation period (all four paired t -tests, $t_{17} \geq 4.24$, $P \leq 0.002$).

Number of plots.—The bootstrap analysis indicated that species richness increased asymptotically as the number of plots surveyed increased (Fig. 3). The variance decreased slightly with sample size. However, after count-

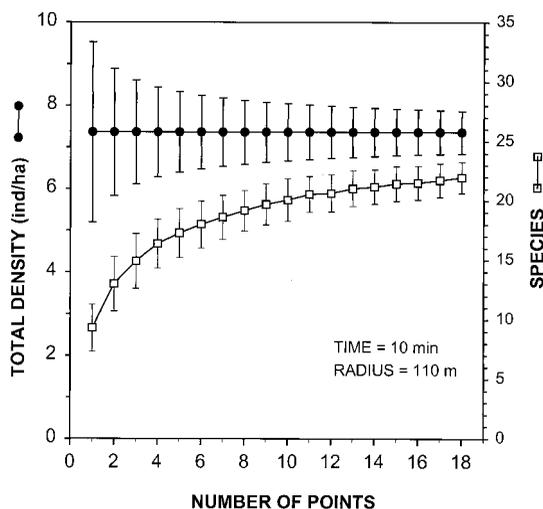


FIGURE 3. Number of species and density of birds estimated for different number of points in Piruquina, southern Chile. Counts were conducted for 10 min per point with radius held constant at 110 m. Each mean and standard deviation shown were generated by bootstrapping 500 times.

ing on 18 plots, the curve did not flatten, reaching only 91.54% of the total (i.e., 24) number of species detected in the counts (Fig. 3). The simulation indicated that when using 50 plots 99.9% of the species recorded could be detected. Recall that bootstrapping draws samples with replacement.

The estimation of the mean bird density was not affected by the number of plots surveyed and was close to the 7.36 individuals/ha found with the largest plot size used (compare Figs. 3 and 1). The precision of the estimate increased considerably as the number of plots increased, especially at the smaller ranges (Fig. 3).

Effects on the most common species.—*Elaenia albiceps* (99 individuals), *Scelorchilus rubecola* (64 individuals), *Sephanoides galeritus* (60 individuals), *Aphrastura spinicauda* (46 individuals), and *Enicognathus ferrugineus* (41 individuals), in that decreasing order, were the five most common species detected (see Appendix). These five species (20.8% of all species) comprised 67.5% of the forest birds by number.

Density estimates of *Elaenia*, *Sephanoides*, and *Scelorchilus*, which were detected in all 18 points (Appendix), followed the general pattern described for the entire assemblage both when increasing the size of the plot and when increasing counting time (Figs. 4 and 5). Compared to the other species, fewer *Aphrastura* and *Enicognathus* were detected at close distance from the observers (i.e., in small plots) than at intermediate distances (Fig. 4). In addition, density estimates for *Enicognathus*

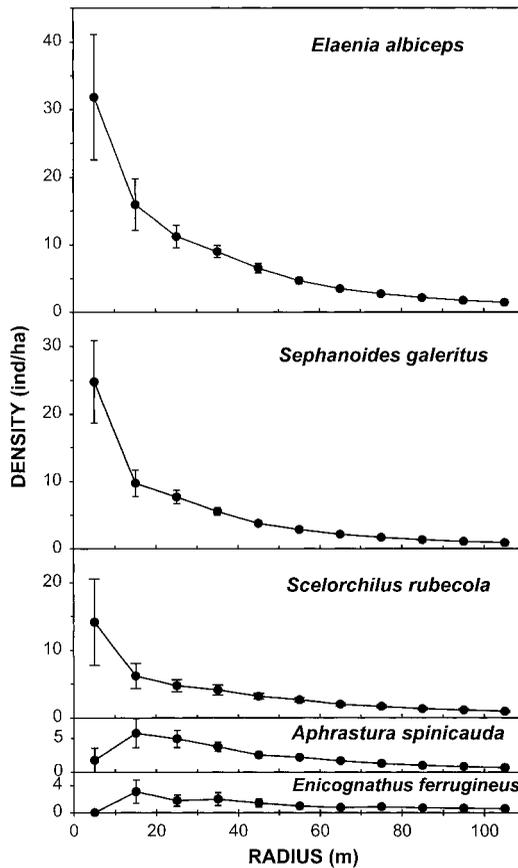


FIGURE 4. Density estimates for different radii for the 5 most common forest birds. Counts were conducted at 18 points for 10 min each, during the Austral summer in a primary forest at Piruquina, Chiloé, southern Chile.

differed from the rest by increasing at a higher rate at the intermediate time intervals than during the first time interval (Fig. 5).

The same data set was used for computing density estimates when counting for 10 min on plots of 40-m radius and 110-m radius. The relative abundances for *Elaenia*, *Aphrastura*, and *Enicognathus* agreed for the two-sized plots used. However, the numerical importance for *Sephanoides* and *Scelorchilus* reversed when computed from the smaller compared to the larger plot size (Appendix).

DISCUSSION

Coincidentally, the methods used here closely followed the guidelines proposed by Ralph et al. (1995). However, based on the lack of previous studies in this habitat, *a priori* decisions, such as selecting the distance

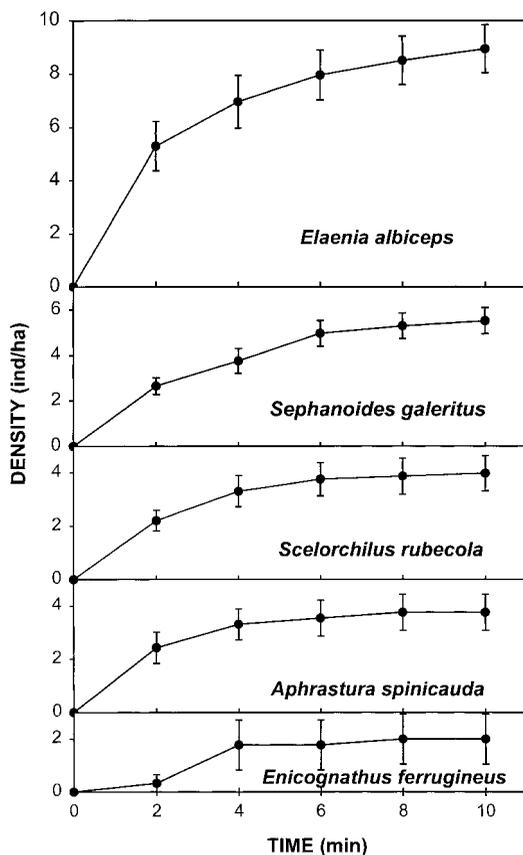


FIGURE 5. Density estimates for different observation times for the five most common forest bird species. Counts were conducted at 18 points held constant at 40 m radii in a rain-forest at Piruquina, Chiloé, southern Chile.

between stations to be 400 m, limited the number of stations that could be sampled (the minimum suggested is 250 m) and the time at the station (see below), turned out to be overly conservative. The data collected indicate that the distance between stations could be reduced to at least 300 m, without compromising the statistical independence of counts on neighboring stations (Pendleton 1995).

The three variables analyzed affected the abundance estimates differently, whereas species richness was similarly affected. An increase in all variables produced increases in the number of species detected without greatly affecting variability (Figs. 1–3).

How large should a radius be?—An increase in the radius results in a non-linear increase in the surface area sampled. Consequently, the number of detected birds should increase proportionally to the square of the

radius, but their densities should remain constant. However, the probability of detection is maximum at the center of the plot (Buckland et al. 1993) and decreases in a non-linear way with distance from the observer in a species- and likely, context-specific way (Verner 1985). Hence, it follows that the density, if not corrected for detectability, will be underestimated (Järvinen 1978, Reynolds et al. 1980, DeSante 1981). An additional complication is that given that the area sampled (in fact, a three-dimensional volume) increases geometrically with the radius, the estimate is very sensitive to distance estimation (Järvinen 1978, Reynolds et al. 1980, DeSante 1981, Verner 1985). In addition, the ability of a person to distinguish two different singing birds—a common event when counting forest birds (Reynolds et al. 1980, Scott et al. 1981, Erazo 1984)—drops as distance increases, which additionally contributes to underestimate densities at larger plot sizes (Wolf et al. 1996). The interplay of these variables likely accounts for the patterns observed (Fig. 1). Changes in detectability may potentially explain the negative exponential decline in the density estimates and the relatively flat “species-area” curve found. The effect of area might produce more counts and therefore might have resulted in less variability in the density estimator. A more obvious factor appears to be the increase in the number of species detected with plot size (see also Savard and Hooper 1995).

For the temperate rainforest bird assemblage studied, it appears that both on graphical and statistical grounds, and compromising species-specific differences, the plot size to be used should have a radius of about 40 m. Plots of that size would detect 78% of the species found in larger plots and would render an overall density of about 34 individuals/ha. Larger plots allow the detection of more species, but compromise density estimates. I emphasize the high sensitivity of the density estimator to the size of the plot (i.e., the steep slope of the curve, Fig. 1), especially at short radii. In this sense, plot size chosen is more critical for estimating density than for studying species richness. Given that the true density and richness values are unknown and that no independent estimates exist, the accuracy of these estimates can not be assessed.

How long to count on a plot?—When the sampling time was increased, estimates of densities and of species richness increased in a similar pattern, but neither curve flattened out within the 10-min observation period used here. Several studies have found similar time-accumulation curves (Fuller and Langslow 1984, Verner 1988, Buskirk and McDonald 1995, Dawson et al. 1995, Petit et al. 1995, Savard and Hooper 1995). Further, Fuller and Langslow (1984) and Petit et al. (1995) did not observe curve flattening off even after 20 min of sampling per plot, unlike findings reported by Reynolds et al. (1980) when counting for 30 min (see also Scott and Ramsey 1981b). I believe it is unlikely that birds became visible only after a few minutes of sampling. As has been pointed out previously the shape of the curves can be an artifact of birds moving into the detection zone and double-counting highly mobile individuals (Reynolds et al. 1980, Scott and Ramsey 1981b, Granholm 1983, Fuller

and Langslow 1984, Wolf et al. 1995). The latter would affect density estimates only. Without an independent estimate it is not possible to rule out or to know the magnitude of such bias. One way to minimize the biases of double-counting and birds moving into the plot is by shortening the time sampling at a plot (Granholm 1983). However, this will underestimate species with larger home ranges, that are less mobile, are infrequent callers, or are less conspicuous (Scott and Ramsey 1981b, Granholm 1983, Fuller and Langslow 1984, Buskirk and McDonald 1995, Dawson et al. 1995, Petit et al. 1995).

With the information available, given that none of the curves flatten out, no statistical or graphical decision can be made. Other criteria to select the giving-up-time at a plot should be used. For instance, if research resources are limited, one goal would be to maximize the time counting at the plots (i.e., counting more birds, but keeping the same plot numbers; but see Barker and Sauer 1995 who found that for certain hypothesis, the maximum power of the test does not coincide with maximum counts), which would only be available after discounting for the time "wasted" to move between stations. Previous studies show that when the amount of time spent moving between stations is considerable (e.g., because stations are too far apart or in a difficult terrain to move through) longer sampling time at the expense of more stations may be more efficient (Fuller and Langslow 1984, Verner 1988, Buskirk and McDonald 1995, Petit et al. 1995, Savard and Hooper 1995). This was true in this study, because the understory was dense, the ground was uneven, and stations were far apart from each other. Thus, relatively long counting times, but not exceeding 10 min (Verner 1988), appear appropriate for this ecosystem. To make results comparable with those in other forests and to comply with other working groups (Verner 1985; Ralph et al. 1993, 1995), I would also recommend an analysis of the subsets of the data for shorter counting times, such as for 4–6 min (Buskirk and McDonald 1995). However, the final decision will depend on the goal of the study (Barker and Sauer 1995).

How many plots?—When deciding how many plots to count, important variables include the area sampled (the sum of the areas of each plot count), amount of spatial variability incorporated into the sampling design, and constraints such as the distance between plots or the time required to get to adjacent plots (see above), roughness of the terrain, and resources available. Regardless of the decision rule, I found that an increase in the number of plots counted improves the precision of the estimated density, but does not affect its mean (Fig. 3). As the sample size is increased (i.e., the number of plots), the variance of the estimator decreases, a well-known relationship in sampling theory (Reynolds et al. 1980, Verner 1985, Barker and Sauer 1995). The estimate of species richness increases in a similar fashion and for similar reasons as the species-area curve (Morrison et al. 1981), and as the number of plots increases species richness estimated will converge toward the actual richness (Blondel et al. 1981, Barker and Sauer 1995). Morrison et al. (1981) found

results similar to mine. For six different habitats they detected more species by incrementing the number of plots from two to eight, and their estimated densities stabilized by about eight plots. The only available data on species vs. number of stations for southern temperate forests are reported by Rozzi et al. (1996a). Their findings for several islands agree with this study, although they found fewer species for the same number of plots on Chiloé Island.

Given that the sample size did not affect the mean density, but did affect the precision of this measure, and that precision improves quickly with sample size, no substantial information is gained when sampling more than 10 points. However, considering the estimation of species richness, only 83.5% of the 24 bird species will be detected when using only 10 points. Rare species (e.g., *Campephilus*, *Glaucidium*, *Strix*, and *Pygarrichas*; Appendix) will likely be missed (Petit et al. 1995). I agree with Edwards et al. (1981) and Savard and Hooper (1995) that plot size appeared relatively more critical than time spent sampling, especially for rare species.

Note that the analysis of point number is based on re-sampling from a relatively small subset of samples and the variability of the data is therefore limited to that sample (Verner and Ritter 1986, Lanyon 1987). For the same reason, the estimates might likely be inflated.

Species-specific responses to density estimates.—In addition to differences in abundances (Appendix), there is considerable variation in behavioral and morphological traits among the bird species counted at Piruquina. All these “bird variables” might bias the estimates, and it is therefore useful to examine some of these traits (Scott and Ramsey 1981b, Verner 1985). The five most abundant species consist of a solitary fruit-eating flycatcher (*Elaenia albiceps*), a small, territorial, and fast-moving hummingbird (*Sephanoides galeritus*), a territorial ground-dwelling tapaculo (*Scelorchilus rubecola*), a social treecreeper (*Aphrastura spinicauda*), and a social parrot (*Enicognathus ferrugineus*). When the area sampled in each plot changed, the three most abundant species showed similar responses in density estimates to those described for the entire bird assemblage (compare Figs. 4 vs. 1, and 5 vs. 2). Nonetheless, their detection functions with distance were different (Reynolds et al. 1980). For instance, the curve for *Sephanoides* is steeper than that for *Scelorchilus* (Fig. 4). Thus, a larger fraction of the former will be detected at closer ranges (probably by its loud high-pitch alarm calls) than the latter (mainly through its loud low-pitch ringing calls). At farther distances the small hummingbird is hardly detected, but the loud-calling tapaculo is still heard. Further, the fact that the curve for *Sephanoides* is less steep over time than that of the other species (Fig. 5), appears to be associated with the species’ relative highly mobility and large home range. Fuller and Langslow (1984) also found species-specific differences in the time-detection curve and caution that counts of different durations will result in different species’ relative abundances. This bias due to different detectabilities can also occur when computing abundances for different radii as seen in *Sephanoides* and *Sce-*

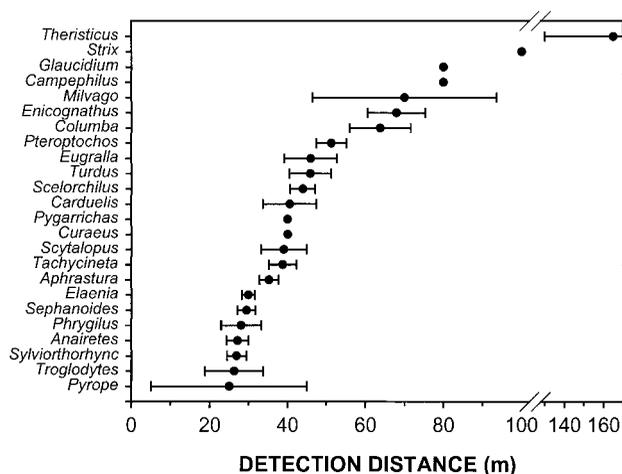


FIGURE 6. Mean (and 1 standard error) detection distances for primary rainforest birds at Piruquina, Chiloé, southern Chile. For sample sizes, complete names and taxonomy of the species see Appendix.

lorchilus. These two species' abundance ranks changed from second and third with a radius of 40 m to third and second with a radius of 110 m, respectively (Appendix).

In contrast to the three most abundant species at Piruquina, *Aphrastura* and *Enicognathus* exhibited lower densities closer to the observers than at medium distances, generating a “donut pattern” (Fig. 4; Verner 1985), probably as a result of moving away from the observer before being detected (Reynolds et al. 1980, Granholm 1983). In addition, *Enicognathus* appeared to first move quietly away and then vocalize, as reflected by its low detection rate during the first 2 min (Fig. 5; see also Scott and Ramsey 1981b). With these data, however, one cannot determine which species were attracted to the observer, in which case an overestimation of their abundances would occur on small plots (Scott and Ramsey 1981b, Granholm 1983) or whether some species attract the observer's attention and thus could be overestimated relative to the others (Reynolds et al. 1980, Fuller and Langslow 1984, Verner 1985). Conversely, due to the observer's “saturation” to distinguish a large number of individuals, abundant species may be underestimated (Järvinen 1978, Scott and Ramsey 1981a, Petit et al. 1995). Another source of underestimation not accounted for here is the fact that most records are aural detections (Reynolds et al. 1980, Scott et al. 1981, Granholm 1983, Erazo 1984) by the songs that are performed mainly by singing males (Mayfield 1981, see also Emlen 1971). Thus, females are less likely to be detected, especially when on nests.

Using body size as an index of conspicuousness (Appendix), I found that larger birds were detected at farther distances than smaller birds (r_s

TABLE 1. Bird studies conducted in Neotropical temperate rainforests. In those studies where more than one forest type was surveyed, I selected the one closest to this study in terms of floristics, location, and timing. This study's abundances were computed based on a 40 m radius plot. Studies are latitudinally arranged.

Locality	Forest type (dominant)	Technique used	Effort	Total spp.	Most abundant species ^a	Authority
PN Ñielol Temuco	<i>Nothofagus Perseetum boldetosum</i> Disturbed	Point counts, but vague ^b	Not reported 3–5 ha 1 time?	17	Eal>Asp>Ccu>Sba>Apa=Tae	Cody 1970
Lago Frías Bariloche	<i>N. dombeyi</i> -conifers Status ?	Strip transect	1 plot: 7.5 ha 2 visits Total 15 h	19 ^d	Asp>Efe>Sga=Sru>Sma=Sba	Vuilleumier 1972
Lago Escondido Bariloche	<i>N. dombeyi-Chusquea</i> Status ?	Point counts	20 stations 10 min/each 1 time	14 ^f	Eal>Sga>Asp>Tae>Sru	Ralph 1985
San Martín Valdivia	<i>Aextoxicon</i> Secondary	Point counts	5 stations 8 min/each 1 time	18 ^e	Sga>Efe>Eal>Asp=Tfa=Pta	Erazo 1984
Gol-Gol Osorno	<i>Myrceugenia-Temu</i> Flooded	Point counts	15 stations 5 min/each 1 time	16 ^{ef}	Tle>Eal>Tae>Tfa>Cpa	García 1982
NE Chiloé Island	<i>N. dombeyi</i> -Myrtaceae Fragments	Point counts	# variable 8 min/each 3–7 times	8–22	Eal>Asp>Sga>Sru>Tfa	Willson et al. 1994
Chiloé Island Piruquina	Myrtaceae- <i>Drimys</i> Primary	Point counts	18 stations 10 min/each	24	Eal>Sga>Sru>Asp>Efe	This study
Chiloé Island Piruquina	Myrtaceae- <i>Drimys</i> Fragments	Strip transect	1 plot: 2.4 ha 3 times/day 10 days	15 ^{ef}	Eal>Tfa>Ele>Sga>Apa=Tae	Sabag 1993

TABLE 1. Continued.

Locality	Forest type (dominant)	Technique used	Effort	Total spp.	Most abundant species ^a	Authority
S. Chiloé Island	<i>Aextoxicon-Drimys</i> -Myrtaceae Primary	Point counts	86 stations 10 min/each	17 ^f	Sga>Asp>Eal>Tfa>Ppa	Rozzi et al. 1996b

^a = Apa: *Anairetes parulus*; Asp: *Aphrastura spinicauda*; Ccu: *Curaeus curaeus*; Cpa: *Cinclodes patagonicus*; Eal: *Elaenia albiceps*; Efe: *Enicognathus ferrugineus*; Ele: *E. leporhynchus*; Ppa: *Phrygilus patagonicus*; Pta: *Pteroptochos tarnii*; Sba: *Spinus barbatus*; Sga: *Sephanoides galeritus*; Sma: *Scytalopus magellanicus*; Sru: *Scelorchilus rubecola*; Tae: *Troglodytes aedon*; Tfa: *Turdus falklandii*.

^b = Identified as *Nothofagus obliqua*-*N. dombeyi* tall forest by Cody (1970:456) and corrected by Erazo (1984:64) as low and disturbed (Jiménez, pers. obs.).

^c = as referred by Cody (1970:455), MacArthur and MacArthur (1961:594) used plots of 5 acres and MacArthur (1964:391) used point counts of "at least an acre."

^d = I assume that the *Geranoaetus* reported, which is not a rainforest raptor, was in fact a juvenile of *Buteo ventralis*.

^e = Only the January count(s) is (are) reported.

^f = I excluded: *Chloephaga* and *Cistothorus* for being of wetlands and open habitats; *Zonotrichia*, *Leptasthenura*, *Sicalis*, *Phrygilus fruticeti*, and *Sturnella* for being of edge, shrubby or open habitats (Jiménez, pers. obs.).

= 0.784, $df = 23$, $P < 0.001$, Fig. 6), but not more quickly ($r_s = 0.004$, $df = 23$, $P > 0.986$). Reynolds et al. (1980) also cautions about the sensitivity to detect rare species, which are generally large-sized, when using large plots. Thus, a positive bias could be introduced for large-bodied species. However, sampling of large but rare or secretive species (e.g., *Strix*, *Glaucidium*, *Campephilus*) with point counts seemed to be inappropriate (Bibby et al. 1993).

In summary, for this temperate rainforest bird assemblage, on average, more than 75% of the species (from all those detected) were detected at distances less than 40 m from the observer, during the first 4 min of sampling on the plots (see also Fuller and Langslow 1984), at five plots (see also Rozzi et al. 1996a). The use of these same criteria also appeared to be justified—but with caution and limitations—for estimating total bird densities. These conclusions should be taken only as guidelines and the specific decisions will ultimately depend on the questions asked. Having this in mind, I hope that the behavior of the data and the patterns shown in this study will help planning future research in Neotropical temperate rainforests (Ralph et al. 1995).

Comparisons with other southern temperate rainforest studies.—A handful of studies have determined the species richness and relative abundances of birds in Neotropical temperate forests. Their findings can be compared cautiously with this study because they either differ in the techniques used, sampling efforts, months sampled, forest type, disturbance regimes, had no replication, or combinations of them (Table 1). All these variables introduce biases and make it difficult to compare studies. For instance, floristics and resources available to birds vary widely through time and space in Neotropical temperate forests (Smith-Ramírez 1993, Sabag 1993, Donoso 1994, Smith-Ramírez and Armesto 1994, Armesto et al. 1996). In addition, disturbance level shapes bird community composition (Willson et al. 1994). Timing of counts is also critical, because the forest bird composition changes seasonally, mainly as a result of migrant dynamics. *Elaenia*, the most abundant species during the breeding season, and *Tachycineta*, are migrants present in these forests only between September and April, and *Sephanoides*, *Turdus*, and *Carduelis* are partial migrants (García 1982; Erazo 1984; Vuilleumier 1985; Sabag 1993; Smith-Ramírez 1993; Rozzi et al. 1996a, 1996b; Espinosa and Egli 1997).

Notwithstanding the many differences among studies, all those reviewed here presented similar numbers of species and the pool of the most abundant species was generally similar (Table 1). Although both metrics were comparable to this study, I detected more species. This could be because I worked on a pristine primary and mid-elevation forest, and that I also included rare species (Table 1).

Elaenia (a frugivore), *Aphrastura* (an insectivore), and *Sephanoides* (a nectarivore) were among the four most abundant species in five of the nine studies and pairs of them were abundant in 6/9 studies (in all combinations; Table 1). *Elaenia* was the most abundant species in 5/9 of the

studies representing more than 21% of all the birds recorded in each of the five studies.

To my knowledge, only Vuilleumier (1972), Ralph (1985), and Sabag (1993) estimated bird densities. Vuilleumier (1972) and Sabag (1993) used a different technique than in this study and had no replication (Table 1). Ralph's (1985) study at Bariloche appears to be the only one comparable to this study. Although birds at Piruquina were almost twice as abundant as in Bariloche (36.4 vs. 18.9 individuals/ha), the two more abundant species (*Elaenia* and *Sephanoides* in both sites) had similar densities (8.9 vs. 7.0 and 5.5 vs. 4.1 individuals/ha, respectively), despite that the two sites seemed to have had more differences than similarities. For instance, compared to the Piruquina site, the Bariloche site had a more continental climate (e.g., less precipitation, more snow and marked seasonality), was located on a lake peninsula on the eastern slope of the Andes, and was a *Nothofagus*-dominated forest (i.e., had fewer fruit-bearing species). Further, in this study I did not correct for detection distance nor did I calculate the effective detection distance when computing densities (Järvinen 1978, Ramsey and Scott 1979, Reynolds et al. 1980, Morrison et al. 1981), which results in considerable underestimation of densities.

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APPENDIX. Species of birds recorded at Piruquina, Chiloé, in southern Chile. Nomenclature and body length data follow Araya and Millie (1989). Frequency of occurrence refers to the species' presence in the 18 plots. Percent by number represents the species' contribution to the total number of individuals counted (459). Densities were computed for the 18 plots, during 10 min per plot, on both, 40 and 110-m-radius plots. Statistics for densities are mean and 1 standard error in the next line.

Scientific name	Common name	Body length (cm)	Frequency of occurrence		Density ind/ha	
			(%)	% by number	Radius 40 m	Radius 110 m
THRESKIORNITHIDAE						
<i>Theristicus caudatus</i>	Buff-necked Ibis	74	11.1	1.09	0.553 0.449	0.073 0.059
FALCONIDAE						
<i>Milvago chimango</i>	Chimango	40	22.2	1.53	0.442 0.257	0.102 0.048
COLUMBIDAE						
<i>Columba araucana</i>	Chilean Pigeon	37	33.3	1.74	0.332 0.180	0.132 0.057
PSITTACIDAE						
<i>Enicognathus ferrugineus</i>	Austral Parakeet	34	61.1	8.93	2.984 1.106	0.599 0.159
STRIGIDAE						
<i>Glaucidium nanum</i>	Austral Pygmy-owl	20	5.6	0.22	0.000 0.000	0.015 0.015
<i>Strix rufipes</i>	Rufous-legged Owl	38	5.6	0.22	0.111 0.111	0.015 0.015
TROCHILIDAE						
<i>Sephanoides galeritus</i>	Green-backed Firecrown	11	100.0	13.07	5.526 0.570	0.877 0.067

APPENDIX. Continued.

Scientific name	Common name	Body length (cm)	Frequency of occurrence (%)	% by number	Density ind/ha	
					Radius 40 m	Radius 110 m
PICIDAE						
<i>Campephilus magellanicus</i>	Magellanic Woodpecker	45	5.6	0.22	0.000 0.000	0.015 0.015
FURNARIIDAE						
<i>Sylviorthorhynchus desmursii</i>	Des Mur's Wiretail	24	33.3	1.74	0.884 0.330	0.117 0.044
<i>Aphrastura spinicauda</i>	Thorn-tailed Rayadito	14	77.8	10.02	3.758 0.680	0.672 0.117
<i>Pygarrichas albogularis</i>	White-throated Treerunner	16	5.6	0.22	0.111 0.111	0.015 0.015
RHINOCRYPTIDAE						
<i>Pterotochos tarnii</i>	Black-throated Heut-huet	25	66.7	4.14	0.774 0.235	0.278 0.058
<i>Scelorchilus rubecola</i>	Chucao Tapaculo	18	100.0	13.94	4.421 0.693	0.935 0.093
<i>Eugralla paradoxa</i>	Ochre-flanked Tapaculo	15	22.2	1.09	0.111 0.111	0.073 0.036
<i>Scytalopus magellanicus</i>	Andean Tapaculo	12	55.6	3.27	0.995 0.332	0.219 0.053
TYRANNIDAE						
<i>Pyrope pyrope</i>	Fire-eyed Diucón	21	11.1	0.44	0.111 0.111	0.029 0.020
<i>Elaenia albiceps</i>	White-crested Elaenia	15	100.0	21.57	8.952 0.899	1.447 0.117
<i>Anairetes parulus</i>	Tufted Tit-tyrant	11	22.2	1.53	0.774 0.398	0.102 0.053

APPENDIX. Continued.

Scientific name	Common name	Body length (cm)	Frequency of occurrence		Density ind/ha	
			(%)	% by number	Radius 40 m	Radius 110 m
HIRUNDINIDAE						
<i>Tachycineta leucopyga</i>	Chilean Swallow	13.5	44.4	3.49	1.437 0.598	0.234 0.085
TROGLODYTIDAE						
<i>Troglodytes aedon</i>	House Wren	12	16.7	0.87	0.442 0.257	0.058 0.034
MUSCICAPIDAE						
<i>Turdus falklandii</i>	Austral Thrush	26	66.7	5.23	1.658 0.433	0.351 0.088
EMBERIZIDAE						
<i>Curaeus curaeus</i>	Austral Blackbird	28	5.6	0.65	0.332 0.332	0.044 0.044
FRINGILIDAE						
<i>Phrygilus patagonicus</i>	Patagonian Sierra-finch	15.5	55.6	2.83	1.216 0.398	0.190 0.051
<i>Carduelis barbatus</i>	Black-chinned Siskin	13.5	27.8	1.96	0.442 0.257	0.132 0.057