THE USE OF MIST-NET CAPTURE RATES TO MONITOR ANNUAL VARIATION IN ABUNDANCE: A VALIDATION STUDY¹

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Abstract. Constant-effort mist-netting has become an increasingly popular tool in longterm monitoring of bird populations. Monitoring programs often assume that variation in the capture rates of adults reflects variation in breeding densities of the sampled population. We test this assumption by comparing annual variation in mist-net capture rates to known variation in breeding densities of four species breeding in coastal scrub habitat at Point Reyes National Seashore, California. For the period 1980 to 1992, breeding densities for each species were assessed using spot-mapping observations of color-banded individuals. These were compared to capture rates calculated from constant-effort mist-netting. Capture rates of adults correlated significantly with breeding density for Spotted Towhees (Pipilo maculatus), Song Sparrows (Melospiza melodia), and Wrentits (Chamaea fasciata), but not for White-crowned Sparrows (Zonotrichia leucophrys). Analysis of covariance confirmed that the relationship of mist-net capture rates to breeding density differed among species. Independent of the effects of breeding density on capture rates, adult capture rates of the four species were higher in years with high rainfall. Among Wrentits and Song Sparrows, approximately 50% or more of adults caught were not occupying territories at the study site; the same bias may exist among other species as well. We conclude that relative changes in breeding density over time can be inferred from variation in mist-net capture rates for some, but not all, species. Additional studies are needed to validate the use of mist nets to assess spatial differences in abundance and to monitor temporal changes in abundance in habitats other than coastal scrub.

Key words: breeding density, constant-effort mist-netting, population trends, Song Sparrow, Spotted Towhee, White-crowned Sparrow, Wrentit.

INTRODUCTION

Mist nets are widely used to monitor changes in species' abundance, especially when other sources of demographic information are not available (Ralph et al. 1993, Dunn and Hussel 1995). Standardized mist-netting programs have been used to provide insight into temporal patterns of abundance (Berthold and Schlenker 1975, Faaborg and Arendt 1992, Vega and Rappole 1994) as well as to estimate breeding success of passerines (DeSante and Geupel 1987, Bibby et al. 1992). Recently, capture rates of adult and hatching-year Swainson's Thrushes (Catharus ustulatus; Johnson and Geupel 1996) and Wilson's Warblers (Wilsonia pusilla; Chase et al. 1997) have been used to provide indices of adult abundance and productivity at a single site. Additionally, large-scale studies in North America (DeSante et al. 1993) and the United Kingdom (Baillie 1990, Peach et al. 1996) have estimated reproductive success from the ratio of juvenile captures to total net-captures.

The studies cited above assume that the number of adults caught is linearly related to breeding density. Although this assumption has never been directly tested, concordance between independent measures of population trends and trends in mist-net capture rates have been noted over broad geographic scales (Dunn and Hussell 1995, Peach et al. 1998). However, studies conducted on a small-scale have had mixed results in comparing trends obtained using mist nets and other methods. Ralph and Fancy (1995) found that monthly variation in mist-net capture rates of color-marked Apapane (Himatione sanguinea) and Iiwi (Vestiaria coccinea) correlated with densities measured by the variable circular plot method at one of two study sites. In contrast, comparing results obtained at 18 sites in Cuba, Wallace et al. (1996) found a poor cor-

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respondence between detections of species using mist nests and detections using fixed-radius point counts; Whitman et al (1997) obtained similar results, working in Belize. Du Feu and McMeeking (1991) found a positive correlation between the number of juvenile Blackbirds (Turdus merula) caught in nets and an independent measure of local productivity, but found no such significant correlation for Song Thrushes (Turdus philomelos). Nur and Geupel (1993a) showed that annual variation in the number of juvenile Song Sparrows (Melospiza melodia) caught in nets was correlated with the number of fledglings produced in the study area. The same comparison did not hold true among Wrentits (Chamaea fasciata).

Recently, Remsen and Good (1996) questioned the ability of mist nets to adequately monitor patterns of abundance in bird communities (see also Jenni et al. 1996). They point out that differences in capture rates may reflect behavioral differences such as spacing systems, activity levels, and flying height, rather than differences in relative abundance. They used computer simulations to demonstrate the potential effect of differences in behavior on mist-net capture rates. Whereas it is important that biologists be aware of potential pitfalls in the use of mistnet capture rates to monitor differences in abundance, the more pressing question is: How well does variation in mist-net capture rates actually reflect differences in abundance, specifically, breeding density?

This question has been difficult to answer, owing to the paucity of long-term studies of a single population using different census methodologies. In this paper we describe such a longterm study conducted by investigators from the Point Reyes Bird Observatory. Since 1976, large numbers of Song Sparrows, Wrentits, Spotted Towhees (Pipilo maculatus), and Whitecrowned Sparrows (Zonotrichia leucophrys) have been captured in a standardized mist-netting program at the Palomarin Field Station (DeSante and Geupel 1987). In addition, as part of the Coastal Scrub Avian Ecology Project (CSAEP; described in Geupel and DeSante 1990), independent estimates of breeding density of these species have been made annually since 1980, using repeated observations of color-banded individuals and the systematic location of nests on the CSAEP study area. The latter encompasses the sites used for our mist-netting study (Fig. 1) and provides a unique opportunity for small scale comparison of monitoring methodologies. We compare mist-net capture rates of adults during the breeding season at the Palomarin Field Station with breeding densities derived from the CSAEP to determine the accuracy with which mist nets measure annual changes in local breeding density.

Our evaluation addresses four specific questions: (1) Is there a linear relationship between capture rates of adults and breeding density for each of four year-round resident species? (2) Is there species variation in the ability of mist nets to track population changes? (3) How large an area are mist nets sampling? To answer this question, we compare the area immediately adjacent and surrounding the mist net complex with a larger area, extending several hundred meters from the mist nets. Finally, because the California central coast experiences marked variation in annual rainfall (DeSante and Geupel 1987), and because rainfall likely influences the amount and quality of vegetation available to animals for food and cover (Rotenberry and Wiens 1991), we ask: (4) Independent of the effects of density on capture rates, are mist-net capture rates correlated with annual variation in rainfall?

METHODS

Data were collected on a study site located at the southern end of the Point Reyes National Seashore, Marin County, California, described in DeSante and Geupel (1987), Johnson and Geupel (1996), and Chase et al. (1997). The site is bounded on the west by the Pacific Ocean and on the east and northeast by mixed evergreen and riparian forest. Coastal scrub vegetation covers the study site and extends across its remaining borders. The scrub vegetation consists primarily of California sage (Artemisia californica), coyote bush (Baccharis pilularis), bush monkey flower (Mimulus aurantiacus), California blackberry (Rubus vitifolius), poison oak (Rhus diversiloba), and Douglas fir (Psuedotsuga menziesii) (Shuford and Timossi 1988).

Twenty permanent 12-m nets were operated daily from April through June, 1980–1992 (Fig. 1), except that nets only were operated three times per week in the month of April from 1989 through 1992. The 20 nets were in 14 locations, that were in, or adjacent to, coastal scrub habitat. Eight locations had single nets, and six had dou-



FIGURE 1. Map of study area. Dashed line denotes the border of the Coastal Scrub Avian Ecology Project study area. Filled circles denote the 14 mist-net locations. Plot A is the breeding census area nearest the nets. Plots A and B together form the larger area considered in this paper, Plots A + B.

ble nets, vertically stacked. Nets were opened 15 min after sunrise and remained open for 6 hr, weather permitting. Ages of captured birds were determined from degree of skull ossification and, when possible, from plumage (Pyle et al. 1987). Repeat captures of individual birds were not included in total counts. The capture rate for each species is the number of distinct individuals captured per thousand-net-hours from 1 April through 30 June. We divided captures by nethours to standardize effort between years; however, net-hours did not differ greatly between years (mean = 10,240; range 7,900–12,200).

Local breeding bird densities, reported as number of breeding pairs per hectare, are derived from detailed territory maps of the CSAEP; territory maps were compiled each year by the same individual (GRG). The CSAEP records the history of color-banded individuals during the breeding season (Geupel and DeSante 1990). The CSAEP study area encompasses 36 ha and includes the breeding bird census plots considered in this project. We used breeding censuses corresponding to a 3.8 ha plot (Plot A) closest to the nets (Fig. 1) and a 16.4 ha region that included Plot A and two additional sub-plots (marked Plot B on Fig. 1) farther from the nets. Note that all mist nets were located within Plot A or were less than 100 m from the edge of Plot A. In contrast, distances from Plot B to the closest mist net varied from 100–600 m, and to the farthest mist net varied from 500–800 m. Thus, comparisons of mist-net capture rates with breeding census results from Plot A, as distinct from Plot A + B, can provide insight into the spatial scale at which mist nets may be able to sample local, breeding populations.

The CSAEP study area was completely surveyed at least twice per month, from late March through late July (Geupel and DeSante 1990). Each year, four observers spent an average of 20 hr week⁻¹ searching for nests and making observations of color-banded individuals. We are confident that no territory holding birds were missed during this intensive field work. Each mapped territory that fell completely within a

breeding census plot is counted as one breeding pair. We counted territories extending beyond the borders of the plots as fractional territories (rounded to the closest one-quarter).

STATISTICAL ANALYSES

We tested the relationship between mist-net capture rate and breeding density for each species using linear regression techniques and the statistical package STATA (Stata Corporation 1993). In these analyses, we regressed mist-net capture rates on breeding bird densities. We confirmed that residuals met assumptions of regression analyses; this included testing residuals for deviation from normality. We examined residuals to determine whether they demonstrated serial autocorrelation, using the Cochrane-Orcutt procedure and the Durbin-Watson statistic (Neter et al. 1985, Stata Corporation 1993). Autocorrelation would violate the assumption made in linear regression analysis that residuals are independent; however, there was no evidence of autocorrelation. Before conducting regression analyses comparing mist-net capture rates and breeding density. we looked for the presence of linear trends in mist-net capture rates or breeding density estimates with time. We found no significant linear trends for these variables for any of the species.

A one-tailed test was used to assess the significance of the regression coefficients because we considered it biologically implausible for net capture rate to genuinely decrease with increasing density. In order to assess the effects of scale, these regressions were performed on breeding densities averaged over Plot A and over Plots A + B.

DeSante and Geupel (1987) observed that capture rates of juvenile (HY) birds at the study area were related to annual rainfall; they interpreted such variation in capture rates as reflecting differences in reproductive success. An alternative explanation is that annual variation in rainfall directly or indirectly influenced capture rates, for example, by altering behavior of juveniles. Thus, we were motivated to consider whether variation in annual rainfall, or some factor correlated with annual rainfall, biases capture rates. We examine the effect of annual rainfall by analyzing a multiple regression model which includes rainfall during the current season (the previous winter plus current spring) as an independent variable.

Where appropriate, individual contributions of rainfall and breeding density to the multiple regression model for a species are depicted in partial regression leverage plots, also called added variable plots (Stata Corporation 1993). These help to visualize the effect of a single ("added") independent variable on the dependent variable while controlling for the effect of other independent variables. We examined whether the relationship of capture rates to breeding density varied among species by testing for the interaction between species and breeding density in an analysis of covariance model (Neter et al. 1985). We further made pairwise between-species comparisons of the slope of net capture rate vs. breeding density. We tested for deviations from linearity in the relationship of capture rates to breeding density by assessing the significance of quadratic and cubic terms in a polynomial regression (Neter et al. 1985).

When comparing data from different species, we first log-transformed capture rates in order to linearize the relationship between capture rates and breeding density and to normalize residuals. Log-transformation of the dependent variable also was recommended by Harvey (1982) for between-species comparisons. A logarithmic transformation is further supported because capture rates likely vary between species in a multiplicative fashion. For example, we might expect that, for species P and Q, capture rates are proportional to breeding density, but with different constants of proportionality for each species (note the null hypothesis is that the constant of proportionality = 0).

RESULTS

For Plot A, the region closest to the nets (Table 1), net capture rate and local breeding density were correlated for Spotted Towhees, Song Sparrows, and Wrentits, but not for Whitecrowned Sparrows. On the larger, more inclusive site, Plots A + B, breeding density was a significant determinant of mist-net capture rate for Song Sparrows and Spotted Towhees, but not for Wrentits or White-crowned Sparrows (Table 1). The constant term, or intercept of the best fit line, represents the expected number of net captures when there are no locally breeding birds. If mist-net capture rates reflect local breeding density, then we would expect the intercept to be zero. Indeed the constant term in the regres-

Net captures 1,000 nhr ⁻¹	Regression coefficient	Standard error	t	Р	<i>R</i> ²
Plot A					
Song Sparrow	0.749	0.320	2.35	0.02	0.333
Wrentit	1.71	0.753	2.28	0.02	0.320
Spotted Towhee	2.18	0.871	2.51	< 0.02	0.364
White-crowned Sparrow	-0.253	0.345	-0.73	а	0.047
Plots A + B					
Song Sparrow	1.46	0.784	1.86	0.04	0.239
Wrentit	1.18	1.01	1.17	>0.1	0.111
Spotted Towhee	2.95	1.37	2.16	0.03	0.298
White-crowned Sparrow	-0.224	0.384	-0.58	а	0.030

TABLE 1. Regression analyses of capture rate of adults in relation to breeding density (breeding pairs ha^{-1}) by species. *P* refers to one-tailed test; see text. n = 13 observations for all analyses.

^a One-tailed test not applicable due to negative coefficient; see text.

sions for Song Sparrows, Wrentits, and Spotted Towhees was close to zero. Only White-crowned Sparrows had a significant intercept (constant = 1.078, P < 0.01). Furthermore, White-crowned Sparrows exhibited no tendency for a positive correlation at either scale; in fact, the correlation was negative for both Plot A and Plots A + B (Table 1).

For the three species that demonstrated a relationship between net capture rates and breeding density in Plot A, the same relationship was weaker when considered over Plots A + B (Table 1). Therefore, we confined our subsequent analyses to Plot A. Note that the decrease in correlation coefficient as the censused area increased (i.e., Plot A + B) was not equivalent for all three species: for Wrentits, the correlation coefficient decreased from +0.566 to +0.333, but for Song Sparrows and Spotted Towhees the change was less marked (decreases of 0.088 and 0.057, respectively).

The relationship of capture rate to breeding density differed among the four species, i.e., slopes of the regressions of capture rates on density were heterogeneous among Wrentits, Song Sparrows, Spotted Towhees, and White-crowned Sparrows ($F_{3,44} = 3.51$, P = 0.023). In addition, pairwise comparison among Wrentits, Song Sparrows, and Spotted Towhees indicated no difference in slope (for each of the three comparisons, *F*-test, P > 0.1). Slopes for the relationship of capture rate to breeding density did not differ between Song Sparrows and Whitecrowned Sparrows (P > 0.1), but slopes comparing White-crowned Sparrows and Wrentits (P< 0.01) and comparing White-crowned Sparrows and Spotted Towhees (P < 0.05) were different.

For Wrentits, both rainfall ($t_{10} = 2.73$, P < 0.05) and breeding density ($t_{10} = 3.31$, P < 0.01) contributed to variation in mist-net capture rates ($R^2 = 0.29$ and 0.43, respectively). The results of the multiple regression analysis are graphically illustrated in Figure 2, which depicts the independent contributions of rainfall (Fig. 2A) and breeding density (Fig. 2B) to explaining variation in Wrentit net capture rates.

For White-crowned Sparrows, Spotted Towhees, and Song Sparrows, considered separately, rainfall did not contribute to variation in capture rates when breeding density was controlled. although the trend was positive for all three species (F-tests, P > 0.1). However, when all four species were analyzed in a combined multi-species statistical model (including a species main effect and breeding density and rainfall effects), there was a significant effect of rainfall on capture rate after controlling for breeding density $(F_{146} = 4.55, P < 0.05, Fig. 3)$. Conversely, the effect of breeding density on capture rate was significant after controlling for rainfall ($F_{1,46}$ = 5.40, P < 0.03). Thus, for all species considered together, and for Wrentits alone, the effect of rainfall on capture rates was positive: capture rates were highest in years with highest rainfall even after adjustment is made for differences in breeding density. Furthermore, there was no significant species \times rainfall interaction ($F_{3,45}$ = 0.12, P > 0.9), implying that the effect of rainfall on capture rates was similar among species.

With the exception of Wrentits, there were no significant quadratic coefficients in a polynomial





FIGURE 2. Added Variable Plots showing the relative contribution of (A) total rainfall (cm year⁻¹) and (B) breeding density (breeding pairs ha⁻¹) in explaining variation in mist-net capture rates in Wrentits (see text). Both the effect of rainfall on capture rates, while controlling for breeding density (A; P = 0.025), and the effect of breeding density on capture rates, while controlling for rainfall (B; P = 0.005), are significant. For both graphs, independent and dependent variables are shown standardized to a mean of 0.

regression relating capture rates to breeding density (Neter et al. 1985). For none of the species were cubic regression coefficients significant. However, for Wrentits, after controlling for the effect of rainfall, the quadratic coefficient for the effect of breeding density on capture rate was no longer significant (P > 0.1). We conclude, therefore, that the relationship of capture rates to breeding density did not deviate from linearity.

DISCUSSION

Mist-net capture rates of Spotted Towhees, Song Sparrows, and Wrentits correlated well with estimates of breeding density over Plot A, the plot that was adjacent to and encompassing the set



FIGURE 3. Effect of total rainfall on log-transformed mist-net capture rates for all four species combined, while controlling for breeding density and for a species main effect. The effect of rainfall is significant (P < 0.05). Rainfall and log-transformed capture rates are standardized to a mean of 0.

of mist nets. Over the larger area, Plots A + B, this correlation was slightly weaker for Song Sparrows and Spotted Towhees, and weaker still for Wrentits. However, for White-crowned Sparrows, no relationship between adult net capture rate and breeding density was apparent at either spatial scale. This species variation in the ability of mist-net capture rate to predict changes in breeding density proved significant.

These results bear on two questions regarding scale. At what spatial scale are we monitoring population trends? Is that scale also species dependent? Plot A is the smallest area we considered. Although not all mist nets were located within the boundaries of Plot A, all nets in this study were at least within 100 m of Plot A. Previous work at this site (Nur et al., in press a) has revealed that even in the Wrentit, a species which is considered especially sedentary (Erickson 1938, Johnson 1972), adults are routinely caught in mist nets up to 200 m from the centers of their territories. Furthermore, territory-holding Wrentits caught in mist nets are observed to cross territory boundaries (Nur and Geupel 1993b). At a greater distance from the nets (about 0.5 km away) there are the two B subplots. For Song Sparrows at this site, it was not unusual to catch individuals 500 m or more away from their territory boundaries (Nur et al., in press b). The results of this study are thus consistent with observations of known territoryholding Wrentits and Song Sparrows: for sedentary Wrentits (whose territorial individuals are rarely caught more than 200 m from their territory centers), there was a correlation of mist-net capture rates with breeding density in Plot A but not in Plots A + B. For the more mobile Song Sparrow, in contrast, capture rates correlated with the density determined in the larger area (0.5 km or more from the mist nets) as well as for the smaller, more immediate area.

O'Connor (1992) suggested that mist nets do

not sample juveniles and adults equally well in the same geographic area. This discrepancy was confirmed by Nur and Geupel (1993b) who found that, among Wrentits, the physical area sampled by the nets varied among age classes. Our results imply that the area sampled by mist nets may differ for adults of different species, but in all cases the efficacy with which nets monitor local population trends decreases with distance from the nets.

The question of scale becomes especially important the more population trends are discordant at different spatial scales. However, few studies have addressed the question of how concordant are population trends determined at different scales. Holmes and Sherry (1988) compared population trends for 19 species on a small study area in Hubbard Brook, New Hampshire, with population trends determined from Breeding Bird Survey (BBS) routes throughout New Hampshire. For 7 species out of 19, trends appeared concordant (r > 0.46, P < 0.05), but for 9 species, there was little correlation between the trends at the two different scales (|r| < 0.2). Examining even larger spatial scales, there appears to be little agreement about the extent of concordance or discordance in population trends (Maurer and Villard 1996); this is especially true for those analyzing BBS data (James et al. 1996).

We have no ready explanation for why there is no relationship between net capture rate and breeding density for White-crowned Sparrows. Like Wrentits, Song Sparrows, and Spotted Towhees, White-crowned Sparrows prefer to breed in the coastal scrub (Shuford 1994). They experience roughly the same year-round weather conditions and food availability as do the other three species. There are few obvious life-history characteristics that distinguish White-crowned Sparrows from all three of the other species in this study. One difference is that White-crowned Sparrows show lower levels of territoriality during the breeding and nonbreeding seasons than the other species (Ralph and Pearson 1971, Mewaldt and King 1977). They initiate egg laying in May, whereas Song Sparrows and Wrentits begin in April (PRBO, unpubl. data). Nevertheless, when data were reanalyzed using May-July capture data instead of April-June data so as to better match the breeding season period of White-crowned Sparrows, qualitative conclusions regarding White-crowned Sparrows remained the same.

If mist nets vary in their effectiveness at measuring variation in breeding densities of four similar species, this suggests that even greater difficulties may beset comparisons among dissimilar species. Our results indicate that mistnetting can give reliable information on trends in breeding densities of local populations for several species; but this evaluation must, at this point, be made on a species-by-species basis. Mist-net capture data likely are more useful for relative comparisons of breeding densities within a species than for comparisons of absolute densities between species. Behavioral differences leading to differences in capture probability likely are more pronounced when comparing different species than when comparing within a species. Use of mist nets to compare abundance among species with different habitat preferences or other behavioral traits is particularly questionable (Berthold and Schlenker 1975, Jenni et al. 1996, Remsen and Good 1996).

At the Palomarin Field Station, rainfall differed considerably among the 13 years of the study; 1982 and 1983 were, for example, extremely wet years, whereas 1987 to 1991 were dry years in central coastal California. Differences in rainfall undoubtedly influence many levels of biological processes (Rotenberry and Weins 1991), including demographic processes in birds (Bryant 1975, Peach et al. 1991). It is conceivable that the behavior of birds could be influenced by seasonal, cumulative rainfall. At Palomarin, annual rainfall appears to be a factor which biases adult capture rates among Wrentits, and perhaps among other species as well.

For all four species, we found a tendency for capture rates to be highest in years with high rainfall. The mechanism linking annual differences in rainfall with annual differences in capture rate is at present unknown. The linkage cannot be very direct: 83% of the year's rain falls during November–March, little falls during May and June. We believe rainfall affects vegetation which in turn affects bird behavior. Our results call for careful consideration of the conclusions of DeSante and Geupel (1987), who concluded that differences in rainfall influenced productivity but did not explicitly consider that rainfall might directly or indirectly bias capture rates.

Despite bias exerted on capture rates because of differences in rainfall, three of the four species demonstrated a predictive relationship between capture rates and breeding density. Although there is certainly a potential for mist-net capture rates to provide misleading indications of differences in abundance (Remsen and Good 1996, Sauer and Link, in press), our study empirically demonstrates that mist-net capture rates can provide valid indices of population change over time.

The relationship between capture rates and breeding densities of Wrentits was manifest even though most adults caught in mist nets at Palomarin were transients rather than local breeders (Nur and Geupel 1993a). Breeding Wrentits whose territories encompass a net, or are adjacent to a net, tend to be captured more than once in the same breeding season; thus, they can be usually distinguished from transient birds. However, as noted above, breeders with territories far from the nets (200 m or more from the closest net) tend to stay on their territories and are rarely caught in nets during the breeding season (Nur et al., in press a). Thus, the mist-netting operation and the CSAEP are, by and large, not counting the same individuals and yet they exhibit the same trends. One possible mechanism linking trends in mist-net capture rates with trends in local breeding density is suggested by Geupel, Williams, and Nur (unpubl. data). These authors found that the number of nonterritorial ("floater") Wrentits detected in the study area at Palomarin increased with increasing number of Wrentit territorial pairs on the study site. Thus, as breeding density increased, there were fewer vacancies available, and thus a higher prevalence and greater capture rate of floaters. For Song Sparrows, territory-holding individuals constitute a larger fraction of all adults caught in nets, compared to Wrentits, but even here 47% of Song Sparrows caught were not local territory-holders (Nur et al., in press b).

Our study validates the use of mist nets to monitor changes in the breeding density for three of four species breeding in coastal scrub habitat. The method failed for the fourth species, White-crowned Sparrows. Mist-netting provides a means to acquire important demographic data (Nur et al., in press b) in a relatively quick and inexpensive manner and is currently gaining widespread use in nationwide standardized monitoring programs (Baillie 1990, DeSante et al. 1993, Ralph et al. 1993). Mist nets may provide a valuable supplement to the Breeding Bird Survey (Holmes and Sherry 1988), if the mist nets are deployed systematically and if results are interpreted on a species by species basis. More studies comparing mist-net capture rates and abundance estimates obtained by other monitoring methods are needed to understand effects of geographic scale, differences among species, and how results of this study generalize to other habitats.

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