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BIRD POPULATION STUDIES IN PUERTO RICO USING MIST NETS: GENERAL PATTERNS AND COMPARISONS WITH POINT COUNTS

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Abstract. Mist nets have been used to monitor size, composition, and survival rates of bird populations in the Guanica Forest of Puerto Rico every winter since 1972. Each line of nets consists of 16, 12-m nets erected end-to-end in a straight line and operated from dawn to dark for three consecutive days. Here we examine features of the netting protocol that could affect quality of results for population studies, including species sampled, length and frequency of netting sessions, and numbers of captures and recaptures. Point counts and mist-net samples gave very different results for relative abundance of species. Number of birds captured for the first time within a sample declined rapidly over three days of netting, with few birds captured the third day, regardless of a species' abundance. Net avoidance was strong within 3-day samples, but not between different netting sessions (which were at least three months apart). We suggest these samples are indicative of avian populations resident within the area of net lines, and that three days is a sufficient length of time to capture the majority of birds using that area, at least in the low-statured vegetation of Guanica Forest. However, in more diverse or structurally complex habitats, mist nets may not sample as large a proportion of the species and individuals present.

Key Words: mist nets, net avoidance, population monitoring, survival.

Mist nets have been used to monitor bird populations in the Guanica Forest of Puerto Rico since 1972, first by J. Faaborg, and later in cooperation with all the authors. A variety of papers has resulted from this work (reviewed by Faaborg and Arendt 1990, Faaborg et al. 2000). Mist-net captures were used initially to compare population levels between islands (Terborgh and Faaborg 1973), and to look for patterns in the morphology of species making up island bird communities (Faaborg 1985). After a severe drought, monitoring was continued to assess the effect of drought on bird populations (Faaborg 1982, Faaborg et al. 1984, Faaborg and Arendt 1992a, Dugger et al. 2000). Captures of winter residents provided observations about site fidelity and territoriality (Faaborg and Winters 1979) and, after 15 years, a severe decline in captures of winter resident warblers was noted (Faaborg and Arendt 1989b, 1992b). With long-term recapture data, we were able to measure demographic traits of both resident and winter resident birds, looking first at longevity (Faaborg and Arendt 1989a) then, using advanced statistical models, survival rates (Faaborg and Arendt 1995). Our latest contribution (Dugger et al. 2000) examined relationships between rainfall patterns and both population and survival rate variation within the resident birds of the forest, using a 26-year data set from a netting site operated since 1973. Because hurricane Georges caused extensive damage to the forest in the fall of 1998, future work will have to incorporate the effects of this event on population and survival parameters.

In this paper, we evaluate our netting protocol. Although it is unlikely that we would change these after 30 years, it is important to understand strengths and weaknesses of our methods in order to better interpret our results, and to make recommendations to others.

METHODS

STUDY SITE

The Guanica Forest is managed by the Department of Natural Resources of the Commonwealth of Puerto Rico. It is a 4,000-ha reserve situated along the southwest coast, composed of approximately 50% natural subtropical deciduous forest and 50% regenerating forest. The relatively undisturbed parts of the forest are considered to be the best remaining examples of this forest type in the New World, and Guanica Forest is listed as a World Biosphere Reserve. Subtropical deciduous forest is short and thorny (see Terborgh and Faaborg 1973 for further descriptions and photographs). Mean canopy height in one study site was 5.2 m (Terborgh and Faaborg 1973), few trees exceeded 8 m, and vegetation height has remained fairly constant over the life of the study. Differences between species in vertical foraging behavior do not appear to be a major means of ecological separation among West Indian species (Faaborg 1985), especially in such a short forest, so nearly all birds found in the forest frequent the zone sampled by mist nets (<2.5 m).

NETTING PROTOCOL

The standard mist-netting protocol involves setting 16 nets, each 12 m long, as close to end-to-end as possible and in as straight a line as possible. From 1972 through 1996 we used 36-mm mesh nets (usually the Association of Field Ornithologists type ATX). Since 1996, we have used 30-mm mesh nets (from Spidertech) because these nets have a fuller bag, which we felt would increase captures of the smallest migrants while not reducing captures of the largest residents. No change in capture rate was apparent with the change in mesh sizes.

Most of the time we have only one netting session with each line annually, in January or early February, but on a few occasions we have operated a line again during the breeding season (June or July) or during early or late winter (October or March). The original net line, situated within undisturbed forest at an intermediate elevation (150 m), has been operated annually since 1973 (except 1977 and 1979). Eight new lines were added during 1989–1991, scattered throughout the central part of the forest to sample a range of locations and vegetation types, including lines in portions of the forest that were heavily disturbed over 60 years ago. All nine lines have been operated annually since 1991.

Two pairs of lines are 100 m apart (from the end of one line to first net of the next line), whereas other lines are at least 1 km from their nearest neighbor. Each line is operated for three consecutive days from dawn (as soon as bats stop flying) to dusk (just before bats start flying). In January, this is from approximately 0700 to 1800 hours. Lines are checked constantly during the first day when capture rates are high, and then regularly (at least every 20 min) after capture rate declines.

Point Count Methods

To determine the relative value of netting versus visual censusing for determining species composition and relative density, J. Faaborg and two colleagues (T. Donovan and B. Woodworth) conducted a series of point counts during 1993, following a modification of guidelines for winter censusing (Hutto et al. 1986). Five points were set up in alignment with each row of nets. The middle point was at the mid-point of the net line, one was at each end (100 m from the center), and the last ones were 100 m beyond the ends of the net line. These points are closer together than is usually recommended, but we felt this was necessary to ensure the points sampled the net line area. We conducted 10 min counts, recording birds both within a 25-m radius of the point and all birds recorded beyond this fixed radius. Each point was visited on three different mornings, when the nets were not in operation. Each visit was conducted by a different observer, each of whom was familiar with the calls and songs of Puerto Rican birds. Counts started 15 min before sunrise, and it took about one hour to complete sampling at each net line. For this paper, we computed average detections per point for unlimited distance for each species.

RESULTS

Species Composition

Guanica Forest supports a typical insular avifauna with relatively few species but high abundances among most of them. Over the course of 30 years, we have captured every bird that we have seen within the Guanica Forest (not counting swallows and similar species that we only see flying overhead). Large raptors and pigeons that are too big for the nets are captured only rarely, as are nocturnal species that generally have stopped moving by the time nets are opened.

We compared the relative frequency of birds detected on all of our point counts with those netted on all net lines during 1993 (Table 1). Although seven of the 10 most abundant species recorded by each technique were the same, their relative frequencies were often very different. For example, the Adelaide's Warbler (see Table 1 for scientific names) was by far the most detected bird on point counts. It is widespread throughout the forest, maintains territories and pair bonds, and sings frequently in the morning, even in January. We feel we caught most of those individuals whose territories occurred along the net lines, but this was often only four to five birds per line, which is a small segment of total captures (4.8%).

The most frequently netted bird, the Bananaquit (31% of captures in 1993), constituted only 10% of point count detections, perhaps, in part, because it sings infrequently at Guanica in mid-winter. High capture rate for this species probably reflected accurately a high density, rather than constant movement of transients, as nearly all cases of individuals caught in two different lines in the same year involved this species. The Puerto Rican Flycatcher is virtually silent in January, so it was rarely recorded on point counts (1.1% of detections) despite accounting for 5.6% of captures. In contrast, species that are large enough that they often get out of the nets but that have loud calls or songs, such as the Puerto Rican Woodpecker, Troupial, and Puerto Rican Lizard-cuckoo, were recorded on point counts more frequently than they were netted. Analyzing birds detected solely within 25 m of the count point would have reduced the number of detections for most species, but would have had little effect on the general relationship between the two inventory methods.

Perhaps the most striking difference in the results of the two techniques was for wintering warblers, which comprised 13% of captures in 1993 but which totaled only 0.2% of total detections on point counts (Table 1). Only two species were detected on point counts (American Redstart and Black-and-white Warbler), whereas nine species were netted. Wintering warblers are relatively quiet in the Guanica Forest in winter and were easily missed on point counts, especially if they foraged on the ground (such as the Ovenbird).

TABLE 1. COMPARISON OF THE TEN MOST ABUNDANT SPECIES FOUND BY NETTING (PERCENT OF TOTAL CAPTURES ON NINE NET LINES) AND BY POINT COUNTS (PERCENT OF ALL DETECTIONS ON ALL POINTS)

Species	Relative frequency
	Percent captured
Netting results	
Bananaquit (*Coereba flaveola*)	31.2
Puerto Rican Bullfinch (*Loxigilla portoricensis*)	18.4
Caribbean Elaenia (*Elaenia martinica*)	11.2
Puerto Rican Flycatcher (*Myiarchus antillarum*)	5.6
Puerto Rican Tody (*Todus mexicanus*)	4.8
Adelaide's Warbler (*Dendroica adelaidae*)	4.8
Puerto Rican Vireo (*Vireo latimeri*)	4.8
Red-legged Thrush (*Turdus plumbeus*)	4.0
Pearly-eyed Thrasher (*Margarops fuscatus*)	4.0
Antillean Mango (*Anthracothorax dominicus*)	4.0
ALL WINTER RESIDENT SPECIES*	13.3
	Percent detected
Point count results	
Adelaide's Warbler	34.0
Caribbean Elaenia	16.6
Bananaquit	10.2
Puerto Rican Vireo	8.7
Puerto Rican Tody	7.1
Puerto Rican Bullfinch	6.5
Puerto Rican Woodpecker (*Melanerpes portoricensis*)	4.0
Troupial (*Icterus icterus*)	2.0
Puerto Rican Lizard-cuckoo (*Saurothera vielloti*)	1.9
Pearly-eyed Thrasher	1.3
ALL WINTER RESIDENT SPECIES**	0.2

* Black-and-white Warbler (*Mniotilta varia*), Swainson's Warbler (*Limnothlypis swainsonii*), Worm-eating Warbler (*Helmitheros vermivorum*), Northern Parula (*Parula americana*), Magnolia Warbler (*Dendroica magnolia*), Prairie Warbler (*D. discolor*), American Redstart (*Setophaga ruticilla*), Hooded Warbler (*Wilsonia citrina*), and Ovenbird (*Seiurus aurocapilla*).

** Black-and-white Warbler and American Redstart

CAPTURE RATES WITHIN THREE-DAY NETTING SESSIONS

The typical capture pattern through a three-day sampling period (all species pooled) was a steep linear decline in daily number of first captures (birds caught for the first time in a netting session). Some samples were very linear (e.g., 1973; Fig. 1), although a few were not (e.g., 1987; Fig. 1). In nearly all samples, however, fewer birds were caught during each subsequent day, and in all cases, capture rates declined over the entire three-day sample. We computed linear regressions of capture rate (number of daily first captures against day of sample for each year), and found similar slopes of capture rates, despite great variation in population levels. Capture rate by sample day, averaged across all years, also showed a strong decline (Fig. 2a), although SE was large due to large annual variation in total captures. When data were treated as percentages of total captures (to reduce variation resulting from varying population sizes), SE was smaller, but the overall pattern remained the same (Fig. 2b). These results, based on 20 years of data from the original net line, were mirrored closely by data from over 60 other net lines during the period 1989–1993 (J. Faaborg, unpubl. data).

Samples with unusual capture patterns generally occurred only when population levels were low, or under exceptional weather conditions (especially high winds). With one exception, unusual patterns involved samples in which captures on the third day were higher than on the second, because of inclement conditions on the second day. In rare cases, we added a fourth day of netting under these circumstances. However, this always resulted in fewer captures than on the third day, suggesting that most of the birds using that area had already been caught in the first three days.

Most species showed daily declines in capture rates similar to the overall patterns illustrated above,

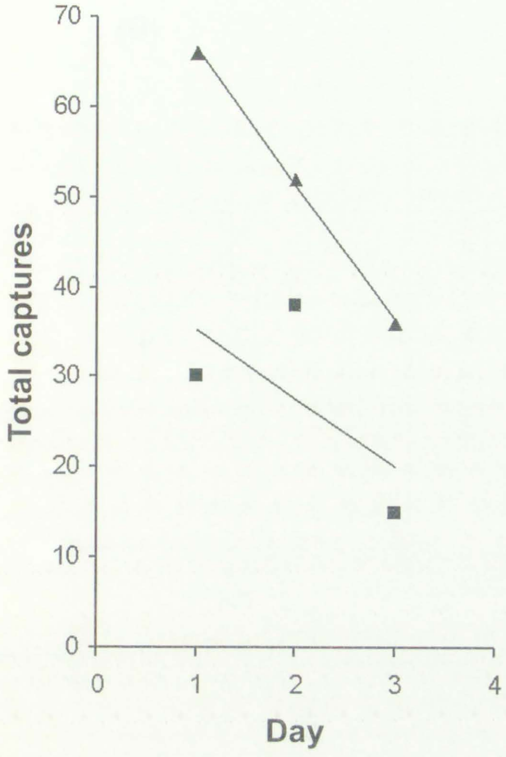

FIGURE 1. Daily capture rates of birds over three-day samples on the original Guanica net line, showing a particularly linear sample (triangles: 1973 sample, $r^2 = 0.99$) and a less linear sample (squares: 1987 sample, $r^2 = 0.41$).

but the pattern was most pronounced for abundant species (Fig. 3a). Less abundant species tended to show a similar trend (Fig. 3b), but when only four or five individuals are captured in three days, the slope of the capture rate will naturally be less steep than for abundant birds. Capture rates for these species are less likely to be linear, probably mainly by chance.

The group of species that migrate to Puerto Rico for the winter, nearly all of them warblers (Parulidae), was captured very rapidly (Fig. 3c). In general, the first two days of netting captured 85–90% of the three-day total of these species.

For species with large numbers of floaters in the population, we might expect captures to continue at a low level for more than three days and, depending upon the characteristics of the floaters, perhaps indefinitely. However, in our knowledge of more than 200 net lines operated throughout the West Indies, we are aware of only two records of an abundant species showing little or no decline in capture rate over a three-day sampling period. Neither was at Guanica and both were on very small islands and apparently associated with extreme drought.

Net Avoidance

Only 5–10% of birds were caught more than once in a three-day sample. Combined with a rapid decline in first captures, this indicates net avoidance. Otherwise, daily capture rates should have remained about constant, with only the proportion of first captures declining. We know that low recapture did not reflect movement out of the area, because we often saw banded birds nearby, and recaptured them in subsequent years. If net avoidance was specific to the exact location of capture, we might expect more than a 10% recapture rate, because birds could be recaptured further along the net line, but avoidance appeared to involve all nets along the nearly 200-m transect of a line. Due to net-avoidance, third day captures often involved 30 or fewer total individuals, compared to 150 or more birds on day one.

We do not know how long net avoidance continues in an individual bird. We occasionally ran net lines in June, between January samples, and saw no difference in expected capture rate in either sample (June or second January). Through more intensive studies of wintering ecology of migrants we have found that nets could be run in October, January, and March with no apparent carry-over of net avoidance (Latta and Faaborg 2001).

Rates of Capture Through the Day

Morning (0700–0930 hours) was the best time to capture birds at Guanica, but there was another burst of activity in the evening (Fig. 4). The midday period (1200–1530 hours) was often slow and few captures occurred after noon on the third day. Because of the short, deciduous nature of the vegetation, many nets were exposed to full sunlight during mid-day, and nets had to be checked frequently at this time to protect birds from heat stress.

Annual Capture and Recapture Rates

Total annual captures of resident birds on the nine net lines varied from 550 to 1,142 individuals. Two species were caught at the rate of about 100 birds/year, three species at around 50 birds/year, and two species at around 30 birds/year. All the others generally are caught 20 times a year or less.

Most of the common species showed patterns of variation that suggested that we were tracking local populations. Annual numbers of the Bananaquit, for

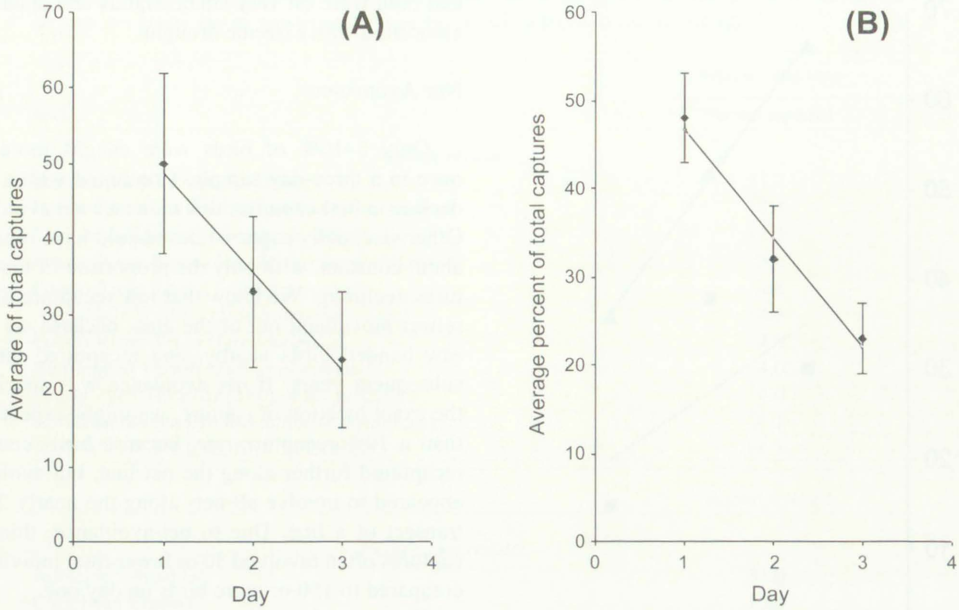

FIGURE 2. (A) Pattern of three-day capture rates by mean of total daily captures (A; $r^2 = 0.972$), or (B) by mean of the percent of total captures caught on each day of the sample ($r^2 = 0.974$) for 18 samples of the original Guanica net line run 1973–1993. Error bars show ±SE.

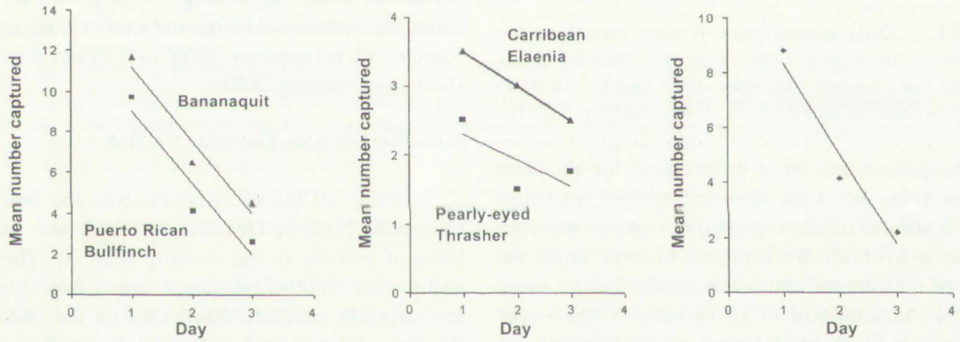

FIGURE 3. Capture rates of species and species groups during the three days of sampling, showing: (A) abundant species with steep declines in capture rates (Puerto Rican Bullfinch [$r^2 = 0.906$] and Bananaquit [$r^2 = 0.945$]); (B) species that have lower and more gradual capture rates (Caribbean Elaenia [$r^2 = 0.998$] and Pearly-eyed Thrasher [$r^2 = 0.590$]); and (C) winter resident species (primarily Parulidae [$r^2 = 0.943$]).

example, ranged from 124 to 485. However, in two ground feeding species, the Common Ground-dove (*Columbina passerina*) and Black-faced Grassquit (*Tiaris bicolor*), numbers varied so dramatically from year to year that dispersal into and out of the forest must have been a factor. For example, ground-doves increased from 5 to 59 to 115 captures in consecutive samples, which must have exceeded local reproductive rates, and they declined from 137 to 11 captures in just a year. Both of these species also showed low rates of recapture of banded individuals.

Annual recapture rates were high enough to allow us to model survival rates for many species, using Cormack-Jolly-Seber mark-recapture models (Pollock et al. 1990, Lebreton et al. 1992) and Program MARK (White and Burnham 1999). As a by-product of survival rate estimation, we can estimate capture probability (the proportion of

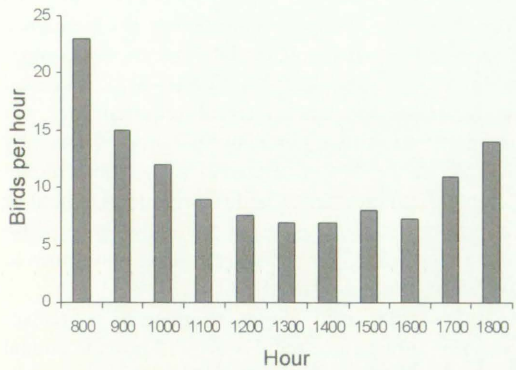

FIGURE 4. Capture rates of birds at the original Guanica net line through the day, averaged for 1990–1995 samples. Birds/hour was computed by counting total captures for the 60-min period ending on the hour (e.g., 0800 hours). First and last hourly periods may include a few birds caught before 0700 hours and after 1800 hours during the net opening and closing process.

previously banded birds present and alive each year that are recaptured). Our current analyses suggest that although recapture rates vary by species, they remain relatively constant from year to year within species and even within some guilds (Faaborg and Arendt 1995, Dugger et al. 2000). Because of this, the raw counts of mist-net capture totals can serve as relatively unbiased indices of population size for many of the species caught in mist nets in Guanica Forest. Estimates of annual recapture rates varied from 10% for some residents to over 35% for three of the common warbler species. Some individuals were extremely site faithful and long lived, including a 17-year-old Puerto Rican Flycatcher and an Ovenbird at least 7 years old.

About 1–2% of individuals were recaptured at a different net line (even when lines were >100 m apart), suggesting that there are some transient individuals in the Guanica samples. These occurred only in some years and almost always with the two most abundant species. Whereas mark–recapture models allow estimation of the proportion of transients in a population, it is sufficient for our purposes to note that population estimates may be misleading for species that show relatively equal capture rates throughout a three-day sample.

DISCUSSION

Results indicate that the netting protocol we use works well in meeting our study objectives. We catch a regular set of species that constitutes the vast majority of the avifauna of Guanica Forest. After three full days of netting, there are relatively few unmarked birds left to catch within a site. Because we rarely catch the same bird in the two net lines that are only 100 m apart, and because capture probability was relatively constant across years, we feel there is no great annual variation in territory or home range size or location. The relative constancy of recapture probability among years indicates that there are not important changes in territory or home range size among years. This stability results in recapture rates that are high enough to give good information on site faithfulness (Woodworth et al. 1999) and to allow estimation of survival rates for many species (Faaborg and Arendt 1995, Dugger et al. 2000), which is often not the case for mist-netting mark–recapture data sets.

In addition, since annual recapture rates appear to remain constant for most species and even across guilds, capture totals over our three-day sample can serve as an reliable index to population levels. Although our methods did not give actual densities, they appeared to give relative densities that could be compared in a meaningful way from year to year within a site or from site to site within the same forest type. For example, we have shown how Guanica bird population variation is highly correlated with certain rainfall characteristics (Faaborg and Arendt 1992a, Dugger et al. 2000), and we see regular variation in relative abundance of bird species in different net lines that seems to be related to variation in vegetation structure within the Guanica Forest.

Mist nets operated as in our protocol may be sufficient to monitor birds in low statured forests such as the Guanica Forest, given the nature of capture rates and the species involved. Recognizing that densities are relative, and noting that the forest here is too short for any sort of foraging stratification, removes the major complaints suggested for many mist-net studies by Remsen and Good (1996). Guanica is perhaps uniquely suited to monitoring with mist nets, because it consists of short, scrubby forest where few birds forage above the area of nets. It also supports a typically depauperate island avifauna with high abundance of most species and few species too large to be captured by a single size of net. Comparisons with sites where many individuals may forage above the nets must be done carefully, as the latter situation is undoubtedly one where only a subset of the overall bird community is being sampled effectively. In forests of tall stature, for example, one would expect that nets run at ground level would only capture the subset of the total bird community that forages and moves near the ground.

Point counts did not add much information on species composition to that of netting within this habitat during the non-breeding season, as no species was detected on point counts that was not netted at least once. This is not surprising, as neither residents nor winter residents are breeding during this, the peak of the dry season, so vocalizations are uncommon in most species. Flocking is also uncommon in this forest. This is not to say that use of point counts would not provide additional valuable information about population trends, particularly for large species that are not easily netted. However, only with detailed, long-term comparisons of the two techniques can we adequately determine the strengths and weaknesses of these two monitoring techniques in this forest.

After three days, capture rates had declined enough that continued netting was unproductive. The fact that for many resident species, third-day captures were very low relative to first day captures supports the idea that we captured a large proportion of the birds whose home ranges included the net line. Adding additional banding days would likely have added few new individuals to the totals. However, habitats with tall vegetation or with species that have much larger home ranges might require longer netting periods to catch as many birds as we get at Guanica in three days (Remsen and Good 1986).

Although it might be tempting to avoid the noontime lull in capture rates by operating nets only until noon or closing them for three to four hours at mid day, this may not be an efficient use of time. Over a six-year period, an average of 43.9% of all captures were made in the second half of the day (after 1200 hours). This suggests that more than three mornings of netting would be needed to catch as many birds as three full days and, to the extent that some birds are active only during the afternoon, these individuals might be missed with morning-only netting.

Although capture rates are often expressed as birds/net-hour (DeSante et al. 1993), our results showed clearly that many more birds were captured on the first day of a sample than on day three. Until we understand more about the characteristics of net-avoidance in birds, we should be careful about comparing netted samples from sessions of different length. In addition, caution is needed in comparing data collected from frequent netting sessions. Running a net line once a year did not seem to have any effect on capture rates, and our data suggest that holding netting sessions as close as three months apart also did not affect capture rates in any obvious way. Net lines operated again before net-avoidance disappeared would produce data that are not comparable to the original samples. Further work is needed to determine the time interval required for net avoidance to be lost. Frequent operation of nets may provide better data on survival rates, local movements, or the production of offspring than annual or infrequent netting does, but it does so at the expense of simple comparisons of short-term capture rates to estimate population sizes.

Any netting protocol that is replicated as precisely as possible on an annual basis will provide annual comparisons of capture rates and insights into population levels. The important rules for the use of mist nets to monitor bird populations involve consistency of effort from year to year within a location, care when comparing different netting regimes within a habitat type, and extreme care when comparing netting results from different habitat types.

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