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INFLUENCE OF MIST-NETTING INTENSITY ON DEMOGRAPHIC INVESTIGATIONS OF AVIAN POPULATIONS

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Abstract. We evaluated capture rates of juvenile and adult passerines, comparing two different netting regimes on the same study plot at the Palomarin Field Station, Point Reyes National Seashore, California. One set of nets was run approximately 5× as often as the other during the breeding season. For four resident species breeding in the immediate vicinity of the nets, results were compared to direct measures of productivity and breeding density as determined from nest monitoring, color banding of nestlings, and known densities of adults from spot-mapping censuses of color-banded individuals. Nets run 6 days/week captured an average of 42% of the Song Sparrows (*Melospiza melodia*) breeding within 100 m of the nets, whereas nets run 1 day/week averaged 10%. Capture rates of adult Wrentits (*Chamaea fasciata*) did not differ significantly between netting regimes. Nets run with higher frequency detected direction of change in productivity in Song Sparrows accurately, whereas nets run with lower frequency did not. The reverse was true for Wrentits, though Wrentit fledglings were twice as likely to be caught in the higher frequency nets. Distance from nest to net also influenced juvenile capture probability. Results indicate the importance of using standardized netting protocol, and show that demographic indices based on mist netting should not be directly compared among species. Optimal netting frequency to attain study goals should be evaluated separately for each species. We caution investigators from drawing conclusions regarding songbird population size and demography based on mist-netting data alone.

Key Words: capture probability, *Chamaea fasciata*, demographic monitoring, *Melospiza melodia*, mist netting, passerine, population size, sampling effort, spot mapping, Song Sparrow, Wrentit.

Constant effort mist-netting has been widely used as a method for monitoring breeding populations of passerines (DeSante 1991b, Ralph et al. 1993), although few studies have attempted to validate the technique (but see du Feu and McMeeking 1991; Nur et al. 2000, *this volume*; S. Baillie et al. unpubl. report).

In this paper we compare capture rates in two arrays of mist nets operated with different protocols, established on a plot where spot-mapping and nest-monitoring of color-banded individuals of four species provided an independent measure of population parameters (Lebreton et al. 1992). The two netting regimes differed in both the frequency of netting and the number of nets employed. We examine whether more intensive mist-netting effort leads to more accurate estimates of population size, productivity, and survivorship.

The use of mist nets to estimate the size of a breeding population requires knowledge of the likelihood of capture of adults (Jenni et al. 1996, Sauer and Link *this volume*). Capture likelihood could vary with many factors, including bird species, distance of territory to nets, number of intervening territories, year, and netting intensity (Nur et al. *this volume*). Here we compare capture rates of adults of four species for individuals known to be breeding within 100 and 200 m of each set of nets in each year.

Another important variable for estimating population size is the breeding status of individuals that are caught. Nur and Geupel (1993b) found that varying percent of breeding season captures consisted of transient individuals that did not breed on the study area, and Nur et al. (*this volume*) found that most Wrentits (*Chamaea fasciata*) captured during the breeding season were not territory holders. Whether or not an individual is recaptured at least once within a season has been used as a means of separating transients from local breeders (Peach 1993, Chase et al. 1997, Gardali et al. 2000). We compare within season recapture rates of known breeders between the two netting regimes.

If mist nets recapture sufficient numbers of individuals from one year to the next, the data may be used in adult survivorship calculations (Clobert et al. 1987, Nur et al. 1999). Knowledge of adult survivorship is important to understanding population dynamics. We examine recapture rates of breeders known to have bred in 1992 that returned to breed on the study plot in 1993, for each netting regime and study species.

Finally, mist netting can be used to estimate productivity of breeding populations (DeSante and Geupel 1987, DeSante et al. 1993, Nur et al. 2000). Capture rates of hatch year (HY) individuals are often assumed to be an index of annual productivity. However, due to variation in natal dispersal strategies and catchability of juveniles produced from nests close to nets, the area being sampled is difficult or impossible to determine (Baker et al. 1995). We compare numbers of HY individuals caught with each netting regime to numbers known to have been produced on the study plot, and we determine the proportion of individuals produced locally and subsequently caught in each netting regime.

METHODS

Field work was conducted on a 36-ha plot at the Palomarin Field Station in the Point Reyes National Seashore in central coastal California. Densities of Song Sparrows (*Melospiza melodia*), Wrentits, Spotted Towhees (*Pipilo maculatus*), and Nuttall's White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) were determined by almost daily spot-map censusing throughout the breeding season (mid-March to July 31). These four species are obligate coastal scrub breeders at Palomarin; that is, 90% of their territories are located in scrub habitat as opposed to in adjacent forested habitats (Geupel and Ballard 2002; Point Reyes Bird Observatory [PRBO], unpubl. data). We located and monitored most nests of the study species, as described by Geupel and DeSante (1990) and Martin and Geupel (1993). In summary, we individually color-banded all nestlings surviving until their primaries broke sheath (usually a few days before fledging). Nestlings missing from the nest after banding were presumed fledged unless there was evidence of depredation. We recorded each nest's location, and its distance from the nearest mist net in each of the two net arrays. Further description of the study site and methods have been provided elsewhere (DeSante 1981, Geupel and DeSante 1990, Johnson and Geupel 1996, Nur et al. *this volume*).

Two arrays of 12-m mist nets were run with different frequency during the summers (May 1 to August 18) of 1992 and 1993 (Fig. 1). One array (the "daily nets") consisted of 20 nets placed relatively close together at 14 sites (6 were stacked 2 high), situated near the southeastern edge of the study area close to the border of coastal scrub and mixed evergreen forest (DeSante and Geupel 1987, Johnson and Geupel 1996). These nets were run at least 6 days/week during both breeding seasons. The other array (the "weekly nets") consisted of 10 nets at ten sites spaced at maximum distances for safe operation (usually 5–20 m), situated in the center of the study area in continuous coastal scrub habitat. These nets were operated once and occasionally twice in 10 days through both breeding seasons. Captured birds were aged by combination of skull pneumatization and plumage characteristics (Pyle et al. 1987). Unbanded birds were given new bands. Netting effort was consistent for the two years of the study. Nets were made by Avinet (Dryden, New York), and were 36- and 30-mm mesh.

We evaluated the differences between netting regimes using log-likelihood tests (G-test) or Fisher's exact tests, depending on sample size (we used the latter where sample size was small). Results were considered significant if $P < 0.05$. We used logistic regression to model the effect of distance from nest to nearest net on capture probability.

RESULTS

CAPTURE RATES OF ADULTS

The weekly nets captured 10% of adult Song Sparrows breeding within 100 m of nets, significantly fewer than the daily nets, which captured 42% (G-test, controlling for year, $G = 7.22$, $df = 1$, $P = 0.007$) (Table 1, Fig. 2). For Wrentits, the netting regimes did not differ significantly, with 42% of those breeding within 100 m captured in the daily nets and 36% in the weekly nets ($G = 0.15$, $df = 1$, $P = 0.69$). There was no significant change in the proportion of breeders captured when we extended the distance to include all breeders within 200 m. No Wrentit breeding more than 150 m from either set of nets was captured (Fig. 2).

WITHIN-SEASON RECAPTURE RATES OF ADULTS

Song Sparrows were more likely to be caught twice or more within a season in the daily nets than in the weekly nets (Table 2). In fact, no Song Sparrows at all were recaptured in the weekly nets (Fisher's exact test, pooling years, $P = 0.025$). The

TABLE 1. CAPTURE RATES FOR BREEDERS NESTING AT DIFFERENT DISTANCES FROM NETS, COMPARING DAILY TO WEEKLY NETS

			Breeders within 100 m			Breeders within 200 m		
				Captured			Captured	
Species	Netting intensity	Year	Number present	Number	Percent	Number present	Number	Percent
Song Sparrow	Daily	1992	13	5	39	22	6	27
		1993	9	4	44	23	4	17
	Weekly	1992	18	2	11	49	3	6
		1993	13	1	8	37	1	3
Wrentit	Daily	1992	18	6	33	32	6	19
		1993	12	6	50	30	7	23
	Weekly	1992	50	20	40	66	20	30
		1993	45	14	31	65	17	26

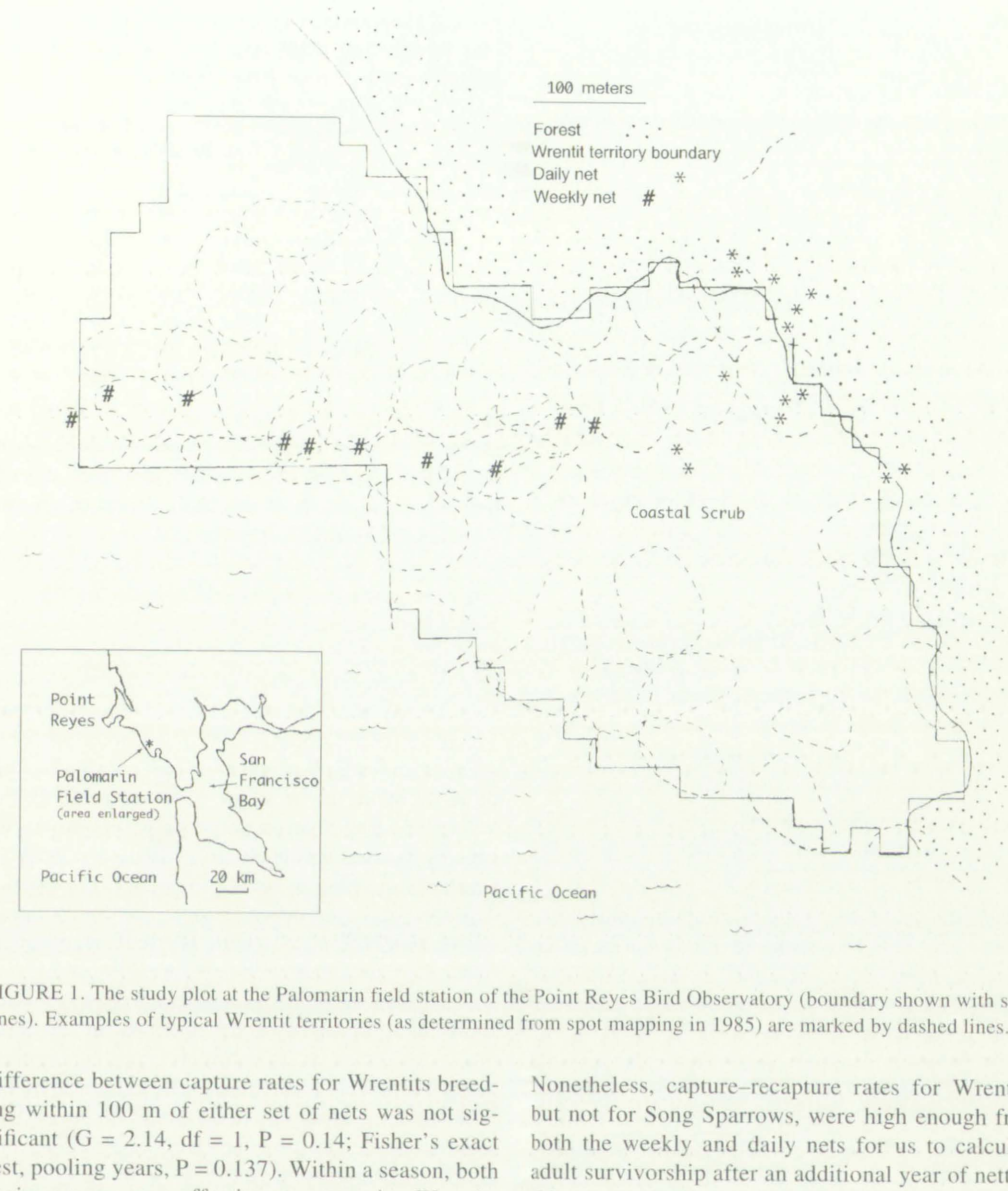

FIGURE 1. The study plot at the Palomarin field station of the Point Reyes Bird Observatory (boundary shown with solid lines). Examples of typical Wrentit territories (as determined from spot mapping in 1985) are marked by dashed lines.

difference between capture rates for Wrentits breeding within 100 m of either set of nets was not significant (G = 2.14, df = 1, P = 0.14; Fisher's exact test, pooling years, P = 0.137). Within a season, both regimes were more effective at recapturing Wrentits than Song Sparrows.

Between-year Recapture Rates of Adults

The daily nets caught more returning Song Sparrows than did the weekly nets, which recaught none (P = 0.044; Table 3). The daily nets caught fewer returning Wrentits than the weekly nets, but this difference was not significant (P = 0.668). Thus, for Song Sparrows, but not for Wrentits, between-year capture rates declined as netting frequency declined. Nonetheless, capture–recapture rates for Wrentits, but not for Song Sparrows, were high enough from both the weekly and daily nets for us to calculate adult survivorship after an additional year of netting (Nur et al. 1999).

Capture Rates of HY Birds Compared to Number Fledged

For Song Sparrows, the capture rates of hatching year birds in the daily nets reflected a decrease in productivity between 1992 and 1993, showing an 11% decrease in HY birds/100 net-h, and thus matched the change in productivity known to have taken place over the entire study plot (–13%), but underestimated the change for birds nesting within

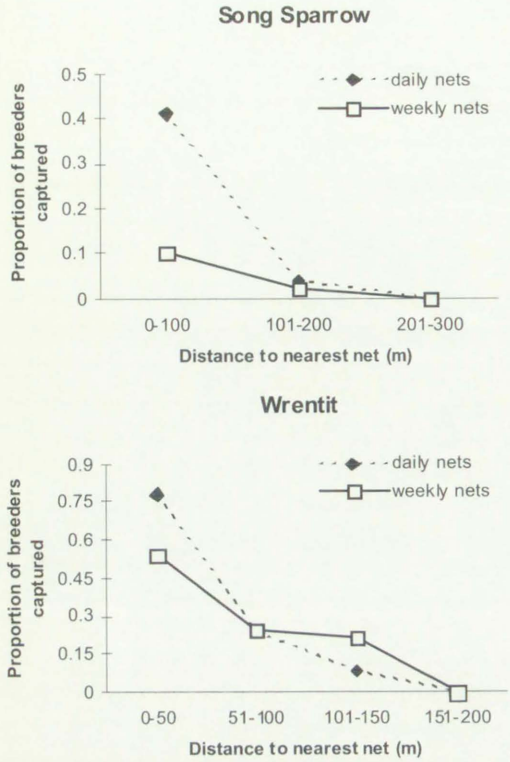

FIGURE 2. Recapture rates of adult breeding Song Sparrows and Wrentits related to distance from nest or territory center to nearest mist net.

200 m of nets (–28%; Table 4). Capture rates in the weekly nets failed to track the number of nestlings known to have fledged at either distance from nets. In fact, capture rates went up whereas the number fledged went down.

For Wrentits, capture rates in the daily nets did not reflect productivity changes at any distance, showing a 32% decrease in HY birds caught/100 net-h between 1992 and 1993 whereas known productivity went up 39% overall, and up 20% within 200 m of nets. The weekly nets performed better; capture rates went up 21% whereas total number fledged on the study plot went up 39%, though within 200 m they went up by 98%. Thus, whereas capture rates

TABLE 2. PROPORTION OF BREEDERS WITHIN 100 M OF THE NETS THAT WERE CAUGHT MORE THAN ONCE PER YEAR, 1992 AND 1993, COMPARING DAILY TO WEEKLY NETS

Species	Netting intensity	Year	Breeders	Captured > once	Percent
Song Sparrow	Daily	1992	13	2	15
		1993	9	2	22
	Weekly	1992	18	0	0
		1993	13	0	0
Wrentit	Daily	1992	18	3	17
		1993	12	4	33
	Weekly	1992	50	9	18
		1993	45	2	4

in the weekly nets reflected the general direction of productivity change on the study plot, they did not reflect the magnitude of this change, particularly for Wrentits breeding closer to the nets.

CAPTURE RATES OF FLEDGLINGS PRODUCED ON THE STUDY PLOT

Compared to weekly nets, the daily nets caught significantly more locally produced White-crowned Sparrows ($G = 8.65$, $P = 0.003$) and Song Sparrows ($G = 20.12$, $P < 0.001$), and more (but not significantly more) Spotted Towhees and Wrentits (Table 5). For White-crowned Sparrows and Song Sparrows, the ratio of captures was about 5 to 1 (daily vs. weekly), similar to the ratio in netting frequency. For Spotted Towhees, the ratio was 2.5 to 1, and for Wrentits, only 1.17 to 1 (i.e., 17% more HY birds were caught in the daily nets compared to the weekly nets).

The number of fledglings captured was biased somewhat by differing distributions of breeding birds in relation to the different netting regimes. That is, the weekly nets were located closer to higher bird densities, especially for Wrentits. Using logistic regression to control for the effect of proximity, the predicted capture probability of a Wrentit fledged 100 m from the daily nets (combining both years) was 0.35. For the weekly nets it was 0.17 (Table 6). This difference was significant ($P < 0.01$). Thus, the daily nets were approximately twice as likely as the

TABLE 3. RETURN RATES OF BANDED BREEDERS NESTING WITHIN 100 M OF THE NEAREST NET, COMPARING DAILY TO WEEKLY NETS

	Daily nets			Weekly nets		
Species	Number returning	Number captured	Percent captured	Number returning	Number captured	Percent captured
Song Sparrow	6	3	50	9	0	0
Wrentit	7	2	29	19	8	42

TABLE 4. DETECTING PRODUCTIVITY WITH DAILY AND WEEKLY NETTING

Species	Netting intensity	Year	HY birds captured	Number/ 100 net-h	Number fledged	
					In study plot	<200m
Song Sparrow	Daily	1992	77	0.75	76	21
		1993	66	0.67	66	13
Percent change				-11%	-13%	-28%
	Weekly	1992	16	1.40	76	47
		1993	13	1.67	66	43
Percent change				+19%	-13%	-9%
Wrentit	Daily	1992	77	0.75	86	24
		1993	51	0.52	120	29
Percent change				-32%	+39%	+20%
	Weekly	1992	41	3.60	86	45
		1993	34	4.35	120	89
Percent change				+21%	+39%	+98%

weekly nets to catch Wrentits fledged 100 m from the closest net. There were too few captures to carry out similar analyses for other species.

DISCUSSION

We demonstrated important differences in capture rates among species and netting strategies, which argue against drawing conclusions regarding adult survivorship, breeding population size, or productivity from mist-netting data alone. For one species, increased effort increased the proportion of the actual breeding population sampled, whereas for another this was not true. Increased effort increased proportion of the locally produced young captured in all four species evaluated, but not to the same extent. There was also substantial annual variation in these parameters, as N. Nur and G. Geupel (unpubl. report), using the same daily nets in the period 1980–1991, found that 71% (versus our 17 to 33%) of Wrentit breeders were caught more than once within a given year. Given this level of annual variation in capture probability, the importance of standardization of techniques among years and study sites cannot be overstated.

Numerous factors have been shown to affect capture rates, and these should be expected to vary among species. For example, differences in post-fledging movement may have been responsible for our low capture rates in weekly nets for locally fledged sparrows, but not Wrentits. Song Sparrows have higher dispersal distances and tend to be less sedentary than Wrentits (Nur and Geupel 1993b; PRBO, unpubl. data). It is likely that young Song Sparrows range farther from their natal territories and do this relatively abruptly, therefore spending less time in the vicinity of mist nets that intersect their territories (Nice 1937). Wrentit juveniles have been observed to stay with family groups near their natal territory an average of thirty days after fledging, and thus have a greater likelihood of being captured in mist nets, even if these nets are run only once or twice per week (Geupel and DeSante 1990). However, Song Sparrows are probably more similar to most North American passerines in dispersal strategy, flying ability, and escape frequency than Wrentits, which are known for their uniqueness in these areas (Geupel and Ballard 2002).

Other studies have also found different capture rates for different species. Du Feu and McMeeking

TABLE 5. PROPORTION OF LOCALLY PRODUCED FLEDGLINGS CAUGHT DURING 1992 AND 1993 COMBINED, COMPARING DAILY WITH WEEKLY NETS

Species	Number fledged	Daily nets		Weekly nets		P	Ratio (daily:weekly)
		Number captured	Percent captured	Number captured	Percent captured		
White-crowned Sparrow	76	12	15.8	2	3.9	0.003	6.0
Song Sparrow	142	34	23.9	8	5.6	<0.001	4.3
Spotted Towhee	39	5	12.8	2	5.1	ns	2.5
Wrentit	206	41	19.9	35	16.9	ns	1.2

TABLE 6. EFFECT OF DISTANCE TO NEAREST NET ON CAPTURE PROBABILITY OF LOCALLY PRODUCED WRENTITS, COMPARING DAILY WITH WEEKLY NETS

	Daily nets		Weekly nets	
Distance from nest to nearest net (m)	Capture probability estimate	95% confidence interval	Capture probability estimate	95% confidence interval
0	0.488	0.33–0.65	0.221	0.14–0.33
100	0.350	0.12–0.47	0.169	0.12–0.23

Notes: Results of logistic regression analysis. P < 0. 001 for model including distance and netting frequency.

(1991) found that a netting regime's captures of Eurasian Blackbirds (*Turdus merula*) was correlated with local productivity, but that with Song Thrushes (*Turdus philomelos*) this correlation did not exist. Also, Nur and Geupel (1993b), using 12 years of data from the same daily nets we used, found that HY Song Sparrow capture rates mirrored true local production whereas capture rates of HY Wrentits did not.

Net shyness is another factor that probably differs among species. The fact that breeding Wrentits were caught less frequently in the daily nets than in the weekly nets may indicate learned net avoidance. If nets are run infrequently, it may be harder for birds (Wrentits, at least) to remember net locations (see also Faaborg et al. *this volume*). However, analyses conducted by Nur et al. (*this volume*) using capture–recapture techniques indicated no evidence of learned net avoidance in Wrentits, as recapture probability in the daily nets was high (71%) 1981–1991, and all breeders with territories within 50 m of nets were recaptured each year. Also (in our study), Song Sparrows were not captured unless nets were run fairly often, and therefore net avoidance did not appear to be a factor.

Habitat may also affect capture rates differently between species (Ballard et al. 2003). In our study, the daily nets were situated closer to and in the forest adjacent to the coastal scrub study plot. All study species nested in much higher densities in coastal scrub habitat at Palomarin than in the forested habitat. Neither Wrentits nor Song Sparrows regularly held territories in the forested habitat, so forest nets were not expected to capture as many of either species. Still, it is possible that Song Sparrows were more likely than Wrentits to venture into the forest habitat, which could also be an explanation for why the daily nets captured more of this species. It would be instructive to evaluate the effect of habitat by repeating our study using a design that varies netting frequency within each habitat type.

We did not test for effects of net density on capture rates, but this factor should also be expected to affect species differently, depending on territory size and movement patterns.

Other authors have related differences in capture rates between species to the birds' different morphologies. Jenni et al. (1996) found that all study species showed similar ability to avoid nets, but that certain species were significantly less likely to escape from the net after being caught. They related this finding to skull width and overall size and mass of the bird. Wrentits and Song Sparrows are relatively similar in size and weight, but Wrentits have longer tarsi, which may be more easily tangled in nets (Wrentit: mean = 25.07 mm, N = 238, SE = 0.24; Song Sparrow: mean = 21.07 mm, N = 216, SE = 0.32).

Capture rates are probably influenced also by the placement of individual nets, but this is difficult to assess (Ballard et al. 2003, Berthold *this volume*). Micro-habitat differences, exposure to sun or wind, and density of net placements relative to number of bird territories are some of the variables that could have significant effects on the effectiveness of different nets for different species. We found that individual nets caught a high percentage of Song Sparrows, and other nets caught a high percentage of the Wrentits. In fact, nets side by side often had completely different capture rates (PRBO, unpubl. data). Jenni et al. (1996) found that exposure to wind and sunlight both affected capture rates, varying by habitat and bird-species composition. These considerations warrant further investigations of sampling effectiveness of various net locations.

For most species at our site, capture rates were not high enough for estimating relative abundance, adult survivorship, or relative productivity of our locally breeding birds. Increased effort generally improved our ability to determine these population parameters, even for species in which net shyness may have been an issue (see above), but never reached an adequate sample size for most other species breeding nearby. Possibly we could increase netting intensity without increasing frequency (e.g., use

100 nets, each run 1 day in 10, rather than running the same 10 nets daily). However, as the coverage area is increased, details of local populations might be lost. Our nets captured a surprisingly small segment of the local population (birds breeding within 200 m, at best), and sometimes only if nets were run with high frequency.

CONCLUSIONS

Our results and others discussed here indicate the importance of standardizing all aspects of mist netting, from using the same net locations to maintaining the same netting frequency throughout a study. However, regardless of netting frequency, different species were not equally represented in mist nets. To obtain sufficient sample size to attain study objectives, it may not be possible to use the optimal netting frequency for each species individually.

Validation of results provided by mist nets requires knowledge of true population size and productivity data, which are best provided by daily nest-searching and territory mapping of color-banded individuals. We recommend continued investigations of true breeding population sizes for disparate species and locales, which will greatly enhance the interpretability of data gathered by mist-netting alone.

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