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SURVEYING BIRDS WITH MIST NETS

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ABSTRACT.—The role of mist nets in the arsenal of field equipment of ornithologists has increased in recent years, especially in studies of banded birds and migration. Advantages of mist nets include reduced variability in data when compared to procedures which depend on extensive experience with sight and sound identification, or judgment in compilation and analysis of field data. Finally, mist nets can provide a wealth of data in a relatively short period.

Use of mist nets has increased in studies of between-season and among-year patterns in avian populations during the past decade. In addition, mist nets can be used to detect differential use of subtly different habitat types in small geographic areas (e.g., forest on dry exposed ridge vs. in moist, sheltered valley). Other uses of nets include studies of avian use of treefall gaps vs. nearby undisturbed forest. My research group recently initiated a study of reproductive success in forest islands in central Illinois. Mist nets operated after the nesting season, but before migration, yield data on the relative abundances of young and adult birds over a range of island sizes.

These and other recent uses of mist nets in avian studies illustrate the kinds of quantitative data amenable to statistical analysis which can be obtained through judicious use of mist nets. However, use of nets, like any counting procedure, must be approached with caution. Potential difficulties of interpretation of mist net results are discussed.

Mist nets were introduced into the United States after World War II. Without doubt, they have revolutionized the study of birds in their natural habitats, especially efforts requiring banding and monitoring of individuals and in collection of specimens for museums. However, their use as a counting procedure has not been great.

Although nets are not a panacea to solve all counting problems, their judicious use can provide considerable insights into dynamics of avian populations and communities. In the present paper I summarize advantages and disadvantages of mist nets in bird count work, and demonstrate inferences that can be developed from use of mist nets. In addition, I illustrate the potential for misuse of results from mist net studies.

ADVANTAGES AND DISADVANTAGES OF NETS

Like any count procedure, nets have both advantages and disadvantages. Important points to keep in mind in selection of a count procedure are objective of the study and type of data required to meet that objective. No single procedure is suitable for all habitats and research objectives.

The primary advantage of nets is that they do not require familiarity with songs and field marks of birds of an area. In addition, nets can be used to standardize sample size (or sample effort). Capture rates for a community or for individual species can be expressed in number of captures per net hour or net day. However, it is important to standardize sample times because capture rates vary with time of day (see below). Another standard sample involves use of a specific number of captures. Some researchers prefer to exclude all recaptures while others include both original and recaptures in a standard sample. I prefer the latter as a measure of bird activity, independent of individuals involved.

In addition, use of a standard time or number of individuals sampled avoids the problem of extrapolating abundance information to standard areas such as 100 acres (40 ha). This advantage is especially attractive in studies of patches of habitat which are small or vary significantly in size.

Like any survey procedure that involves handling of organisms, those organisms tend to avoid the nets after a few days (when most individuals have been captured). Capture rates become vanishingly small after the third day of net operation (when only permanent residents are present). During periods with considerable day-to-day turnover in individuals (e.g., migration periods), capture rates are less likely to decline so obviously; indeed, they may markedly increase as waves of migrants pass through an area.

In my experience a 100-capture sample is the best compromise between the number of captures and time, especially in view of the fact that capture rates decline throughout the period of netting. For a more detailed discussion of these and other related subjects, see Karr (1979, 1980).

Finally, with mist nets it is possible to accumulate quantitatively reliable information in a relatively short period. Repeatability of results of mist netting for several major population and

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community metrics is also an advantage (Karr 1980).

Reduction of observer-related biases and rapid accumulation of standard samples are major advantages. The latter is especially important in areas with high species richness or where many of the assumptions of more classical procedures (territoriality, monogamy, etc.) are not met.

However, like all procedures, netting is not without problems. The value of mist nets is minimized in inclement weather, especially during periods of rain and/or, in more open habitats, high winds. Other general problems are placement of nets in the field, and variability in tension and spacing of shelf strings when nets are erected. Finally, it is important to avoid inferences which are not supported by the data base provided by mist-netting; e.g., avoid reference to densities.

In some cases it seems clear that mist nets are useful, perhaps only to provide a mechanism to band many of the birds in a local population for studies of population dynamics and behavior. In other cases, mist nets are useful for provision of population and community data. However, great care should be used in the application of mist nets to counting problems.

FIELD METHODS

A wide variety of factors should be considered in establishment of field protocols involving use of mist nets in collection of ecological data. Perhaps the most significant net attribute to determine capture rates is mesh size. Generally, larger meshes capture larger birds (Heimerdinger and Leberman 1966). I find 36 mm mesh nets to be the most effective for the widest range of birds found in most terrestrial habitats. Birds less than 5 to 8 g are not efficiently captured, nor are birds above about 100 g (Karr 1979). In addition to standardizing mesh size, it is essential that net length and height (thus net area) be standardized for production of the most valuable comparative data.

Habitat type also is an important factor affecting efficiency of mist nets and thus capture rates. In grassland, for example, nets tend to be more visible than in forest. In second-growth areas a greater proportion of the fauna (species and individuals) is likely to be captured in ground level nets. Thus, it is unwise to compare capture rates between forest and second growth as if they are equally good indexes of the relative densities in the two habitats (Karr 1979).

Deployment of nets also can play a major role in the success of a data collection effort. Generally, I place nets in a loop covering about 2 ha. Others use a line of nets placed end to end (Terborgh and Faaborg 1973, Wright 1979). The major deployment problem to be avoided is concentration of nets in too small an area. Capture rates are depressed under such conditions.

One major disadvantage of mist nets is the difficulty and expense of using them in canopy and subcanopy levels. A number of systems have been developed to operate nets in the canopy and subcanopy (Greenlaw and Swinebroad 1967, Humprey et al. 1968, Whitaker 1972, Sappington and Jackson 1973, Karr 1979). They vary with respect to net mobility, cost, and ease of use.

Time of day also is an important determinant of net capture rates. Bird activity varies throughout the day and nets change in their visibility with shifts in sun angle. Generally bird activity peaks in morning and in late afternoon or early evening. Precise time of the peaks varies with day length, length of twilight and, in some areas, evening and morning temperatures. Habitat type and season may also be important variables (see below).

Frequency with which nets are checked must also vary with several factors. I find that nets left for up to 90 minutes are not a problem in forests or other habitats where birds are not exposed to direct sunlight. In more open areas, nets must be checked as frequently as every 15 to 30 minutes to avoid major mortality. Another disadvantage of long intervals between net runs is that birds get increasingly tangled and difficult to extract with increase in time between runs. For most of my research, I check nets every 60 minutes. Careful, regular checking of nets typically keeps mortality below one percent.

Like any other procedure, an important factor in use of mist nets is regular and reliable measurement and recording of data. Recording of time of day that nets are opened and closed to the nearest 5 minutes is essential to allow precise determination of the duration (in hours or days) of sampling. Additionally, records of age, sex, moult, and other natural history information can be valuable in interpreting many aspects of population and community characteristics. Since vegetation affects avian use of an area, careful measurement of vegetation attributes must be made.

DATA ANALYSIS AND INTERPRETATION

In this section I select a few examples of the kinds of biological insights that can be derived from studies employing mist nets as a census technique. These are meant to be illustrative examples only.

No counting procedures can be expected to provide absolute density information without total disturbance of the organisms under study. Capture rates from mist net studies are simply relative population estimates; their use should be tempered with that realization in mind. Relative density data provided by mist-net sampling can be used to evaluate changes in populations in both space and time.

Temporal Pattern

During the past two years I have collected 100-bird mist net samples from each of four forest study plots in central Panama. Each site has been sampled four times—twice in wet and twice in dry seasons. The four study plots are located in an area of about 2 km^2 on the Pipeline Road, Parque Nacional La Soberania. One area, Limbo Hunt Club, has been described in more

TABLE 1
MINIMUM AND MEAN HUMIDITIES FOR DRY AND WET SEASONS IN THE UNDERGROWTH OF THREE FOREST STUDY PLOTS IN CENTRAL PANAMA. MEANS DETERMINED FROM HOURLY OBSERVATIONS ON ONE DAY AT SEVEN SITES IN EACH STUDY PLOT

	Minimum		Mean (*n*)	
Study plot	Dry	Wet	Dry	Wet
Ridgetop	50	94	67 (72)	98 (80)
Limbo	62	95	74 (28)[a]	97 (80)
Valley	79	98	81 (54)	100 (88)

[a] Observations every three hours.

detail elsewhere (Karr 1971, 1976b). Local rainfall averages about 2600 mm per year with a rainy season that begins in April and extends, in most years, into December. The late December to early April period is typically dry, with less than 100 mm of rain per month. Temperatures average 27°C throughout the year. Macroclimate does not vary among areas. However, because of topographic differences among the areas, microclimate of the undergrowth does vary (Table 1). Only three areas will be described here. At one extreme is a flat elevated area with no stream within the study plot. Temperatures are higher and relative humidities lower (as low as 50%) at midday during the dry season at this site (Ridgetop). An intermediate area (Limbo Hunt Club) is a mixture of an upland and stream-edge environment with a maximum topographic relief of about 8 meters. Dry-season temperature and humidity profiles in the undergrowth are intermediate between those at Ridgetop and the next study plot (Valley). The Valley plot is adjacent to the Limbo Hunt Club plot but is a deep stream valley with a narrow basin and high, steep slopes. Dry-season temperature and humidity profiles at midday in the undergrowth are different from the two earlier sites. Humidities rarely go below 60% at any location. Daily rains during the wet season modify the microclimate

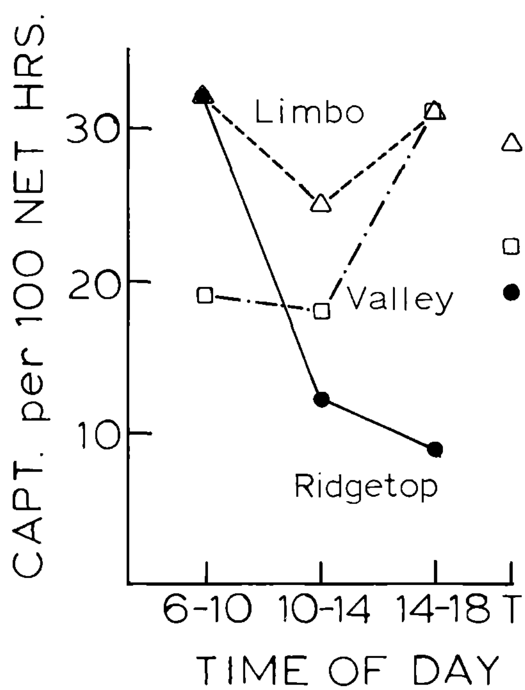

FIGURE 1. Capture rates in birds per 100 net hours for first three days of netting on three study areas in Central Panama, dry season 1979. *T* = average per day.

of the sites to the extent that temperature and humidity profiles are nearly identical. A fourth site not described here, intermediate between Ridgetop and Limbo, is somewhat more similar to Limbo. When bird capture data for each season are combined from all four study sites, capture rates are strikingly consistent within seasons and between years (Table 2). However, they are lower in wet season than in dry season.

TABLE 2
SUMMARY OF MIST NET RESULTS (COMPOSITE OF 4 SAMPLE PLOTS) IN LOWLAND WET FOREST IN CENTRAL PANAMA

	1979		1980	
	Dry season	Wet season	Dry season	Wet season
Number of				
Captures	415	364	416	370
Net hours	1809	2102	1851	2096
Captures per 100 net hours	22.9	17.3	22.5	16.7

TABLE 3
DRY-SEASON CAPTURE RATES AND SPECIES RICHNESS FOR SEVERAL LOWLAND WET FOREST SITES IN CENTRAL PANAMA. NOTE THAT 1979 WAS A RELATIVELY DRY DRY SEASON WHILE RAINFALL DURING 1980 DRY SEASON WAS ABOVE NORMAL

	Study site		
Year	Ridgetop	Limbo	Valley
Capture rates (capt./100 net hours)			
1979	19.1	29.3	21.9
1980	26.7	30.5	15.5
Species richness (spp./100 captures)			
1979	32	38	33
1980	36	30	33

TABLE 4
DRY SEASON CAPTURE RATES FOR BIRDS IN UNDERGROWTH MIST NETS IN "UPLAND" AND "LOWLAND" LOCATIONS AT LIMBO HUNT CLUB, PARQUE NACIONAL LA SOBERANIA, PANAMA

			Number of			Captures per 100 net hours
Year	Season	Region	Net hours	Captures	χ^2	
1979	Dry	Lowland	149	59	9.18[a]	39.6
		Upland	209	46		22.0
	Wet	Lowland	247	50	0.04	20.2
		Upland	256	50		19.5
1980	Dry	Lowland	161	59	3.79	36.6
		Upland	187	47		25.1
	Wet	Lowland	244	49	1.47	20.1
		Upland	208	53		25.5

[a] Sign at $P < 0.05$ at $\chi^2 = 3.84$.

TABLE 5
NUMBER OF WET AND DRY SEASON CAPTURES OF *PIPROMORPHA OLEAGINEA* AT 5 STUDY AREAS IN CENTRAL PANAMA—1979–80

	Number of captures		
	Dry season	Wet season	Probability level[a]
Study plot			
Limbo Hunt Club	20	7	0.0006
Ridgetop	4	16	0.0018
Roadside	17	9	0.0019
Valley	28	4	0.0001
Barro Colorado Island (1980 only)	11	0	0.0017

[a] Based on binomial probability test with expected values (p and q) based on number of net hours at each site in wet and dry seasons.

Diurnal variation in capture rates is also obvious (Fig. 1). Thus, mist nets can be used to examine year-to-year, seasonal, and diurnal variation in avian activity.

SPATIAL PATTERN

Diurnal variation in capture rates depicted in Figure 1 clearly shows that bird use varies among microhabitats. Bird activity is highest in early morning at the driest site (Ridgetop). The wettest site (Valley) shows essentially the reverse pattern. The area is avoided in early morning due to steep slopes and increased energy demands of considerable vertical movement by foraging birds. However, as the day progresses, birds may be attracted to this area because insects remain active in the sheltered, more humid environment. There is also some evidence that permanent water supply attracts birds to the valley during late afternoon. Several species that are rarely seen below canopy levels have been captured during dry season at the Valley site as they descended to drink and bathe from the stream. The intermediate site (Limbo) illustrates an intermediate pattern.

Although regional activity of birds is consistent for each season between years (Table 2), capture rates vary independently among the four study plots. Patterns of variation are clearly explicable in light of microhabitat patterns. For example, note that bird activity was higher at the Ridgetop site in the wetter 1980 dry season than in the drier 1979 dry season (Table 3). The reverse was true in the wetter Valley site. The intermediate Limbo site had essentially the same capture rates in the two years.

But even this consistent intermediate pattern masks habitat selection dynamics within the study plot. The Limbo Hunt Club plot consists of a flat area along a stream, a small rise of about 8 m, and a flat upland. Capture rates vary between upland and lowland areas between years. Capture rates were significantly higher in lowland than in upland during the especially dry dry season of 1979 (Table 4). Only three months later, during wet season, capture rates were identical (Table 4). During the following relatively wet dry season of 1980, there were no differences in the capture rates between the two regions of the 2 ha study plot. Again, recall that these capture rates are for areas only 8 m apart in elevation. Overall, birds tend to shift their spatial use of habitat in response to temporal variation in microclimatic conditions.

Species richness of the samples also varies among the three sites (Table 3). At Limbo Hunt Club, number of species in 100-bird samples (range 30–38) is inversely correlated with March (sample month) rainfall (Karr 1980). At Ridgetop, species richness (like capture rates) was higher in the wetter year while the reverse was true at Limbo. The Valley samples contained the same number of species in both years.

In addition to general community metrics, it is possible to discern variation in abundance of species with mist-net sampling. For example, Karr et al. (in press) found that 10 species were captured at significantly ($P < 0.05$) different rates in samples collected nearly a decade apart. In some cases, shifts were due to habitat changes (especially increased area of treefall gaps) while in others seasonal movements of temperate zone migrants were important.

Variation between seasons in capture rates of birds also has been documented (Karr et al. in press). Insectivore-nectarivores were more common during the dry season, a period of peak

TABLE 6
COMPARISON OF OBSERVED AND PREDICTED NUMBERS OF RESIDENT SPECIES IN FOREST ISLANDS IN EAST-CENTRAL ILLINOIS (SUMMER 1979; BLAKE AND KARR, UNPUB. DATA).

		Point census		Mist net samples	
Study area	Size (ha)	Ob-served	Pre-dicted	Ob-served	Pre-dicted
Rittenhouse Woods	1.8	8	9.6	7	7.9
Brownfield Woods	24.3	20	20.2	10	18.4
Hart Woods	28.0	31	31.3	21	28.2
Funks Grove B	65.0	26	28.2	17	21.4
Allerton Park	600.0	34	34.1	29	38.2

flowering activity, while species that follow army ants were more common in the wet season.

The frugivorous Ochre-bellied Flycatcher (*Pipramorpha oleaginea*) showed distinct seasonal changes in capture rates in the past two years. On four of five study plots the species is captured at higher rates in dry than in wet season (Table 5). The only exception is Ridgetop, which apparently is not suitable for high densities of many species during dry season (see above).

In another study in central Panama, Schemske and Brokaw (in press) tested the hypothesis that bird communities of treefall gaps in tropical forest differ from those of adjacent intact forest. They found that species richness was greater in gaps but capture rates were nearly identical in gaps and intact forest. Of 31 species with sample sizes adequate for analysis, 5 were caught more regularly in gaps (3 species) or in intact forest (2 species).

An ongoing study of forest islands as habitat for birds is providing additional examples of the use of mist nets in studying birds (Blake and Karr, unpubl. data). When the number of species observed in a forest tract is plotted against number of 15 minute observation periods (or number of mist net captures), an asymptote is approached. To achieve some degree of statistical confidence in the estimated number of species in a particular forest tract, these values can be fitted to an equation for a hyberbola:

$$\frac{1}{S} = K\left(\frac{1}{T}\right) + \frac{1}{S_{\max}}$$

where S = number of species observed (captured)
T = number of 20-minute observation periods (or number of species captured)
and $S_{\max}$ = the predicted maximum number of species present.

This equation is equivalent to the Lineweaver-Burk equation, a transformation of the Michaelis-Menten equation, the rate equation for one-substrate, enzyme-catalyzed reactions (Lehninger 1975). The predicted maximum should be equal to or greater than the number actually observed. Deviation from the predicted number could be due to sampling error (not all species were seen or captured) or to an ecological deficiency of the forest tract, such that the predicted maximum will not actually be achieved.

Number of species predicted from netting data was significantly correlated with both number of species predicted from census data and number of species actually observed (Table 6) during census periods (r = 0.940 and 0.956, respectively; $P < 0.01$ in both cases). Predicted number of species derived from netting data is based on lower observed (captured) totals than is the predicted number derived from census periods. The advantage of this model is that it may allow predictions of species richness with small samples, or conversely, an indication of the minimum number of census periods needed to achieve a given level of precision.

An additional component of the island study is use of mist nets after the fledging period to try to determine adult-juvenile ratios before dispersal. It is our hope that these can be used as a measure of reproductive success. If such success varies within and between species over a range of island sizes, it may be possible to more clearly understand effects of island size on small population survival.

In this section I have tried to provide examples of the uses of mist nets in the study of avian ecology. Other population and community metrics have been studied by other researchers. These include guild signatures (Karr 1980), turnover dynamics (Terborgh and Faaborg 1973, Karr in press), migrant abundances (Karr 1976a, 1979, Terborgh and Faaborg 1980a), community saturation (Terborgh and Faaborg 1980b), and habitat selection (Willson and Moriarty 1976). Clearly, use of nets as a procedure for counting birds is limited only by the originality of future generations of ornithologists.

FINAL COMMENTS

Lest the reader conclude that mist nets provide a foolproof way to count birds and study population and community dynamics, I hasten to add a few words of caution. It is essential that researchers recognize deficiencies and biases of mist nets as a sampling tool.

It is not, in my opinion, appropriate to use mist nets (or any other procedure) for "fishing expeditions." Researchers should have precise study objectives (hypotheses) in mind and select sampling protocols to yield highest quality data for those objectives.

The most important caution is that mist net capture rates do not constitute a measure of absolute density. Thus, scientists should avoid discussing them as if they were. As an example, I earlier concluded that the Ochre-bellied Flycatcher is less regularly captured in wet than dry season on four of my study plots. Several possible explanations of that pattern could be advanced. Perhaps the abundance of the species does indeed shift. If so, where do the birds go? Perhaps the birds are less active in wet season (due to nesting, more uniformly dispersed food supplies, or water) and thus are captured less frequently. It is not possible at this time to clearly distinguish among these and other alternatives. The fact that the dry site is out of phase with the others suggests that it is indeed a shift in spatial use of habitat. This example reinforces the principle that there is no substitute for knowledge of the organisms under study. Mist nets can be used to provide reliable quantitative data but interpretation of results requires caution. They can be even more valuable if backed up with other quantitative and qualitative observations about the birds under study.

Readers should note that rate of capture of birds in ground level mist nets will be in proportion to the percent of activity by species in the sample space (within 3 m of the ground). Comparisons of abundances of species with different activity levels in the ground layer obviously should be avoided. Similarly, two species should not be directly compared if their activities (flight distance, flight frequencies, etc.) are not similar.

Mist nets combined with color banding of birds also allow more precise determination of movement patterns and the extent of overlap of territories. Red-capped Manakins (*Pipra mentalis*), for example, are typically the most regularly captured species in the undergrowth of Central American lowland forest. Capture rates of the species vary significantly from month to month (Karr et al. in press) with extensive almost day-to-day turnover in individuals (Karr 1971, unpubl. data). Careful examination of capture-recapture rates provides considerable insights into the populations dynamics and movements of this species relative to others. But they must be interpreted carefully.

In summary, mist nets are valuable tools for bird counting. They should be used more extensively, but with precision, if the greatest possible yield of scientific conclusions is to be forthcoming. They can be especially useful when familiarity with birds in the field is minimal, when many shy and/or secretive species are present, and in areas (or seasons) where birds rarely sing. Further, they are valuable where assumptions of other procedures (territorial systems, monogamy) are not met.

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