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MISUSE OF DATA FROM MIST-NET CAPTURES TO ASSESS RELATIVE ABUNDANCE IN BIRD POPULATIONS

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ABSTRACT.—Capture data from mist nets are used frequently to quantify the relative abundance of birds. In spite of obvious confounding variables, most of which have been mentioned previously in the literature, relative capture of birds typically is equated directly to relative abundance. Through modeling, we quantify the potential magnitude of the effect of those variables among species and between age/sex categories of the same species. We demonstrate that differences in proportional use of vertical-height categories, including differences below the resolving power of visual estimates, can produce substantial differences in the capture rates of birds with identical abundance. To simulate capture on the horizontal plane, we designed a computer program that models how frequently birds strike nets with respect to home-range size and overlap, number of flights, and mean flight distance. The quantitative results of these simulations show that differences in spacing system, flight distance, and flight frequency have strong effects on capture rates. We also list additional problems with interpretation of differences in capture data. We think that these influences on capture data combine to preclude quantitative comparisons of relative abundance of birds, either among species or within species in different habitats, by use of mist-net capture data under most current research protocols. Although our analyses refer directly only to birds and mist nets, the outcomes of the analyses are relevant to any method that estimates relative abundance from captures of mobile organisms by stationary traps during brief sampling periods. *Received 3 July 1995, accepted 3 October 1995.*

MIST NETS ARE an effective tool for capturing birds, typically those found primarily within 2 to 3 m of the ground. For more than two decades, analysis of capture rates of birds by mist nets has played a prominent role in studies of avian ecology. Many studies have compared relative abundance in mist-net samples of species, sexes, or age categories to make inferences concerning their relative abundance in different regions, communities, habitats, guilds, seasons, or years. Interpretations based on these data are now presented in at least one textbook (Ricklefs 1990:740).

The most enticing advantage of mist nets for assessing relative abundance is that their use avoids the obvious biases of censusing techniques that rely on the visual and auditory ability of human observers (Karr 1981, 1990). The number of birds captured in nets of standard length over standard time periods thus, is, often considered to be a superior measure of relative abundance, particularly in permitting comparisons among studies that involve different investigators (e.g. Karr et al. 1990). Mist-net sampling also allows quantitative comparisons of secretive or rarely vocal species that are ineffectively sampled by visual-auditory censuses, and of nonterritorial species that are inappropriate for some census techniques (Karr 1981).

Disadvantages of mist nets for comparing relative abundance of birds have been mentioned frequently. Obviously, ground-level mist nets sample only that portion of the avifauna that moves within 2 to 3 m of the ground. MacArthur and MacArthur's (1974) seminal paper on quantitative use of mist-net capture data for comparing bird populations noted that: (1) because birds captured in nets learn to avoid those nets ("net avoidance"), and because species vary in learning ability, capture data cannot be used for capture-recapture analyses; (2) even within a species, the degree to which individuals are territorial versus wandering complicates any comparisons of capture rates because of the differing probabilities of recapture. MacArthur and MacArthur (1974) provided a method for compensating for the difference in probability of capture for birds whose spacing systems differ. Karr (1981, 1990) reviewed the advantages of mist nets and pointed out several additional factors that influence capture other than relative abundance of the birds sampled: (1) weather; (2) differences in net location; (3) variability in net tension; (4) habitat structure; (5) differences in vertical movements and the proportion of time spent within the 2-m sampling zone; (6) differences in flight distance; and (7) differences in flight frequency. More generally, Karr (1981) noted that "interpretation of results requires caution," "great care should be used in the application of mist nets to counting problems," and, in reference to direct use of capture rates as a measure of relative abundance, "there is no substitute for knowledge of the organisms under study." Thus, in a paper devoted to discussing mist nets as a tool for surveying bird populations, Karr clearly outlined the problems with interpretation of capture rates as reflecting only relative abundance.

Unfortunately, most papers that use mist-net data to infer relative abundances do not take into account the factors mentioned by MacArthur and MacArthur (1974) and Karr (1981). Interpretations of relative numbers of birds captured typically are given as if reflecting relative abundance alone. We have found only two papers (Terborgh and Faaborg 1973, Waide 1980) that inferred relative abundance from capture data that also attempted to control directly for influences on capture rate other than relative abundance (and in these two cases, only for differences in spacing systems).

The crucial conceptual and methodological point in using capture data is the assumption that differences in numbers of birds captured are determined primarily by relative abundance and that other influences have no significant effect. For this to be true, the spatial-movement patterns in both the vertical and horizontal planes must not differ significantly among the birds being compared. In other words, unless the proportion of flights at mist-net level, the spacing system, the average flight distance, the number of flights per sample period, the degree of net avoidance, and the "catchability" of the birds compared are statistically indistinguishable, the number of birds captured in mist nets during a sampling period is determined by much more than relative abundance. Direct use of capture data from mist nets to make precise comparisons of relative abundance implies an assumption that the birds compared all move around like identical molecules in a vacuum. However, the few data that exist on movement patterns (see Discussion) show substantial differences even within the same age/sex category at different sites or during different seasons.

We suspect that lack of quantitative documentation of the potential magnitude of these influences on mist-net capture in part explains why many authors fail to discuss the cautionary points presented by MacArthur and MacArthur (1974) and Karr (1981). For this reason, we attempt to quantify the potential magnitude of these influences. Our purpose is to discuss the shortcomings of the direct use of mist-net data in estimating relative abundances, not to compare the use of mist-net surveys to auditory-visual censusing techniques. Problems with auditory-visual estimates have been analyzed directly and reviewed thoroughly (e.g. Verner 1985, Verner and Milne 1990); problems with mist-net data have not. Although our analyses and simulations focus on mist nets and birds, the results are relevant to any technique that estimates relative abundance of mobile organisms by capture rates in stationary traps.

We conclude the discussion by suggesting a partial solution to some problems that confront the use of mist-net data in estimating relative abundances. We also point out, however, that, even incorporating that partial solution, mist-net capture data cannot be used to estimate accurately the relative abundances without incorporating corrections based on detailed knowledge of the ecology and behavior of the birds involved.

METHODS

Insufficient data exist on vertical-activity patterns in birds to predict realistically the distribution of activities by a single mathematical model; different species (and even individuals of one species in different forest conditions) probably exhibit different activity distributions. We calculated patterns of vertical space use on the assumption that vertical activity is normally distributed. We do not claim that such distributions are normal in reality, but only that this is a useful first approximation. The normal distribution is simply an easily calculated distribution, and we use it to demonstrate the kinds of effects on mist-net capture rates that probably will be evident with any uneven vertical-height distribution.

In our calculations, the part of the activity distribution that occurred (impossibly) "below ground level" was assumed to represent birds caught by the net. This assumption, as opposed to considering the below-ground tail of the distribution to represent birds that walk under the net, biases the results in favor of capture. This is conservative with respect to the effects discussed in this paper.

Mist-net capture data on the horizontal plane were obtained from computer simulations (program written in Think Pascal and performed on a Macintosh IIX). Territory size, net length, number of nets, distance between nets, flight number, flight distance ($\bar{x}$ and SD), flight angle ($\bar{x}$ and SD), and net-avoidance distance, all described below, were defined by the user. The program first constructed a 10 × 10 grid to simulate 100 equal-area territories. For each simulation a new line of nets was superimposed on this grid and bird-movement simulations were conducted for all birds whose territories intersected the net line (i.e. those possible to catch). The number of simulations was set by the user (see below).

Net placement was accomplished as follows: A point within the 10 × 10 grid was chosen at random for one end of a simulated line of nets. This and all other random values herein were calculated using the standard Macintosh toolbox random-number generator (by Apple Computer 1985). A direction was then randomly chosen (to the nearest degree), and the other end of the net line was placed at the appropriate distance in that direction.

Once the territories and mist nets were set, a bird was "released" in each territory crossed by the net line. All other territories were ignored because there was no chance of catching birds in them. Each bird was released by randomly choosing a starting point inside the territory. The bird then moved a distance calculated from a normal distribution determined by the predefined mean and standard deviation of the flight distance. The first flight was made in a completely random direction; all subsequent flights started at the endpoint of the previous flight and were calculated from a circular-normal distribution with the mean set as the same direction as the last flight and a predefined standard deviation. Distances for all flights were governed by the same normal distribution as the first flight. Bird movements were constrained to remain within the territory; if the endpoint of a calculated flight fell outside the territory, then a new random angle was chosen until the resulting endpoint fell within the territory. The procedure then returned to varying the flight angle according to the circular-normal approach until the next time the bird contacted the edge of its territory. Choice of a large angular standard deviation resulted in relatively random movements; an angular standard deviation of zero resulted in movement in straight lines except when a territory margin was reached. The number of flights could be varied by the user. In most simulations, 100% of the individuals were captured by at least 3,000 flights. Although data for flight frequency are available for a few bird species while foraging, we cannot find such data for movements throughout the day, including quiescent periods. We suspect that most bird species average fewer than one flight per minute for an entire 12-h day (=720 flights/day).

Each bird moved within its territory until the predefined maximum number of flights was reached or until the bird contacted one of the nets. Contact occurred when a calculated flight path intersected a net. A predefined net-avoidance distance also was programmed into the simulation such that no flight beginning less than the net-avoidance distance from the net would intersect that net. This simulated the bird seeing and, therefore, avoiding the net if it landed within the net-avoidance distance.

The number of iterations for this entire process, including net-placement and bird-movement parameters, was set by the user. The program recorded the proportion of birds in all 100 territories that were captured, the proportion of birds captured of those whose territories were intersected by nets (i.e. those possible to catch), and the number of territories crossed by nets for each iteration. Means and standard deviations were then calculated for each set of parameters.

Nonterritorial birds were simulated also. We modeled two types of nonterritorial spacing systems. In one (Type 1), we used home ranges smaller than, and randomly placed in, the hypothetical study area; thus, the degree of overlap was determined by chance. This spacing system might approximate that of, for example, the Wedge-billed Woodcreeper (*Glyphorynchus spirurus*; Gradwohl and Greenberg 1980) or the Northern Parula (*Parula americana*) in winter (Staicer 1992). For all home ranges that intersected the net line, bird flights were simulated as described above. In the other nonterritorial spacing system (Type 2), we set home range size as equal to the entire hypothetical study area, thereby simulating total overlap in home range boundaries. This might be equivalent to the spacing system of wandering individuals that do not hold territories within a matrix of territorial individuals. All parameters other than territory placement were identical to those in the territorial simulations described above.

In all simulations, we used the following parameters: net length, 12 m; net height, 2 m; net number, 15; and internet distance, 10 m (values typical of many studies). We used territory sizes of 1, 2, 5, 10, and 25 ha. Terborgh et al.'s (1990) estimates of territory sizes for tropical forest birds, often the targets of mist-net studies, show that most species frequently netted in the undergrowth have territories in the 5 to 15 ha range, with no species having a territory smaller than 3 ha. We included smaller territory sizes, however, to encompass estimates of territory sizes from other regions and habitats (e.g. Rappole and Warner 1980, G. Rosenberg 1990). In the absence of published data on net-avoidance distance or inter- and intraspecific differences in this distance, we used a distance of 1 m in all simulations. We strongly suspect that this avoidance distance is conservative because many birds probably detect the presence of a net from farther than 1 m, depending on vegetation density and structure. In all simulations, the bird population is stable, with no immigration or emigration. In all simulations presented, an individual could be "captured" only once. This is equivalent to studies that mark individual birds and do not count recaptures. We emphasize, however, that many published studies that compare

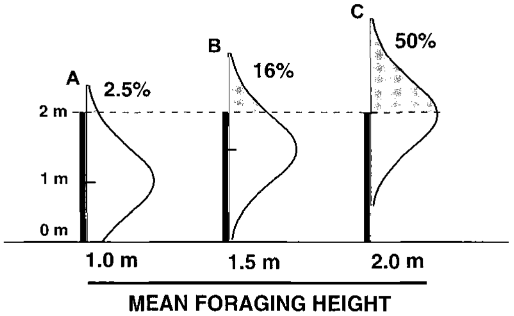

Fig. 1. Effect of mean activity height on frequency of mist-net captures. Mean activity height is (A) 1.0 m, (B) 1.5 m, and (C) 2.0 m. SD of activity height is 0.5 m, and mist-net height is 2 m. That portion of curve "below" 0 m is included in "captured" portion of distribution (see Methods).

relative abundance either do not mark birds or count known recaptures in their sample, thereby magnifying problems in interpreting their results as reflecting only relative abundance. We encourage all those involved in such studies to mark individual birds and to exclude recaptures from calculations.

Our simulations encompassed a broad range of mean flight distances and flight frequencies that presumably bracket actual values for most land birds. For the standard deviation of flight distance, we arbitrarily used one-half of the mean flight distance. Flight-distance SD was chosen to be proportional to distance because it seemed reasonable that a bird with a larger mean would have a larger SD, and one-half seemed a reasonable proportion (e.g. using our assumption of a normal distribution, 95% of the flights with a mean of 2 m would fall between 0 and 4 m, and 95% of those with a mean of 10 m would fall between 0 and 20 m). For the SD of flight angle, we chose 10°; this makes all flights roughly the same direction, but not in a straight line.

As in almost all simulations, some parameters are unrealistic to varying degrees. Our use of square territories is clearly simplistic; whether this shape biases the outcome of our simulations will be examined in subsequent analyses. Movement patterns within a territory were randomized rather than directed toward defense of a perimeter or some other nonrandom movement pattern. In all simulations, only one bird occupied each territory or home range, clearly an unrealistic feature, at least for the breeding season. We simplified the simulations by using only one bird in part because we were uncertain how to incorporate the potential effects of pair bonding on captures. In our experience, when one member of a pair is captured, the other often flies around its struggling mate until it too is captured; in other cases, however, the other member clearly avoids the net after seeing its captured mate. Because our comparisons are based largely on percent individuals captured rather than absolute numbers, our use of only one bird per territory would not bias the results. Similarly, we did not incorporate movements of territorial birds outside of their territory boundaries, although such movements are well known. Because such movements would increase the probability of capture of an individual bird, incorporation of them into the simulations would decrease the time needed to capture all birds but would not effect the overall patterns observed.

Our use of a 100% capture rate for birds striking nets clearly favors quick completion of the simulations. Also, the simulations presented do not incorporate any "learning" factor; in other words, if a bird lands within the 1 m net-avoidance distance, the probability of return to that net is not lowered. This also favors rapid completion of simulations. In both cases, the effect on our results is that the percent of individuals captured for a given number of flights is unrealistically high, a bias that conservatively diminishes the importance of the variable modeled in affecting capture rates. For example, Karr (1981) noted that net avoidance often results in "vanishingly small" number of birds captured after the third day of operation.

In all figures, each point refers to the mean value of 100 simulations unless stated otherwise. Similarly, the percent individuals captured refers only to those whose territories were crossed by the randomly placed net line unless stated otherwise. The percent captured over the entire 100-territory sample area would be much smaller because most territories would be unaffected by the nets.

RESULTS

Vertical movements.—Birds with different vertical-activity patterns are expected to have different capture rates in mist nets. At the extreme, birds that spend their time in the canopy (say at 20–30 m) will rarely be caught in a 2-m-high mist net, whereas birds that spend all of their time within 2 m of the ground are likely to be caught frequently. However, even slight changes in activity height can have a notable effect even on understory species.

If, in a hypothetical species, vertical activity is normally distributed with a mean of 1 m and SD of 0.5 m, then 2.5% of the activity of that bird will occur above the net, where birds cannot be caught (Fig. 1A). If the mean shifts up only 0.5 m, but the SD remains the same, then the proportion of the bird's activity that occurs above the net is 16% (Fig. 1B); another 0.5-m

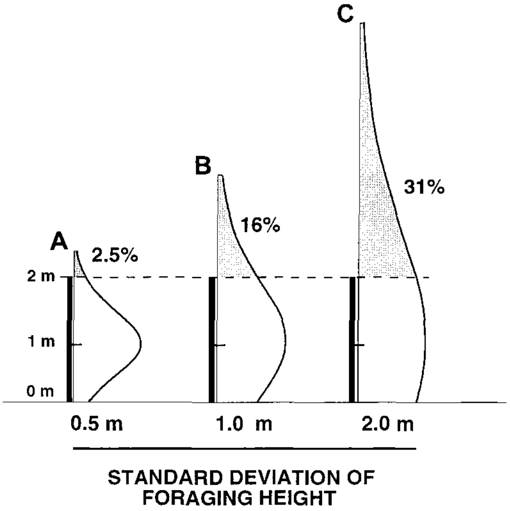

Fig. 2. Effect of SD of activity height on frequency of mist-net captures. Activity-height mean is 1.0 m, and SD is (A) 1.0 m, (B) 1.5 m, and (C) 2.0 m. Mist-net height is 2 m. That portion of the curve "below" 0 m is included in "captured" portion of distribution (see Methods).

increase in mean activity height (to 2 m) results in fully 50% of the activity above the net (Fig. 1C). Hence, an increase of only 1 m in mean activity height yields a 20-fold increase in the proportion of time a bird spends in a region where it cannot be caught by the net, which in turn affects strongly the probability of capture.

Similarly, variance in the distribution of activity height strongly affects the proportion of a bird's activity that occurs above the net. Figure 2A illustrates a hypothetical normal activity height distribution with a mean of 1 m and SD of 0.5 m. As in Figure 1A, 2.5% of the activity of that bird occurs over the net. If the SD is increased to 1 m (Fig. 2B), 6.4 times as much (16%) of the bird's activity occurs above the net. With a SD of 2 m (Fig. 2C), this value becomes 31%, or a greater than 12-fold increase over the time spent above the net at a standard deviation of 0.5 m.

Variation in the mean and SD of activity height also can have important effects on capture rate in birds that spend most of their time well above the net. Figure 3 illustrates the proportion of a bird's activity under various conditions of mean and standard deviation of normally distributed activity height in a forest with a 30-m canopy. The difference in proportion of activity at net height between a bird with an average activity height of 5 m and one with an average of 10 m varies with standard deviation. At standard deviations of 1 and 2 m, less than 1% of the birds' activity occurs at the level of the net. However, at a standard deviation of 5 m, approximately 27% of the activity of the bird with the mean of 5 m occurs at net level, whereas only 5.5% of the activity of a bird with a 10 m mean occurs there. This difference decreases as the SD increases until the difference reaches zero at a standard deviation of ∞ (i.e. when activity is equal at all heights).

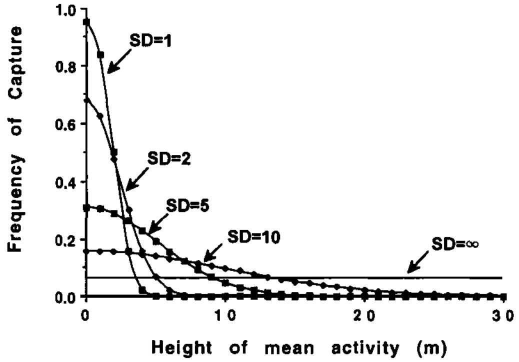

Fig. 3. Effect of variation in mean activity height on frequency of mist-net capture for five levels of variation; SD is standard deviation in activity height.

Small differences in mean activity height can have a substantial effect on capture values. For instance, if the SD in both cases is 5 m, an activity height mean of 10 m will mean that 5.5% of the bird's activity will be at net height, whereas an 11 m mean will mean that only 3.6% of the activity will occur at that level. Hence, a 1-m difference in mean foraging height 8 to 9 m above the top of the net can result in a 1.5-fold difference in potential capture rate. This difference in height is beyond the level of accuracy of most observers in the field and, for that reason, studies of vertical movement patterns of birds seldom attempt to estimate vertical height with greater resolution than 1 m. However, smaller than 1.5-fold differences are frequently discussed in mist-net-generated data on relative abundance.

Skewed distributions of activity heights (which are certainly more common than the normal distribution discussed here) would show a pattern of relative capture that differs in magnitude from that discussed above. However,

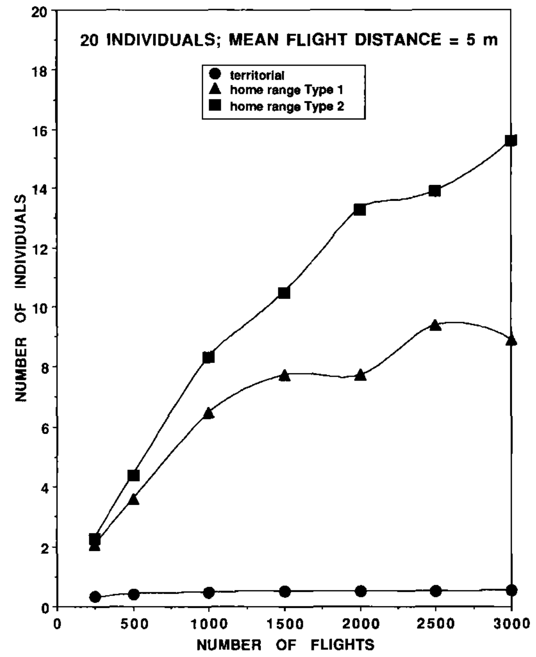

Fig. 4. Effect of spacing system on capture rates. Each curve represents number of individuals captured from population of 20 for each of three spacing systems.

such a distribution would still show qualitatively similar differences in capture rate with changes in activity height median, mean, and variance.

Territorial vs. nonterritorial species.—Birds that occupy nonoverlapping territories are expected to be caught less often than birds with overlapping home ranges, all else being equal, because the potential number of individuals captured per net is higher if spatial movement patterns allow more than one individual to occupy an area. To simulate the differences in capture values among species, sexes, or age classes that differ only in spacing system, we compared capture data for territorial birds to those for nonterritorial birds, using both Type 1 (partial overlap) and Type 2 (total overlap) nonterritorial systems (see Methods). In the simulation presented, the same number of individuals (20) of each type of spacing system was placed in a standard 1-km^2 site, and the mean flight distance was standardized at 5 m. The latter is probably unrealistically small for birds that have large (25-100 ha) home ranges (Type 2); however, this conservative bias minimizes the number of nonterritorial birds caught (i.e. it makes values for territorial and nonterritorial birds more similar than they otherwise would have been). Home-range size for Type 1 birds was 25 ha. As expected, many fewer territorial birds were captured than nonterritorial birds (Fig. 4), although densities were identical. For example, after 1,500 flights, mist nets captured 15 times as many Type 1 and 20 times as many Type 2 as territorial birds.

Effect of differences in flight distance.—Birds that fly farther per flight are expected to be caught by mist nets more often than those that fly shorter distances, all else being equal; the probability of intersecting a net is positively associated with the total distance flown. To quantify the importance of this influence on capture values, simulations were performed that measured capture rates for birds that differed in mean flight distance (see Methods), while controlling for spacing system, territory size, and flight frequency. In this and all simulations below, we emphasize that, if mist-net capture rates were influenced only by relative abundance, there would be no influence of the factor under discussion, and the results would produce a horizontal line with a slope not statistically different from zero. Therefore, only when the curves presented in our simulations reach asymptotes can the variable in question be ignored as an influence on the number of individuals captured per sampling period.

For territorial birds in our simulation, mean flight distance strongly influenced the percent individuals captured after 250 flights with, as expected, individuals making longer flights captured more frequently (Fig. 5A). The difference between capture rates of individuals with mean flight distances of 2 versus 10 m varied from a 43% increase for individuals with 1-ha territories to a 133% increase for individuals with 25-ha territories. After 1,000 flights (Fig. 5B), capture rates of birds with 1- and 2-ha territories and flight distances greater than 3 m tended to approach an asymptote, as did capture rates for birds with 5- and 10-ha territories for flight distances of more than 5 m. Otherwise, substantial differences existed (e.g. a 5% increase from flight distances of 2 to 4 m for 1-ha territories and 102% increased from flight distances of 2 to 10 m for 25-ha territories). After 2,000 flights (Fig. 5C), many curves approached asymptotes, but birds with large territories and small flight distances did not. After 3,000 flights

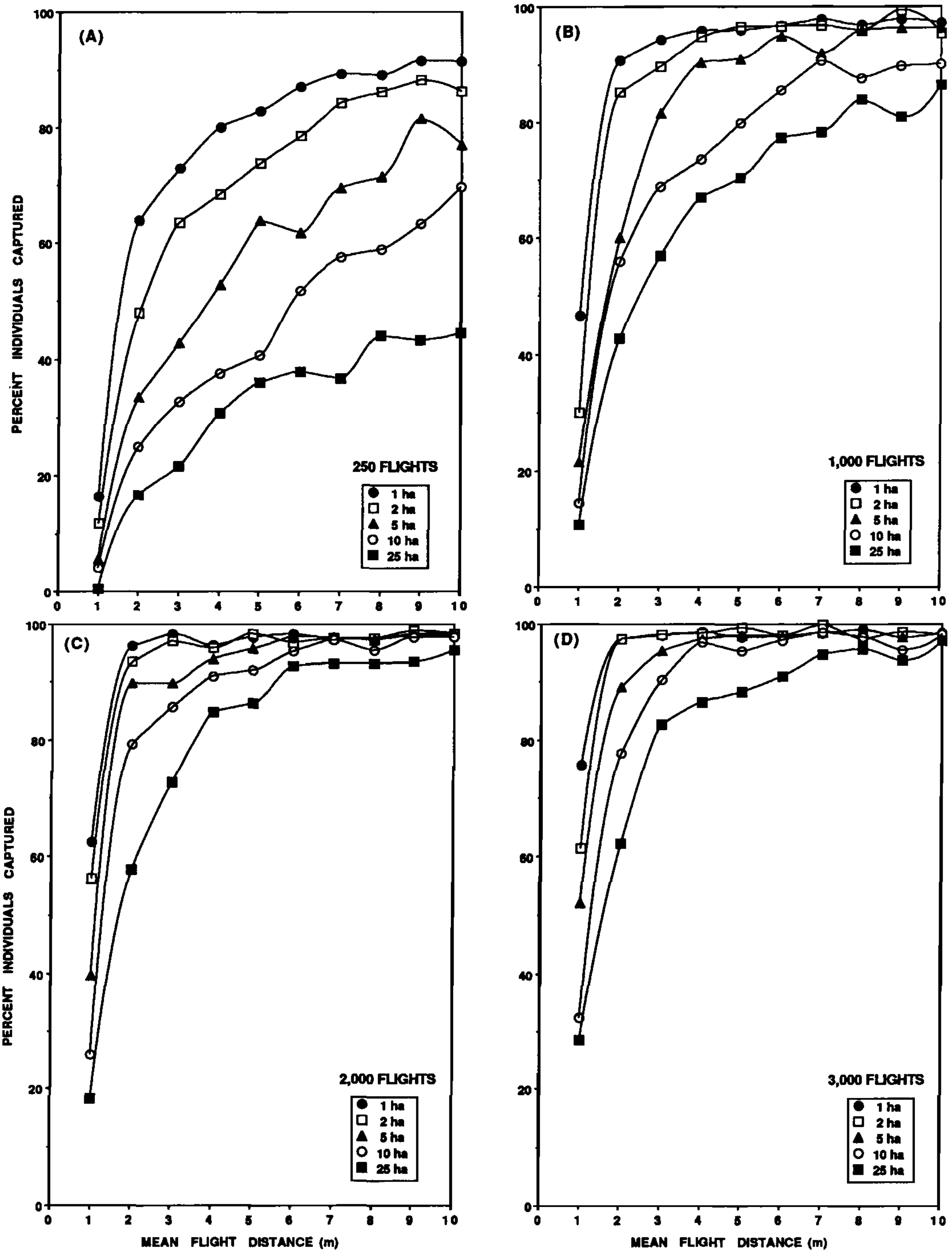

Fig. 5. Effect of differences in mean flight distance on capture rates for territorial species (for five territory sizes after (A) 250 flights, (B) 1,000 flights, (C) 2,000 flights, and (D) 3,000 flights.

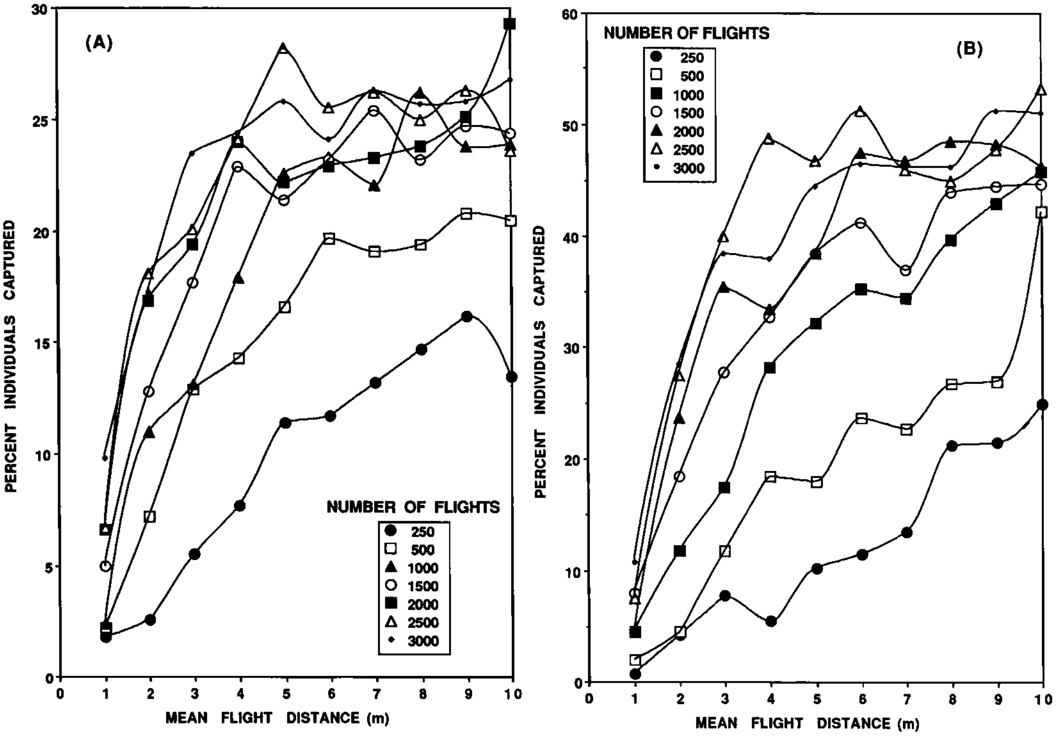

Fig. 6. Effect of differences in mean flight distance on capture rates for nonterritorial species with partly overlapping home ranges of 10 and 25 ha.

(Fig. 5D), the capture rate curves generally approached asymptotes for flight distances above 2 m except for birds with 10- and 25-ha territories.

For Type 1 (partial overlap) nonterritorial birds with home ranges of 10 ha, differences in mean flight distance dramatically influenced the number of birds captured, except after 2,500 flights at mean flight distances greater than 4 to 5 m (Fig. 6A). For Type 1 birds with home ranges of 25 ha, the influences of differences in mean flight distance were even more dramatic (Fig. 6B). Until the number of flights reached 2,000, the relationships between flight distances and capture rates approximated straight lines. For 2,000 flights or more, capture rates began to show asymptotes at flight distances greater than 4 to 6 m, and there was little indication of capture rates reaching an asymptote over the range of values in the simulation.

For Type 2 (total overlap) nonterritorial birds in a 1-km^2 area, the number of birds captured was likewise influenced dramatically by flight distance (Fig. 7). For this simulation, we included mean flight-distance values much larger (>10 m) than in other simulations because we hoped to encompass the extreme range of potential values of some bird species that fly long distances and have large home ranges. Examples of such birds are some undergrowth hummingbirds (especially the trap-lining phaethornine species) and perhaps some manakins (e.g. *Pipra, Manacus, Chiroxiphia*). These birds are particularly common in mist-net samples. For flight distances under 10 m, the relationships between flight distances and capture rates were nearly straight lines. For flight distances of 25, 50 and 100 m, there were substantial differences in capture rates at 250 and 500 flights, but for 1,000 flights or more, virtually all individuals were captured.

Effect of differences in flight frequencies.—Birds that fly more frequently are expected to be caught more often than those that fly less frequently, because the probability of intersecting a net is related to the number of times a bird flies. To quantify the importance of this influence on mist-net capture, simulations were performed that measured the number of individuals captured for birds that differed in flight rates (see Methods) while controlling for spacing system, territory size, and flight distance.

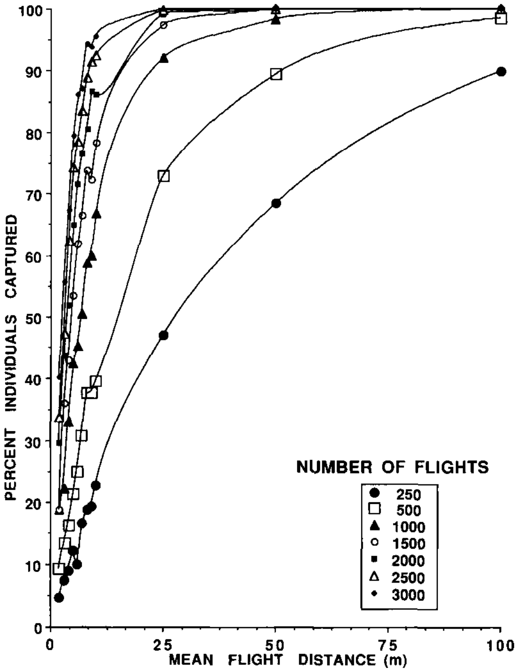

Fig. 7. Effect of differences in mean flight distance on capture rates for nonterritorial species with completely overlapping home ranges of 100 ha.

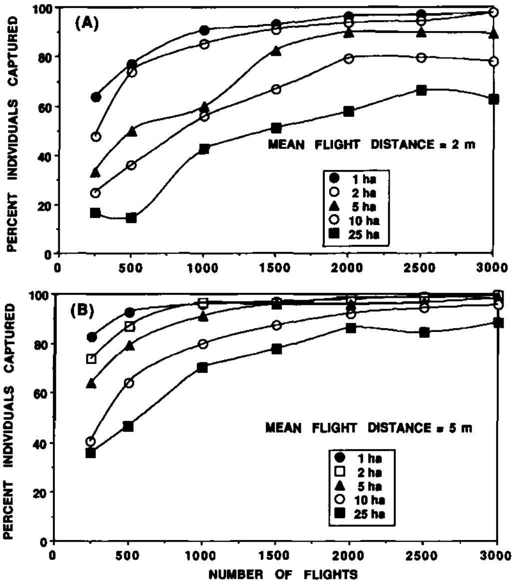

Fig. 8. Effect of differences in flight rates on capture rates for territorial species (for five territory sizes) with mean flight distances of (A) 2 m and (B) 5 m.

For territorial birds with small mean flight distances (e.g. 2 m), substantial differences in capture rates were found among birds that fly 500, 1,000, 1,500, and 2,000 times per unit time period for territory sizes of 2, 5, 10, and 25 ha (Fig. 8A). For example, for birds with 25-ha territories, one that flew 1,000 times/sample period was captured 2.5 times as frequently as one that flew 250 times/period and, for birds with 2-ha territories, one that flew 1,000 times/sample period was captured 1.8 times as frequently. Thus, in this example, mist nets would capture 1.8 to 2.5 times as many individuals of the species that flies more frequently even though both have identical relative abundances. For birds with very small (1-ha) territories, differences in number of birds captured were relatively small above 1,500 flights/sample period. For territorial birds with a mean flight distance of 5 m, the results were similar, but with asymptotes reached at lower numbers of flights, generally at 1,000 to 1,500 flights/sample period (Fig. 8B). For territorial birds with mean flight distances of 10 m, asymptotes were reached at about 1,000 flights/sample period; however, 10 m is probably much longer than the mean flight distance for most territorial species of the understory.

For nonterritorial birds with Type 1 (partial overlap) home ranges of 10 ha, substantial differences in capture values were found for birds with mean flight distances of 6 m and shorter for birds that made 250, 500, 1,000, 2,000, and 2,500 flights/sample period, and for birds with 8 to 10 m mean flight distances, substantial differences are found among birds that make 250, 500, and 1,000 flights/sample period (Fig. 9A). For example, for two species with mean flight distances of 2 m, one that flew 1,000 times/sample period was captured 4.4 times more frequently than one that flew 250 times/sample period, and for two species with mean flight distances of 8 m, one that flew 1,000 times/sample period was captured 1.8 times more frequently than one that flew 250 times/sample period. Thus, in this example, mist nets would capture 1.8 to 4.4 times as many individuals of the species that flies more frequently even though both have identical true relative abundance. For birds with Type 1 home ranges of 25 ha, even fewer asymptotes were reached before 3,000 flights (Fig. 9B); only for flight distances of 8 and 10 m and flight frequencies of at least 2,000/sample period did the capture-rate curves reach asymptotes. Differences among birds with different flight frequencies were again substantial. For example, for two species

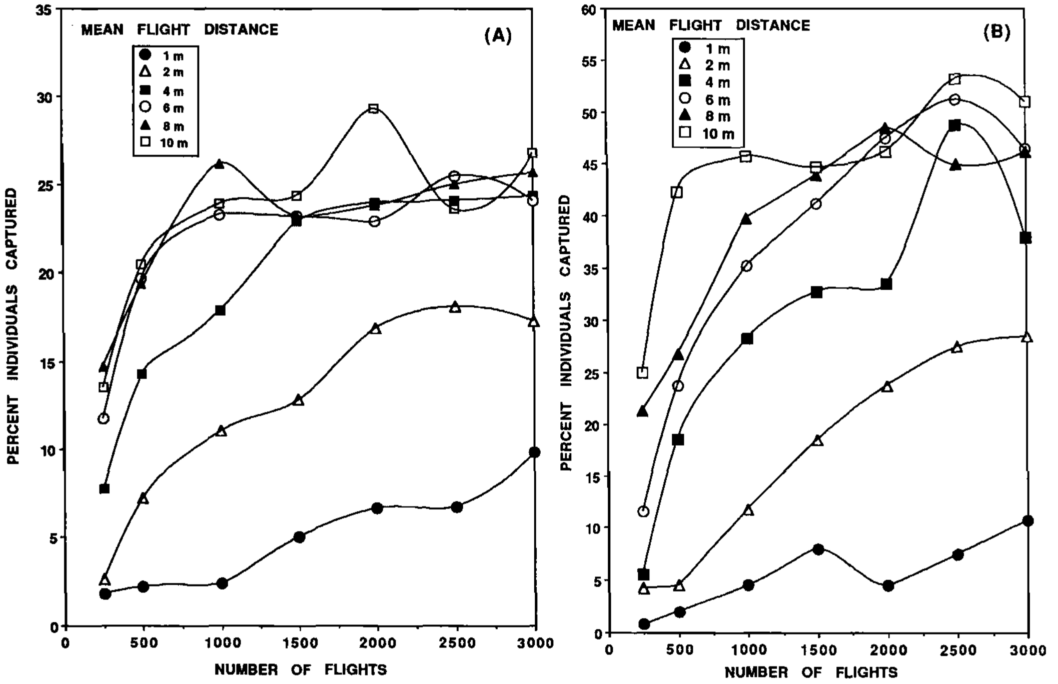

Fig. 9. Effect of differences in flight rates on capture rates for nonterritorial species with partly overlapping home ranges of (A) 10 ha, and (B) 25 ha.

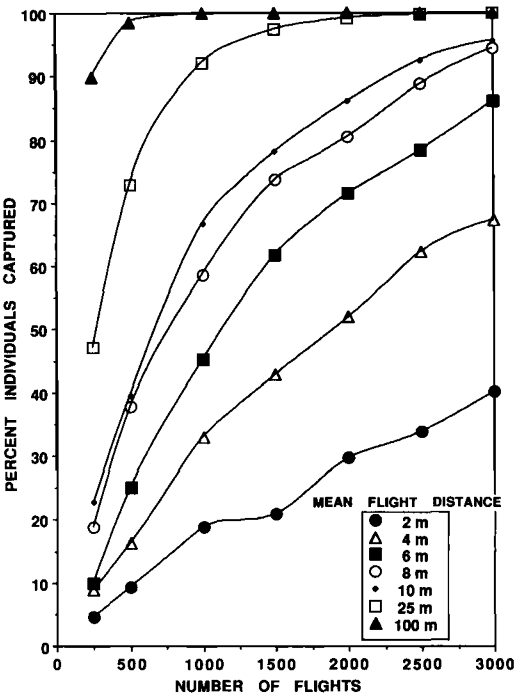

Fig. 10. Effect of differences in flight rates on capture rates for nonterritorial species with completely overlapping home ranges of 100 ha.

with mean flight distances of 2 m, one that flew 1,000 times/sample period was captured 2.5 times more frequently than one that flew 250 times/sample period. Thus, mist nets would capture 2.5 times as many individuals of the species that flies more frequently, even though both have identical relative abundances.

For nonterritorial birds with Type 2 (total overlap) home ranges of 100 ha, substantial differences in capture values were found among birds with mean flight distances of 10 m and shorter and that made 250, 500, 1,000, 2,000, and 2,500, and 3,000 flights/sample period. At a 25-m mean flight distance there were substantial differences among birds that made 250, 500, 1,000, and 1,500 flights/sample period (Fig. 10). For two species with mean flight distances of 4 m, one that flew 1,000 times/sample period was captured 3.7 times more frequently than one that flew 250 times/sample period. Thus, mist nets would capture 3.7 times as many individuals of the species that flies more frequently, even though both have identical relative abundances. Only for birds with extremely large (100-m) mean flight distances (trap-lining hummingbirds?) was there no effect of flight frequency on capture rate, at least for flight frequencies >250 times/sample period.

Survey of papers using mist-net capture data.—Do published studies that use mist-net captures to estimate relative abundance take any of these factors into account? Because three edited volumes (Keast and Morton 1980, Gentry 1990, Hagan and Johnston 1992) contain a number of mist-net studies (9, 4, and 11, respectively), we used the papers in those three volumes as a convenient sample of the literature. We searched the methods sections of each paper (or papers cited for methods outlined elsewhere) to see if any assumptions were stated concerning differences among the units compared in (a) vertical movements, (b) spacing system, (c) flight distance, or (d) flight frequency. We also searched the methods sections for statements concerning other parameters that would be essential for evaluating the data, comparing the data to other studies, or repeating the study itself: (a) number of nets; (b) duration of sampling period; (c) distance between nets (which influences the number of bird territories and home ranges potentially sampled); (d) whether birds were individually marked and recaptures discounted; and (e) mesh size of net.

Not one paper explicitly stated the assumption that differences in capture rates were determined only by differences in relative abundance (although two papers cited a paper published elsewhere that stated this assumption). However, all papers proceeded with that assumption. Only four papers (Bierregaard 1990, Blake and Loiselle 1992, Karr 1990, Petit et al. 1992) acknowledged that problems exist in comparing species or habitats. Eight of 24 papers (33%) did not report the number of nets used. Eight papers (33%) did not clearly indicate the duration of mist-net sampling periods. Eleven papers (46%) did not provide the distances between nets. In 10 studies (42%), individual birds were not marked, but three of them used methods to estimate the percent recaptures in the sample; however, at least two of the studies in which birds were marked included known recaptures in the data used to estimate relative abundance. Thus, at least nine (38%) counted recaptures without qualification in their estimates of relative abundance. Eight papers (33%) did not provide the mesh size of nets used, a variable long known (Heimerdinger and Leberman 1966) to influence species composition of net captures, with capture rates varying within some size classes by more than 100% (Pardieck and Waide 1992). Likewise, Pardieck and Waide (1992) found that only 3 of 12 papers surveyed that compared relative abundance of species also reported mesh size, and only 1 of 12 single-species studies reported mesh size (without which the study cannot be replicated). Overall, 17 papers (71%) in our survey did not provide the information needed to replicate the study.

DISCUSSION

Several alternative hypotheses can be proposed to explain many results of mist-net studies that are typically interpreted as reflecting only differences in relative abundance. We explore the following hypothetical example: the number of the same age/sex category of species X captured is 25% higher over the same time period at site A than at site B (using same deployment pattern of nets in space and time and nets of the same mesh size; both sites in the same habitat type). The usual interpretation of such a result by most researchers working with mist-net captures is that the density is 25% higher at site A than at site B (differences of far less than 25% often are discussed). Assume that the rate of escape from nets and the degree of net avoidance is the same (a reasonable assumption for same age/sex category, but probably not otherwise valid), and that all recaptures are excluded from the calculations. We offer the following five alternative explanations for a 25% difference in capture rates with identical relative abundance:

1. The mean height above ground of movements is lower at site A than at site B. For example, a bird with a normally distributed vertical activity pattern with a mean height of 1.62 m and a SD of 0.5 m has a 78% chance of being caught on any given flight that crosses the net lane. A 25% higher chance of capture (97.5%) can be explained by a decrease in mean foraging height of 0.62 m if the SD remains constant. Such small absolute decreases in mean foraging height are probably beyond the resolution of studies that rely on visual observation.

2. The SD of the height above ground of movements is smaller at site A than at site B. For the bird discussed in the preceding paragraph with a normally distributed vertical activity pattern, a mean activity height of 1.62 m, an activity-height SD of 0.5 m, and a probability of being caught of 78%, a 25% increase in capture rate can be the result of a 0.31 m decrease in the activity-height SD to 0.19 m.

3. The spacing system of species X at the two sites differs. For example, all of the individuals at site B might be territorial, whereas floaters are present at site A. Using the simulated values illustrated in

Figure 4, approximately 3% of the territorial birds at each site will be captured after 1,000 flights. However, after the same number of flights approximately 8% of floaters will be captured as well, assuming that the floaters' home ranges consist of the entire study area (Type 2 home range). In such a system, a 25% increase in number of birds captured would be effected by the presence of approximately nine floaters, or fewer than one floater for every two territorial birds. If floaters have home ranges that are smaller than the entire site area (Type 1 home ranges), this value decreases, at least if the parameters are similar to those simulated in Figure 4. Under such circumstances, approximately 64% of the floaters will be captured after 1,000 flights. In such a case, only one floater for every 25 residents would be necessary to increase the number of birds captured by 25%.

4. The mean flight distance at site A is longer than at site B. For example, approximately 25% more birds will be captured at site A than at site B after 1,000 flights for a species with 5-ha territories if the mean flight distance at site A is 2.5 m, whereas that at site B is 2.0 m (values estimated from Fig. 5A).

5. The flight frequency is higher at site A than at site B. For example, in a case in which the mean flight distance is 2 m and the territory size is 5 ha at both sites, approximately 25% more birds will be captured at site A than at site B if the number of flights/sample period is 1,300 at site A and 1,000 at site B (values estimated from Fig. 8A).

All of these alternative hypotheses are reasonable (see below). Yet, we found no paper that considers in detail such alternative explanations for differences in relative mist-net capture values. It is possible that some of the influences on capture data other than relative abundance may cancel each other out. For example, birds with longer flight distances, which would increase capture values, may have lower flight frequencies, which would decrease capture values. Also, it seems likely that, as the mean height above ground increases, so does the variance, thereby compensating in part for the influence of differences in vertical movement patterns. Other influences, however, more likely have additive and perhaps multiplicative influences. For example, birds with large, overlapping home ranges, which would increase the likelihood of capture, probably have longer flight distances or greater flight frequencies, which also would increase the likelihood of capture.

Is there reason to worry about differences in vertical-movement patterns? Interspecific differences in use of space with respect to mean height above ground have been quantified so many times that they are regarded as a major axis of ecological segregation among bird species, even in habitats with low vegetation (e.g. Cody 1966). Only for those species with all vertical movements within 2 m of the ground would the assumption of "no differences in vertical distribution" not be violated, unless, of course, identical distributions can be demonstrated.

However, we know of few such bird species, other than completely terrestrial species that seldom strike nets. For example, for 50 tropical forest species that Bell (1982) recorded in the zone below 2 m (excluding strictly terrestrial species), only 1 species was found exclusively in that zone. Even for those species that forage almost exclusively on the ground, some often spend some proportion of time above 2 m during other activities, particularly singing. As for intraspecific differences, vertical distribution of movements or foraging behaviors may differ with respect to study site (e.g. Willis 1966, Morse 1971, 1980, Bennett 1980, Keast 1980, Rabenold 1978, 1980, Wiedenfeld 1992), habitat or microhabitat (e.g. Rabenold 1980), year (e.g. Williams 1980), season (e.g. Chipley 1980, Robinson 1981, Waide 1981), age (McDonald and Smith 1994), or sex (e.g. Morse 1968, Williamson 1971, Rabenold 1980, Hooper and Lennartz 1981, Peters and Grubb 1983, Bell 1986, Holmes 1986 and references therein, Petit et al. 1990). In spite of these examples of vertical differences in movement patterns, and Greenberg and Gradwohl's (1986) warning that fluctuations in vertical movements would generate fluctuations in mist-net capture rates when bird population size is actually constant, most studies that analyze mist-net captures have not considered this problem.

The only study of which we are aware that explicitly analyzed vertical height distributions using mist nets was that of Fitzgerald et al. (1989), who sampled the entire range of vegetation in a New Zealand forest from undergrowth to canopy (13.5 m) with stacked sets of nets. Their analysis demonstrated that vertical distribution can have a profound effect on capture rates in birds. For example, if their study had been conducted using only the lowest tier of nets (hence, approximating most mist-net studies), Fitzgerald et al. would have found the proportional abundance of the Sacred Kingfisher (*Halcyon sancta*) to be six times lower and that of the Dunnock (*Prunella modularis*) to be four times higher than when all six nets were used.

In fact, only 1 of the 14 species studied (the Rifleman, *Acanthisitta chloris*) would have appeared to have the same relative abundance with one net as with all six.

Fitzgerald et al. (1989) also found that several species varied in vertical activity with time of day (e.g. the mean activity height for the New Zealand Bellbird [*Anthornis melanura*] was more than 2 m higher at 1300 than at 1100) and season (e.g. the mean activity height for the Blackbird [*Turdus merula*] was more than 2 m higher in July than in August). Also, for some species, the vertical distribution of birds when first captured differed from the vertical distribution of recaptures. Fitzgerald et al. hypothesized that transient birds traveled through the forest at different heights from those most frequently used by residents.

Perhaps the most telling finding by Fitzgerald et al. (1989) was that the activity height distributions for some species differed distinctly among net sites, even though all were placed within a 4-ha plot of a single forest type. For example, 28% of the *Turdus merula* in one set of nets were caught in the lowest net, whereas the same net in another set caught only 12%. Fitzgerald et al. suggested that this was due to: "1) differences in local topography of trees and foliage around the nets, making parts of some sets of nets remain in sunlight and therefore visible longer than others; 2) differences in height of natural 'flight-lines' through the forest that are intercepted by each set of nets; 3) differences in spatial distribution of important food resources near each set of nets; and 4) variations in vegetation profile through the forest." All of these factors certainly vary in any forest and will play a role in capture rates in any mist-netting study.

The problems in comparing capture rates of species, sexes, or age classes that differ in spacing systems is so obvious that we consider a computer simulation to demonstrate quantitative differences in predicted capture values as "over-kill." Remsen and Parker (1983), Greenberg and Gradwohl (1986), and Bierregaard (1990) pointed out that capture rates of birds with different spacing systems will differ even if their relative abundances are identical, and Graves et al. (1983) even used the large differences in capture rates among age and sex classes of the same species to infer differences in spacing systems, rather than the traditional interpretation that they differed in relative abundance. Stiles (1992) noted that the high frequency with which the Long-tailed Hermit (*Phaethornis superciliosus*) was captured in nets (because of its trap-lining behavior) had led to overestimates of its relative abundance. Westcott and Smith (1994) found that wandering individuals in a lekking tyrannid flycatcher moved between leks as far as 700 m in only 1.5 h. Yet, only a few studies (e.g. Bierregaard 1990, Robinson et al. 1990) mention differences in spacing systems as a problem for interpreting mist-net data.

As noted by Remsen and Parker (1983), inspection of every data set on capture rates of Neotropical forest birds (e.g. Karr et al. 1990) reveals that the most "abundant" species are those with nonterritorial, highly mobile spacing systems, namely: hermit hummingbirds (particularly *Phaethornis*); manakins (particularly *Pipra, Manacus, Chiroxiphia,* and *Corapipo*); army-ant-following antbirds (*Pithys, Gymnopithys, Hylophylax,* etc.); frugivorous, lekking flycatchers (*Pipromorpha, Mionectes;* Willis et al. 1978, Snow and Snow 1979, Westcott and Smith 1994); and the Wedge-billed Woodcreeper, a species with large, overlapping home ranges (Gradwohl and Greenberg 1980). Even among territorial insectivores, those species most frequently captured in nets tend to be ones that make long horizontal flights (e.g. *Thamnomanes* [Schulenberg 1983], *Platyrinchus* [J. W. Fitzpatrick pers. comm.], dead-leaf-searching *Myrmotherula* and *Automolus* species [Remsen and Parker 1984, K. Rosenberg 1990]). Rather than interpret such data as indicating that these are the most common species in tropical forest undergrowth (e.g. Snow and Snow 1979, 1981), we believe that such data indicate that these species are simply more highly prone to capture by mist nets because of differences in horizontal movement patterns, as strongly suggested by the outcomes of our simulations.

Likewise, the problem in comparing birds that differ in mean flight distance or flight frequency, regardless of spacing system, was mentioned by Karr (1981) and Remsen and Parker (1983), but is widely overlooked. We doubt that any two species at any study site have mean flight distances or flight frequencies that are statistically indistinguishable with reasonable sample sizes. Robinson and Holmes (1982) found substantial differences in flight distances and frequencies among 10 species of passerine birds. Holmes and Robinson (1988) found that the

Veery (*Catharus fuscescens*) and the Swainson's Thrush (*C. ustulatus*) flew more than twice as often per minute as did the closely related Hermit Thrush (*C. guttatus*). Data on intraspecific differences in flight distances or flight frequencies also are scarce. Rabenold (1980), Waide (1981), and Riley and Smith (1992) found substantial seasonal differences in flight distances. Gochfeld and Burger (1984) and McDonald and Smith (1994) found significant differences in movement rates of adult versus young birds. Movement patterns during the breeding season would be expected to differ dramatically within any species between incubation and nestling periods. Indirectly, age-based differences (e.g. MaGrath and Lill 1985, Maccarone 1987, Wunderle and Martinez 1987) and sex-based differences (e.g. Selander 1966, Morse 1968, Hogstad 1978, East 1980, Power 1980, Martindale 1983, Bell 1986, Holmes 1986, Teather 1992) in diet, foraging height, foraging maneuvers, and substrate use probably generate differences in flight distances. Karr and Freemark (1983) even used mist-net capture data to estimate activity levels of bird species at different seasons rather than relative abundance. Given the many variables that presumably influence flight distances with respect to foliage distribution and resource availability, there is every reason to predict substantial intraspecific differences in mean flight distance with respect to season, site, habitat, age, and sex.

In all our simulations, an individual could be "captured" only once. This is equivalent to studies that mark individual birds so that they are counted only once. We emphasize, however, that if our sample of published studies is a fair representation, then many published studies (38% of our sample) that have compared relative abundance of birds did not mark their birds or included recaptures in their estimates without any method to compensate for their inclusion. Failure to mark individual birds, or the inclusion of recaptures, accentuates the influence of every variable that we consider in our simulations. If we had conducted simulations that counted recaptured individuals, all of our graphs would show virtually straight-line relationships between dependent and independent variables, because the asymptotes are caused by depletion of the pool of previously uncaptured individuals. As a first approximation, the slopes of such straight-line relationships would be similar to those of the lines between the first two points on any graph.

We designed our simulations to maximize capture rates by assuming that every time a bird strikes a net, it is captured. Those familiar with mist netting know that such an assumption is conservative. In the absence of published data, we asked 14 people familiar with mist netting to provide us with their "best estimate" on the percent of individual birds that strike a net that then bounce out or escape. These estimates (J. M. Bates, R. O. Bierregaard, D. F. DeSante, F. B. Gill, R. Greenberg, M. Cohn-Haft, N. J. Klein, N. Krabbe, A. W. Kratter, S. M. Lanyon, M. Marín A., P. P. Marra, M. B. Robbins, D. Willard) ranged from 4 to 50% (mean 18%). Using this mean, all simulations involving number of flights could be extended by a factor of about 18%. Even this would be a conservative adjustment because it is likely that, once a bird has escaped from a net, the probability of it hitting that net again is reduced through learning.

As pointed out by Levey (1988), another problem with interpreting mist-net captures is that when a bird is captured in a mist net, it does not necessarily mean that it was using the area around the net except to fly through that air space. Therefore, the validity of interpretations of capture data with respect to habitat and microhabitat use at the net depends on the likelihood that the bird was just passing through. For species with short flight distances, that likelihood is clearly low (although dispersing individuals may have been using the area near the net only as a "stepping stone"). For species with medium and long flight distances, however, that likelihood is higher. In fact, because nets capture only flying birds, capture-rate data applied to small areas might indicate avoidance, not use or preference. We suggest that use of mist-net captures to determine habitat and microhabitat preferences of species that typically make flights longer than the distance from the nets to the variables measured is of dubious validity. Regardless of problems in detection, at least visual observations allow direct assessment of the most critical fact in any assessment of habitat or microhabitat preference, namely whether the bird in question was actually using that resource.

Use of mist nets is often praised as a method to compare bird populations among sites in that it removes the inherent biases in visual and auditory census techniques associated with differences among observers. Use of mist nets is often portrayed as free or nearly so of any researcher-dependent biases, as if they were an automatic device that recorded all birds in their vicinity, and with identical results no matter who sets them and where they are set. On the contrary, important individual differences exist among those who set nets, and these differences might affect inter- and intraspecific capture rates strongly. Subtle differences in the way a net is set affect capture rates and species composition. In our experience, a net set in dense vegetation will capture a higher proportion of species that have short flight distances and a lower proportion of those with long flight distances; the converse is true for nets in relatively sparse vegetation. Experienced mist-netters recognize spots where nets will yield the highest overall capture rates (Ralph et al. 1993). For example, nets along ridge lines or crossing gullies often catch relatively high numbers of birds. Capture rates are strongly affected by the tension with which a net is set, the angles and frequency of light striking it, the frequency with which it is cleaned of debris and of captured birds, the frequency of human disturbance, the degree to which nearby vegetation is cleared from the net line, the proportion of time the net is exposed to wind, the wind direction, the frequency of moisture condensation on the filaments, and how soon such pre-dawn condensation is shaken out of the net each morning. Whether these differences are equivalent in their impact on results to those known for observer differences in other census techniques is unknown. Nonetheless, use of nets does not necessarily remove interinvestigator variables, and comparison of results among studies done by different investigators is not straightforward.

Mist-net capture data have been used to estimate long-term population trends of birds (e.g. Faaborg and Arendt 1992, Hagan et al. 1992), and a major new program has been instituted to estimate long-term trends in migratory bird populations in North America through capture data (DeSante et al. 1993). Although we see no *a priori* reasons to expect long-term unidirectional changes in the variables such as spacing system, mean flight distance, or flight frequency that could confound such analyses, we do see one reason for concern: changes in vegetation structure at the sampling stations. Because both the horizontal and vertical movement patterns (and bird species composition, even in migration) are strongly affected by vegetation structure, any change in this structure, such as succession, would confound any true population trend or create a "population" trend when none exists. Those who direct some of these programs are clearly aware of this problem and have stated that such programs must be established where the vegetation is "relatively stable" (Ralph et al. 1993). Our calculations on the effect of vertical movements on capture rates indicate, however, that vegetation structure must be very stable.

Mist nets are a powerful tool for detecting the presence of undergrowth bird species, particularly secretive species or those that vocalize infrequently. Although mist nets should be included in the sampling protocol (presence/absence or qualitative comparisons of abundance) for any avifaunal survey of densely vegetated habitats, their ability to sample the entire avifauna is limited (Remsen 1994). For example, Bierregaard (1990) found that even after seven years, 136,000 net-h, and 25,000 captures, mist nets detected only 41% of the species in a tropical forest. Even in habitat of low stature, mist nets do not detect the presence of all species. For example, Robinson and Terborgh (1990) found that after nearly 700 individual captures, only 86% of the bird species known to occur regularly in low riverine scrub were netted. Although nets placed in the canopy increase the proportion of a local avifauna detected by nets, canopy nets are logistically much more difficult to set up and maintain than ground nets and often catch many fewer birds, sometimes so few that some studies discontinued their use (e.g. Rappole and Warner 1980); recent technical advances, however, may make their use in the canopy more practical (Meyers and Pardieck 1993).

Can mist-net capture data be used to estimate relative abundance accurately? We believe that they cannot be used to do this with any methods currently in use, and we are unable to see how the relative abundance of birds with different spacing systems can ever be compared accurately using the technique. However, if netting is carried out until the capture rates of new individuals reach an asymptote, then the number of captures approximates relative abundance for birds with the same spacing system. A corollary of this observation regarding asymptotes is that capture rates are best compared only among birds for which the capture rates reached asymptotes during the study. This requires marking of all individuals and presumably an extension of netting operations for many more days than currently in the protocols of most mist-net studies. Therefore, we regard many conclusions of published mist-net studies concerning comparisons of relative abundance as open to question.

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