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COPING WITH CAPTURE RATE BIAS: CANOPY HEIGHT AND SEVERAL EXTRINSIC FACTORS

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Abstract. Many factors other than a species' actual abundance can affect mist-net capture rates. We used ANCOVA models to quantify some potential biases and control their effects, producing adjusted estimates of capture rates that are more directly comparable among mist-net stations. Data came from 46 two-day mist-net sessions from September 1990 to May 1992 at six subtropical forest stations in the Rio Bravo Conservation and Management Area, northwest Belize. Factors evaluated included canopy height at net sites, long-term net shyness (days elapsed between first and last netting day of the entire study period), season (wet vs. dry), total rainfall during a netting session, and temperature. Number of individuals and species captured/10 net-h declined at each net with increasing canopy height above the net. Capture rates differed significantly among some of the stations. Elapsed days and rainfall caused significant bias in capture rates, which were statistically controlled within the ANCOVA, whereas season and temperature did not. Capture rates varied among sessions, but there was a slight and significant decline over the entire study period for all stations combined. Rainfall significantly depressed capture rates somewhat on a daily basis, but capture rates did not differ between wet and dry seasons. When we replaced the station variable in the ANCOVA with mean canopy height, the model was still highly significant, but did not explain as much of the variation in capture rates. Statistical analysis provides an objective means of interpreting data and estimating reliability, but only if statistical assumptions of the analyses are met. We discuss the need for including randomization in the experimental design, standardizing netting protocol, and quantifying sources of bias in the field, before ANCOVA or other parametric statistical techniques can be used to partition effects of biases.

Key Words: Belize, bias, canopy height, capture rates, experimental design, mist net, multivariate statistics.

In the tropics "a bird in the hand" may be worth more than "two in the bush" because bird vocalizations are relatively unknown, and observers require extensive experience with the bird community before becoming proficient at conducting point counts. For some cryptic or secretive and rarely vocal species in the understory, mist netting may be the best, or only, method of detection (Terborgh 1985, Remsen 1994). Thus, mist netting has several advantages over other kinds of counts and has often been used to describe bird species composition and relative abundances in tropical forests (Whitman *this volume*).

Nonetheless, mist netting is criticized as a technique for counting birds because susceptibility to capture depends on a bird's spatial and temporal activity, which varies according to species, age, sex, weather, season, time of day, experience with nets, and foraging stratum (Karr 1981a, Remsen and Parker 1983, Martin and Karr 1986, Rappole and Ramos 1995, Jenni et al. 1996, Remsen and Good 1996). Bird-community composition is often related to vegetation structure (Brokaw and Lent 1999), but differences in vegetation structure confounds species-to-species, habitat-to-habitat, station-to-station, and even net-to-net capture rate comparisons, because the proportion of individuals sampled of midstory, subcanopy, and canopy species will likely decline as canopy height increases and the proportion of vegetation within net level decreases (Whitman et al. 1997).

Researchers using mist nets in the tropics have dealt with variable height-related capture probabilities, where some species seldom come down to mist-net level, in one of the following ways: (1) define the study species as only those species that occur at mist net level (the forest understory or second growth); (2) limit analyses to only those species or guilds known to be vulnerable to capture; or (3) combine point counts and mist net results (e.g., Loiselle and Blake 1991, Petit et al. 1992, Stouffer and Bierregaard 1995, Gram and Faaborg 1997, Whitman et al. 1997). In principal, mark–recapture techniques can be used to estimate capture proportion and population size separately for each species caught (Kendall et al. *this volume*). However, mark–recapture cannot give good estimates for species rarely caught, and the method involves assumptions that cannot always be met. These four approaches may reduce, but not eliminate, height-related "species detectability" bias within forests of different height and vegetation structure.

Bias is "the difference between the actual population value and the mean of a sampling distribution" (Dixon 1993:292). If the sample capture rate is centered on the true population mean and is not consistently too low or too high, then it is unbiased. If biases are strong and unaccounted for, the results of field studies will be erroneous. If a method does not detect individuals equally under all the conditions being compared, estimates of the true population differences among habitats and times will be biased, unless the counts are adjusted for the differing capture probability (Thompson 2002, Sauer and Link *this volume*). Part of the solution is to design studies to account for potential biases, quantifying them in the field when netting, and adding them as variables during analysis. In this way, the effect of each factor on capture rates can be determined. If bias is detected, and the data meet the statistical requirements, capture rates from netting samples can be statistically adjusted for the biases within a multi-factor analysis (e.g., Ramsey et al. 1987, Boulinier et al. 1998). We use that approach in this paper, to investigate the effects of a selected set of potential biases on mist-net capture rates using data from our work on bird communities in several subtropical forest types in Belize.

METHODS

STUDY AREA

Data were collected from September 1990 to May 1992 in the Rio Bravo Conservation and Management Area (RBCMA), then a 92,000 ha preserve in northwest Belize (17°45'N, 89°00'W), managed by the Programme for Belize. The RBCMA is in the "subtropical moist" life zone, with a mean annual rainfall of about 1,500 mm, and a dry season that generally extends from February-March through May.

The six stations used in our analysis were established in relatively mature natural forest. The stations were named after the locally predominant vegetation: Mesic Upland Forest I and II (two stations), Dry Upland Forest (I and II), Riparian Forest, and Palm Forest. The nearctic migrants captured at stations in this study ranged from 16.7% of species and 15.7% of individuals at Mesic Upland Forest I to 25.6% of species at Riparian Forest and 24.7% of individuals at Dry Upland Forest I.

Each station consisted of a 1-km transect located near a road, but far enough from the road to avoid edge effects. The start of each transect was a random number between 100 and 350 m perpendicular into the forest from the first randomly selected point along the road that fell into the appropriate forest type. The direction each transect took from the starting point was also selected at random, from bearings not heading back toward the road. Transects were laid along a compass bearing and marked every 20 m with PVC pipe. The bearings of a few transects were adjusted at the 100-m point, or a gap was inserted, where the forest type changed appreciably or there was some habitat anomaly. The distances separating transects ranged from 1.6 to 28 km.

MIST-NETTING PROCEDURES

On each transect we put up 13 36-mm mesh and two 30-mm mesh mist nets on collapsible tent poles. Nets were set up within a 500-m section of each 1-km transect, selected for ease of access and to avoid features that would not be comparable among transects. We stratified the 500-m section into 100-m segments, within each of which we established three net sites at randomly selected points for a total of 15 nets/transect. Placement of the two 30-mm mist nets was determined by chance at each netting session.

We netted at least seven times at each of the six stations, spanning two wet and two dry seasons. Each station was netted in one session during the first wet season, that is, in the third and fourth quarters of 1990 when transects were established. Afterwards, we netted each station once each quarter of the year during the study, for a minimum of two netting sessions from each of the wet and dry seasons per year. We ran additional sessions at two upland forest stations, to improve sampling with respect to migration.

We opened nets at first light each day, ran them until dusk on the first day, and in most cases ended on the second day once we reached approximately 300 net-h for the session. We continually patrolled nets during light rain, brief showers, or during "rain drip" from the foliage after heavy rain, keeping nets open as long as we felt that captured birds were not in danger of becoming wet. We recorded the opening and closing of each net to the nearest 5 min, including closures for heavy rain or when an individual net was exposed to hot sun. There were several exceptions to the protocol of 300 net-h/session. The first session at stations ranged from 257 to 288 net-h due to our initial caution when netting on rainy days. Also, in January and February 1991, C. Robbins conducted 3-day sessions at these stations as part of his own survey work (Robbins et al. 1992). Only captures during the first 300 net-h in his sessions were used in our analyses. The actual mean net-hour/session was 335.1 ± 67.8 SD, but was reduced to 292.4 ±18.47 SD when only captures during net hours up to and including 300 net-h were used. In total, 3,245 captures during 13,450 net-h were used in this analysis.

We aged and sexed wintering or transient nearctic migrants following Pyle's (1987) guide and our experience with birds in North America. For year-round residents and summer residents we based age and sex designations on plumage descriptions (Stiles and Skutch 1989, Howell and Webb 1995), presence of brood patch or cloacal protuberance, eye or gape color, feather condition, synchrony of growth bars on feathers, and, with caution, degree of skull pneumatization.

DEPENDENT VARIABLES

Capture rate (number of captures/10 net-h) were calculated for data pooled from the fifteen nets at each station for each 300 net-h session, the sample unit in most of our

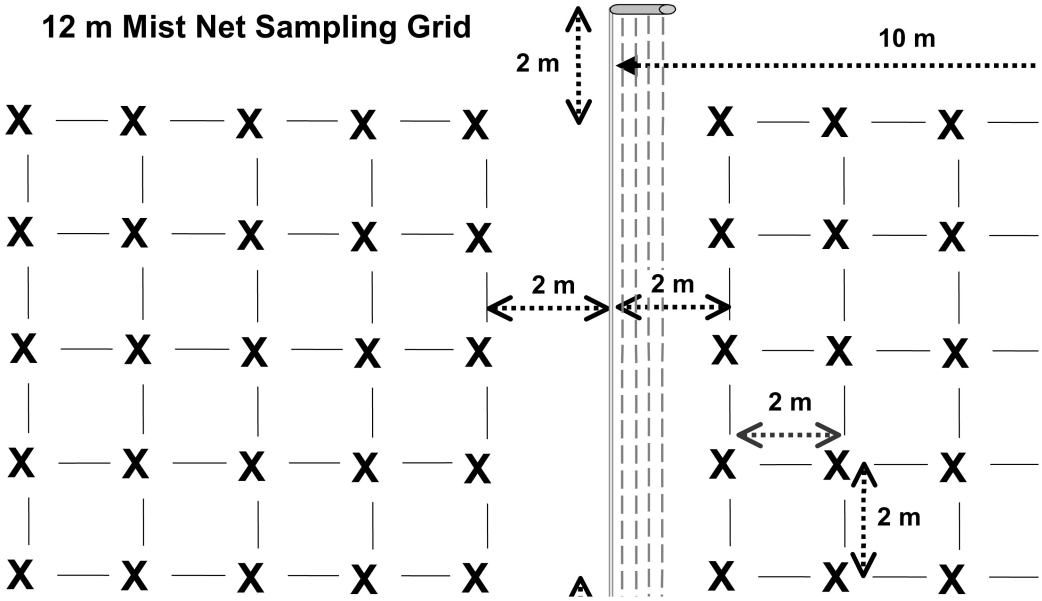

FIGURE 1. Layout of canopy height sample points (X's) at each net.

analyses (in all cases except the analysis of canopy height). Separate capture rates for each session provide repeated measure "snap-shots" of the local avifauna.

We examined six variations of capture rates, three involving total number of captures within a session (including recaptures), calculated separately for all species combined, for resident species alone, and for migrant species alone. Recaptures were included in these indices to give an index of overall bird activity. We also calculated rates for number of separate individuals captured (first captures within a session, including birds banded at any previous session), individuals recaptured (re-caught within a session and more than 2 h from the previous capture), and the number of species caught within each session. For evaluation of canopy height, we calculated capture rates as described above, but on a net-by-net basis rather than averaged for each of the six transects, because vegetation structure can vary widely among nets within a transect.

INDEPENDENT VARIABLES

Concurrent with our netting we recorded additional data to use as independent variables in our analyses of capture rates.

CANOPY was the mean maximum canopy height at each net, based on 50 sample points regularly distributed as shown in Figure 1. At each point we used a one-inch diameter, 2.5 m-long PVC pipe to sight an imaginary vertical line to the forest canopy, and then estimated the maximum canopy height along that line. Although the method requires estimating heights, we deemed it adequate for comparing vegetation height among stations because we regularly checked our estimates with a rangefinder.

STATION was a class variable for station.

DAYS was the number of days from start of the study, including days between netting sessions (values ranged from 0 to 571).

SEASON was a class variable describing dry season (mist-netting sessions from 9 January to 19 May 1991 and from 15 February to 21 April 1992) and wet season (sessions from 5 September to 25 November 1990 and 23 August to 9 November 1991).

RAIN indicated total rainfall during each netting session, taken from daily records of rainfall at Chan Chich Lodge, about 30 km from the stations. Given the local nature of tropical rainstorms, rainfall at Chan Chich may not have been directly related to rainfall at stations, but we felt that similarity was sufficient to justify inclusion of this factor.

TEMPERATURE was the maximum daily temperature recorded daily at Chan Chich during a netting session. Minimum temperatures were correlated with the maximums, so were not included in the analyses.

STATISTICAL ANALYSES

All numeric variables were tested for normality and homogeneity of variances among class levels, and converted to ranks if necessary for use in parametric or non-parametric statistics. We used a $\log_{10}$ transformation of the number of individuals/10 net-h and a square root transformation of the number of species/10 net-h to normalize distributions, and a $\log_{10}$ transformation to equalize variance of CANOPY.

We used a One-Way ANOVA to test for differences in CANOPY height at nets among STATIONs. For other factors, we used ANCOVA instead of a repeated-measures ANOVA, because our experimental design was unbalanced (three wet season versus four dry season sessions), and we had a combination of numerical and class variables we wished to examine simultaneously. ANCOVA combines numerical and class factors to (1) adjust for sources of bias to see whether class differences remain or become insignificant when adjusting a covariate (thus, we can adjust for the repeated-measures in a time series by incorporating a variable measuring time over the course of the sampling); (2) produce adjusted least-square means once sources of experimental error have been removed; or (3) study regressions in multiple groups to see if relationships between dependent and independent variables are the same within categories of the groups (Snedecor and Cochran 1967).

ANCOVA was used to test effects of CANOPY and STATION on capture rates for number of individuals and number of species, and to evaluate effects on capture rates of STATION, DAYS, SEASON, RAIN, and TEMPERATURE. The effects of these factors on capture rates were first tested in a full model ANCOVA. Non-significant factors and non-significant interactions among significant factors were then removed from the model before re-running ANCOVA again to produce final results. We then replaced the variable STATION with CANOPY in the final full-model ANCOVA to determine if this simple index of vegetation structure could explain a greater amount of variation. This variable substitution converted the six station classes to six ordinal measures. We used type III sums of squares to evaluate factor significance, type I sums of squares to investigate importance of interactions among independent variables, and adjusted least-square means (LSM) to produce probabilities for the hypothesis that one least square-estimated mean equals another.

We used SAS procedures PROC GLM, PROC UNIVARIATE, and PROC CORR for tests of significance (SAS Institute 1999). We calculated the Bartlett test scores and PROC REGRESSION to verify homogeneity of variances and slopes among class variables before using a parametric GLM.

RESULTS

CANOPY HEIGHT (CANOPY)

Mean canopy height at nets differed significantly among stations (ANOVA, $r^2 = 0.704$, $F = 40.04$, $P < 0.001$; Table 1). Mesic Upland Forest II nets had higher CANOPY and Riparian Forest nets had lower CANOPY than nets at all other stations ($P < 0.001$). The only other difference among stations was that CANOPY at Palm Forest nets was higher than at Mesic Upland Forest I nets ($P < 0.001$).

On a net-by-net basis, the number of individuals captured/10 net-h declined significantly with increase in mean canopy height ($r = -0.79$, slope = -0.327/m, $P < 0.001$; Fig 2A). Both STATION ($F = 13.36$, $P < 0.001$) and CANOPY height ($F = 5.4$, $P < 0.05$) had significant independent effects, explaining 60.9% of the variation in capture rates (ANCOVA, $F = 21.58$, $P < 0.001$).

Similarly, the rate at which new species were caught at the nets declined with increasing canopy height ($r = -0.78$, slope = -0.316 species/m, $P < 0.001$; Fig 2B). The ANCOVA was significant ($r^2 = 0.623$, $F = 22.87$, $P < 0.001$), and both STATION ($F = 13.52$, $P < 0.001$) and CANOPY ($F = 4.1$, $P < 0.05$) affected species capture rates. Capture rates at Riparian nets, where CANOPY was lowest, were higher than capture rates at other stations (Fig. 2), but capture rates at other stations overlapped considerably despite a wide range of CANOPY heights.

MULTIFACTORIAL ANALYSES

All species combined.—The full ANCOVA model was highly significant, explaining 89.7% of the variation in total capture rates of all species combined (Table 2). STATION and the two covariates DAYS and RAIN were significant factors, whereas SEASON and TEMPERATURE were not. There were no significant interactions among the independent variables, and no autocorrelation between the residuals of the significant variables, DAYS and RAIN ($D = 2.318$, $> d_U = 1.622$, $N = 46$, $P < 0.05$). Capture rates at Riparian Forest were significantly higher than at other stations ($P < 0.001$). Palm Forest capture rates were significantly higher than those at both Dry Upland stations ($P < 0.05$).

TABLE 1. MEAN CANOPY HEIGHT AT MIST NET STATIONS IN SIX TROPICAL FOREST STATIONS, RIO BRAVO CONSERVATION MANAGEMENT AREA, BELIZE

	Canopy height (m)				
Station	Mean	SE	SD	CV	N
Dry Upland Forest I	15.52	0.498	1.928	12.42	15
Dry Upland Forest II	15.22	0.882	3.416	22.44	15
Mesic Upland Forest I	14.95	0.821	3.179	21.26	15
Mesic Upland Forest II	20.96	0.800	3.099	14.79	15
Palm Forest	14.53	0.741	2.87	19.76	15
Riparian Forest	7.742	0.468	1.812	23.40	15

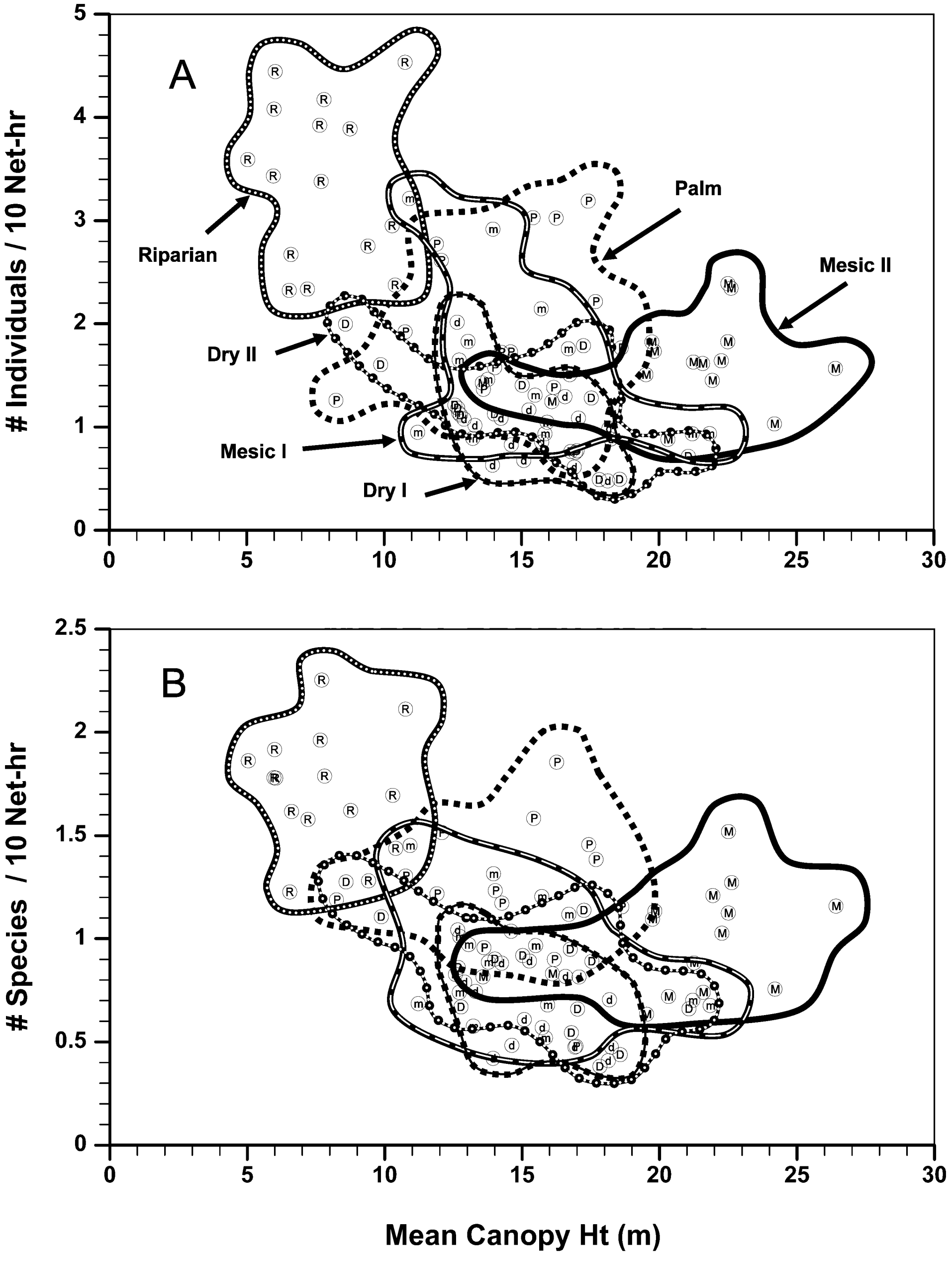

FIGURE 2. Capture rates versus mean canopy height (m) around each mist net (N = 90) at six forest stations in the Rio Bravo Conservation and Management Area, Belize (plotted on untransformed axes). (A) Total number of individuals from all species combined /10 net-h; (B) Total number of species/10 net-h. Each net is represented by a letter and the 15 nets at each station are delimited by polygons.

Capture rates clearly vary from session to session (Fig. 3). Nonetheless, there was a slight, yet significant, decline over the entire study period for all stations combined (slope = -0.017/10 day, t = 45, $P \leq 0.001$), and at Dry Upland Forest I, Palm Forest, and Riparian Forest separately. Riparian also had a significant positive interaction with RAINFALL.

Along with examination of the residual plots against DAYS, we found no evidence of autocorrelation in error terms within stations (D ranging

TABLE 2. ANALYSIS OF COVARIANCE (ANCOVA) OF CAPTURE RATES, COEFFICIENTS OF DETERMINATION (r^2), AND ADJUSTED LEAST SQUARE MEANS (LSM) (N = 46)

		Captures/10 net-h					Species/ session
		All species	Residents	Migrants	Individuals	Recaptures	
FULL MODEL	F[a]	15.83***	12.43***	4.86***	9.24***	6.59***	7.38***
	r^2	0.897	0.873	0.728	0.836	0.784	0.803
	LSM	2.43	2.07	0.36	1.85	0.579	25.72
Class Effects							
STATION	F	43.53***	32.20***	11.91***	22.41***	15.56***	19.23***
Dry Upland I	LSM	1.30	1.05	0.255	1.04	0.262	18.94
Dry Upland II	LSM	1.56	1.38	0.176	1.15	0.403	21.45
Mesic Upland I	LSM	2.10	1.78	0.321	1.56	0.538	23.46
Mesic Upland II	LSM	2.05	1.82	0.231	1.73	0.324	23.73
Palm	LSM	2.70	2.3	0.408	2.05	0.641	28.82
Riparian	LSM	5.17	4.25	0.923	3.90	1.27	38.04
SEASON	F	0.40 ns	0.12 ns	0.72 ns	0.08 ns	0.63 ns	0.24 ns
Dry	LSM	2.42	2.10	0.324	0.018	0.630	26.16
Wet	LSM	2.54	2.09	0.447	0.020	0.516	25.32
Covariates							
DAYS	F	15.83***	16.62***	0.04 ns	24.44***	8.45**	0.89 ns
RAIN	LSM	9.06**	7.63**	1.19 ns	5.63*	1.51 ns	0.49 ns
TEMPERATURE	LSM	0.73 ns	2.96 ns	4.43	1.61 ns	1.23 ns	1.12 ns
Interactions							
STATION * SEASON	F	1.99 ns	1.79 ns	0.62 ns	1.38 ns	0.33 ns	1.52 ns
RAIN * SEASON	F	0.08 ns	0.03 ns	1.52 ns	0.02 ns	0.12 ns	0.07 ns
TEMPERATURE*SEASON	F	0.37 ns	0.12 ns	0.56 ns	0.06 ns	0.70 ns	0.27 ns

[a] F values for Type III Sums of Squares, probability of significance: P < 0.05 *, P < 0.01 **, P < 0.001 ***; ns = not significant.

from 1.81 at Mesic Upland Forest II to 3.05 at Dry Upland Forest I), except that at Dry Upland Forest II, D = 1.26, which is inconclusive. With seven to eight sessions at each station, we used the bounds for two independent variables for the smallest sample size available for the Durbin-Watson statistic (d_L = 0.95, d_U = 1.54, N = 15, $P \leq 0.05$). Total capture rate for all species combined did not differ between wet and dry seasons, either before (F = 0.29, df = 45, ns) or after controlling for the effects of other factors (Table 2). However, capture rates were depressed with increasing rainfall during sessions (regardless of season), after adjusting for the other factors in the ANCOVA (slope = -0.811/10 day, P < 0.001). Riparian Forest was the only single station at which rainfall significantly affected overall capture rate (slope = -5.3, t = -5.47, P < 0.01; with significant interaction of DAYS).

A simple ANCOVA on overall capture rates (total captures, all species combined) for the 46 sessions with mean CANOPY as a class variable instead of STATION, and including DAYS, gave identical results as when class STATION was used (r^2 = 0.796, F = 25.43, P < 0.001; either STATION or CANOPY F = 29.65, P < 0.001; DAYS F = 8.42, P < 0.01). When CANOPY was entered as a continuous variable, the model was still highly significant, but CANOPY did not explain the variation in capture rates as well as did STATION (r^2 = 0.451, F = 33.56, P < 0.001; DAYS F = 2.54, ns).

Other capture rates.—Separate multifactorial analyses were conducted for number of birds captured/10 net-h of resident species, migrant species, individuals of all species combined (excluding within-session recaptures), recaptured individuals of all species combined (within-session recaptures), and for the rate at which new species were detected within each session. Although there were differences in significance levels, patterns were similar to those described above for all species combined (Table 2). Migrant species stood out as having capture rates unaffected by DAYS, and this was the only group affected by TEMPERATURE, which probably reflects the seasonal difference in presence of these species in the study area. Rate at which new species were captured was significantly affected only by STATION. Numbers of species captured at the Riparian and Palm Forest stations were significantly higher than elsewhere, and were higher at both Mesic Upland Forest stations than at Dry Upland I.

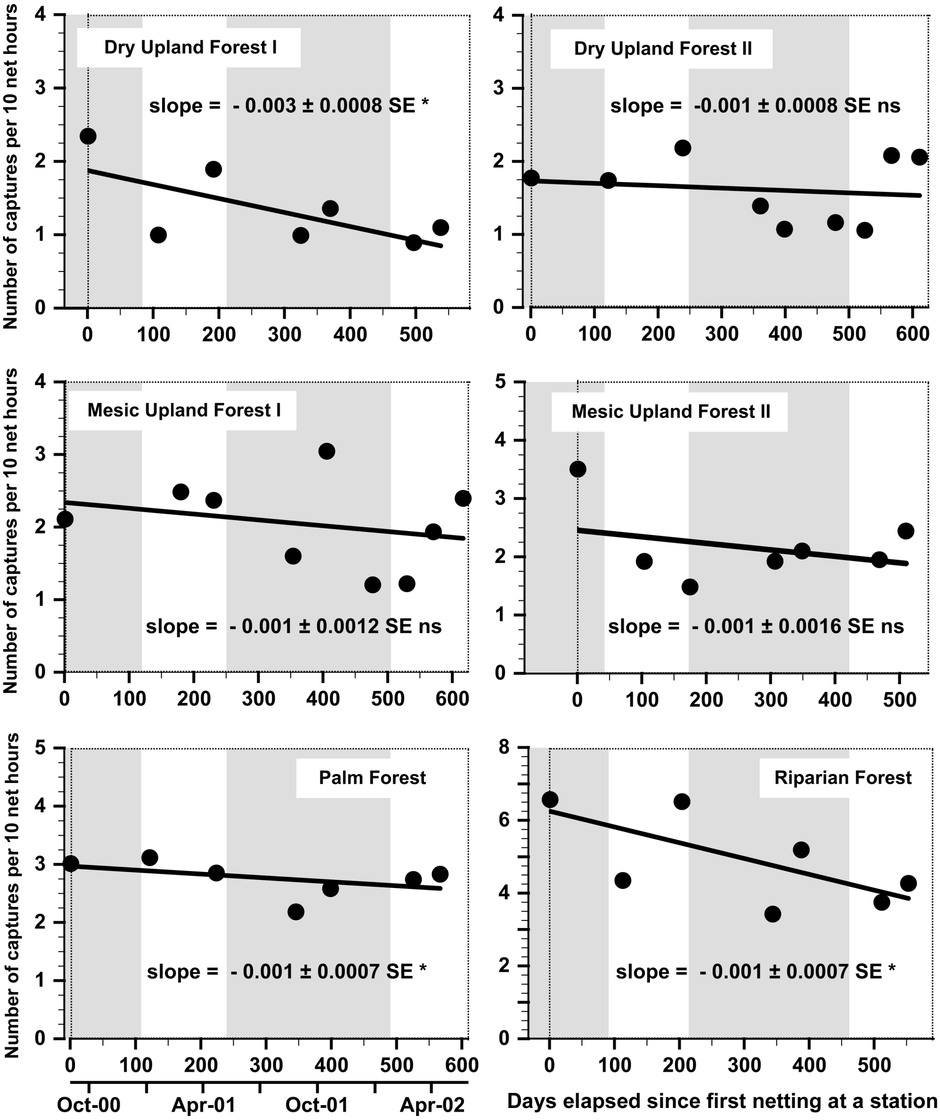

FIGURE 3. Mean capture rates (total captures, all species combined) for 46 sessions among six stations, in four forest types, netted from September 1990 to May 1992 in the Rio Bravo Conservation and Management Area, Belize. Sessions are in chronological order by the number of days elapsed since netting first began at each station, starting at zero along the horizontal axis. The *y*-axes are off-set in each plot to synchronize the *x*-axes by date (second axis on lower left). Wet seasons are shaded; dry seasons are unshaded. Slope of the regression ±SE is shown for each station, along with significance (asterisk indicating P < 0.05).

There was no autocorrelation among capture rate residuals for resident species ($D = 2.072 > d_U = 1.622$, $N = 46$, $P < 0.05$), migrant species ($D = 1.879 > d_U = 1.622$, $N = 46$, $P < 0.05$), individuals ($D = 2.461 > d_U = 1.622$, $N = 46$, $P < 0.05$), recaptures ($D = 2.226 > d_U = 1.622$, $N = 46$, $P < 0.05$), or species ($D = 2.463 > d_U = 1.622$, $N = 46$, $P < 0.05$).

DISCUSSION

EFFECT OF CANOPY HEIGHT (CANOPY)

We chose canopy height as an index of vegetation structure because it is simple to measure and interpret, although structural complexity and density below the canopy will also influence the height distribution of birds and their probability of capture. The net-by-net decline in the number of individuals and number of species captured/10 net-h as canopy height increased demonstrates how capture rates may be biased by canopy height differences among habitats (see also Gram and Faaborg 1997, Whitman et al. 1997), but not all of the differences in capture rates among stations were explained by canopy height (Fig. 2.).

There are at least two reasons why relative capture rates among locations with vegetation of differing height would not reflect true relative abundance of some species. First, taller forests usually have more distinct vegetation layers than do shorter forests in the tropics, supporting midstory and subcanopy specialists, which rarely venture into the understory and get caught in mist nets. Some of these specialist species rarely occur in shorter forests, but many of them will shift their foraging lower as canopy height decreases, thereby increasing their probability of capture (Rappole and Ramos 1995, Remsen and Good 1996). Second, canopy and subcanopy species at times follow the foliage–air interface into shorter second-growth (Stiles 1983). In both cases, these specialists will be caught disproportionably higher in nets in shorter vegetation than in nets in taller forest, their primary habitat.

Unfortunately, measuring vegetation structure around nets cannot be used to adjust capture rates for canopy height bias unless the species-specific capture probabilities are known. Timed behavioral observations documenting the height distribution of many individuals of each species, in a variety of habitats, are needed to quantify these probabilities.

MULTIFACTORIAL ANALYSES

The ANCOVA statistically isolated the effect of STATION on capture rate, and determined the significance of independent effects of SEASON, TEMPERATURE, RAINFALL, and DAYS elapsed since the first netting session at a station. Thus, potential biases that could affect comparisons of STATION were either controlled or dismissed, using objective statistical tests, such that comparison of results among stations should be less biased by the factors we measured.

STATION.—ANCOVA results indicated that Riparian Forest capture rates (all measures) were significantly higher than at all other stations, and that there were also other station differences. However, it is important to remember that the GLM models do not indicate causes. Stations could differ for ecologically meaningful reasons, because of biases not tested, or as a result of noise from random errors. Further analyses, for instance testing for capture rate differences by taxon, guild, breeding status, flocking behavior, or foraging strata, could reveal why capture rates are different among stations.

DAYS.—Declining capture rates over time at a study location could be evidence of the development of long-term net shyness, caused by local birds learning to avoid net locations. Except for migrant captures and the number of species caught/10 net-h, the ANCOVAs detected significant declines in capture rates over 500–600 days since netting first began at stations. However, this represents a modest decline of about 1 fewer captures/100 net-h/60 days elapsed. Although unlikely given the length of our study, the decline could be a result of true decline in population size. This could be tested by simultaneous population monitoring with a method that does not involve capture.

We designed our protocol in part to minimize disturbance during set up and operation of nets, and to minimize net visibility and effects of net shyness. We used 15 nets, relatively few compared to some other studies, at randomized locations. Although it is currently unknown whether randomness of net site affects development of net shyness, it is certainly possible that linear net arrays, or placement of nets in “good” sites for capture (where bird activity is high) would give birds a relatively high chance of gaining experience with specific net sites. When we first established the net sites we cut and removed as little vegetation as needed to avoid net tangling. We did not cut net poles, but used tent poles. Following establishment, net sites needed little further maintenance. The frequency of days between our netting sessions at stations was bimodal (modes = 41, 122 days; min = 38, max = 179). Usually nets were open on only two sequential days, an average of less than 3.4% of the days between first and last netting day at each station. Thus, any individual bird should have had few encounters with nets, and minimal visual cues for learning net sites.

Nonetheless, we have indirect evidence that some individuals might learn to avoid nets for several months. A number of migrant warblers first banded in the fall 1990 and not recaptured during that overwintering season, were recaptured the next year. Also, the proportion of migrants recaptured from the fall to following spring for each of the two over-wintering seasons were much higher during the second year than the first year, long after obvious visible cues to net site had disappeared.

SEASON.—In most tropical areas the distribution and behavior of animals changes with distinct wet and dry seasons (Karr 1976, Bell 1982, Karr et al. 1982, Terborgh 1983, Levey 1988). In our study, capture rates were lower during rainy netting sessions, but did not differ between wet and dry seasons. This apparent contradiction could be a result of the fact that the dry seasons during our study were relatively wet (in fact, the two wettest sessions occurred in the dry season), and the wet seasons relatively dry. It can rain on any given day in either season, so capture rates on occasional netting days can, by chance, be unrepresentative of seasonal rainfall. Of note with respect to canopy height biases, Pearson (1971) suggested that foraging height in several species shifted seasonally.

On the other hand, we did not look at the effects on capture rates of several other factors that vary temporally, such as the breeding schedule of year-round residents, or timing of residency for nearctic migrants. Breeding in year-round residents is tied to the seasonality of food resources, and begins in February with a small pulse of young and immatures produced in March and a larger cohort produced starting in May, peaking in August and tapering off in December when hatching year plumages become undistinguishable. Nearctic migrants start arriving in August, and most depart by mid April. Migrant captures peak in November and April, likely the result of both passage-migrants wintering further south and local movements of winter residents settling in after arrival or becoming restless in preparation for their departure to the north. Riparian Forest had the most passage-migrant species of all stations, but transients are commonly observed in more open habitats in the RBCMA during migration (Mallory et al. 1998).

RAIN.—Except for migrants and species numbers, rain depressed capture rates. However, although significant, the effects were small relative to other variables in the ANCOVA. One might expect birds to be less active during rain and more active between rain showers. However, this was not borne out when capture rates from rainy and dry days are compared on the basis of time that nets were actually open. Flocks often continue moving or foraging during rain (Poulsen 1996; E. Mallory, pers. obs.). Elsewhere in the tropics with more rainfall or a harsher dry season, rain or the lack thereof may have larger effects on bird activity and capture rates. Also, if netting were repeated in the RBCMA during more typical wet or dry seasons than during this study, results could be different from what we report here.

CANOPY.—There are several reasons why average CANOPY height did not explain capture rates better than STATION in the ANCOVA model. First, almost all the variation in canopy height among the nets was lost when reduced to the average values for the six stations (therefore reducing the power to adjust for this bias in capture rates). This indicates that single estimates of canopy height, even when based on data pooled from the exact net locations, are not adequate to statistically adjust for CANOPY height bias. Instead, statistical adjustments in capture rates would have to be calculated net-by-net, before averaging the results for a station. Second, the highest net canopies were at Mesic Upland II, but net capture rates there were not substantially different from those at other upland stations (Fig. 2), and the most productive nets there tended to be under the highest canopy. Third, true population differences in species richness and relative abundance exist among forests that are not directly related to canopy height. Fourth, other factors differing among stations, but not included in this model, could have had significant effects on capture rates and interacted with canopy height effects.

Tropical residents versuss nearctic migrants.—Because 16–25% of captures were of migrants, which are absent from the study area for at least four months each year, our results were heavily influenced by the abundance and behavior of resident species. Migrant capture rates, and the number of migrant species captured, were significantly higher at Riparian Forest but showed no other differences. Migrants sample sizes may have to be enlarged to detect other effects.

CONCLUSIONS AND STATISTICAL CONSIDERATIONS

We have demonstrated the effects of several biases and how they can be controlled statistically. However, many other factors should be considered that may affect capture rates more than those we included in our study, such as sex, age, stage of molt, fat level, breeding condition, the successional stage of vegetation, distance of nets from a road, and habitat disturbance.

The goals of a mist-net study are usually a variant of the questions: how many birds of which species are present, where and when are they present, what they are doing, and why. Statistics provide an objective means of interpreting data, providing probabilities of reliability, as long as the data meet the assumptions of the models. Frequently, testing the assumptions of normality, independence, and homogeneity of variances among observations is ignored, invalidating the use of parametric statistics. For instance, it is rare that stations and their mist-net locations are randomized. We were able to control bias in our analyses with multivariate techniques because our experimental design incorporated randomization of our station locations, we standardized our netting protocol, and we quantified the sources of bias in the field. We urge all mist-net operators to consider potential sources of bias, and design studies to incorporate measurements enabling statistical removal of these biases in the analysis stage.

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