TABLE 1. CONTINUED

Species	Captures/1,000 net-h	CV
Hooded Warbler (*Wilsonia citrina*)	27.97	0.65
Wilson's Warbler (*W. pusilla*)	0.05	2.24
Yellow-breasted Chat (*Icteria virens*)	3.45	0.72
Chestnut-sided Warbler (*D. pensylvanica*)	2.41	0.67
Summer Tanager (*Piranga rubra*)	20.20	0.20
Scarlet Tanager (*P. olivacea*)	13.16	0.60
Dark-eyed Junco (*Junco hyemalis*)	0.05	2.24
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	18.47	0.68
Blue Grosbeak (*Guiraca caerulea*)	4.15	0.42
Indigo Bunting (*Passerina cyanea*)	43.85	0.54
Painted Bunting (*P. ciris*)	7.33	0.83
Dickcissel (*Spiza americana*)	0.38	1.56
Bobolink (*Dolichonyx oryzivorus*)	0.13	2.24
Orchard Oriole (*Icterus spurius*)	26.92	0.41
Baltimore Oriole (*I. galbula*)	4.49	0.49

were netted at each of our stations each year. Daily patterns of arrival at stopover sites varied considerably from year to year, as illustrated by five years of capture data from East Ship Island (Fig. 2). Numbers of individual birds captured/recaptured on East Ship Island each year were: 873/70 (1987), 2,327/385 (1988), 3,080/306 (1989), 2,585/437 (1990), and 2,151/240 (1991); and on Horn Island 2,022/419 (1992). The annual percent of birds recaptured one or more times ranged from 8.0–20.7% (mean = 13.05 ± 4.36%). Annual spring capture rates, first captures, and recaptures combined for all species, ranged from 0.35 to 0.70 birds per net hour.

The mean number of birds netted annually/1,000 net-h varied considerably within species (Table 1). Coefficients of variation (CV; Zar 1984) for annual mean rates from 1987 to 1991 on East Ship Island provide an index of annual within-station capture rate variability. For example, over all years, approximately 63 White-eyed Vireos were captured/1,000 net-h, but annual capture rates were highly variable (CV = 74%). In contrast, Black-and-white Warblers were caught less often (16/1,000 net-h), but annual capture rates were much less variable (CV = 27%).

Most of the birds captured at our study sites had low fat reserves. Overall, slightly over 50% were scored "0 fat," although there was some variation in the average condition of birds from year to year (Fig. 3).

FIGURE 1. Study sites on the north shore of the Gulf of Mexico. Site 1 = Peveto Beach, Louisiana, Site 2 = Ship and Horn Islands, Mississippi.

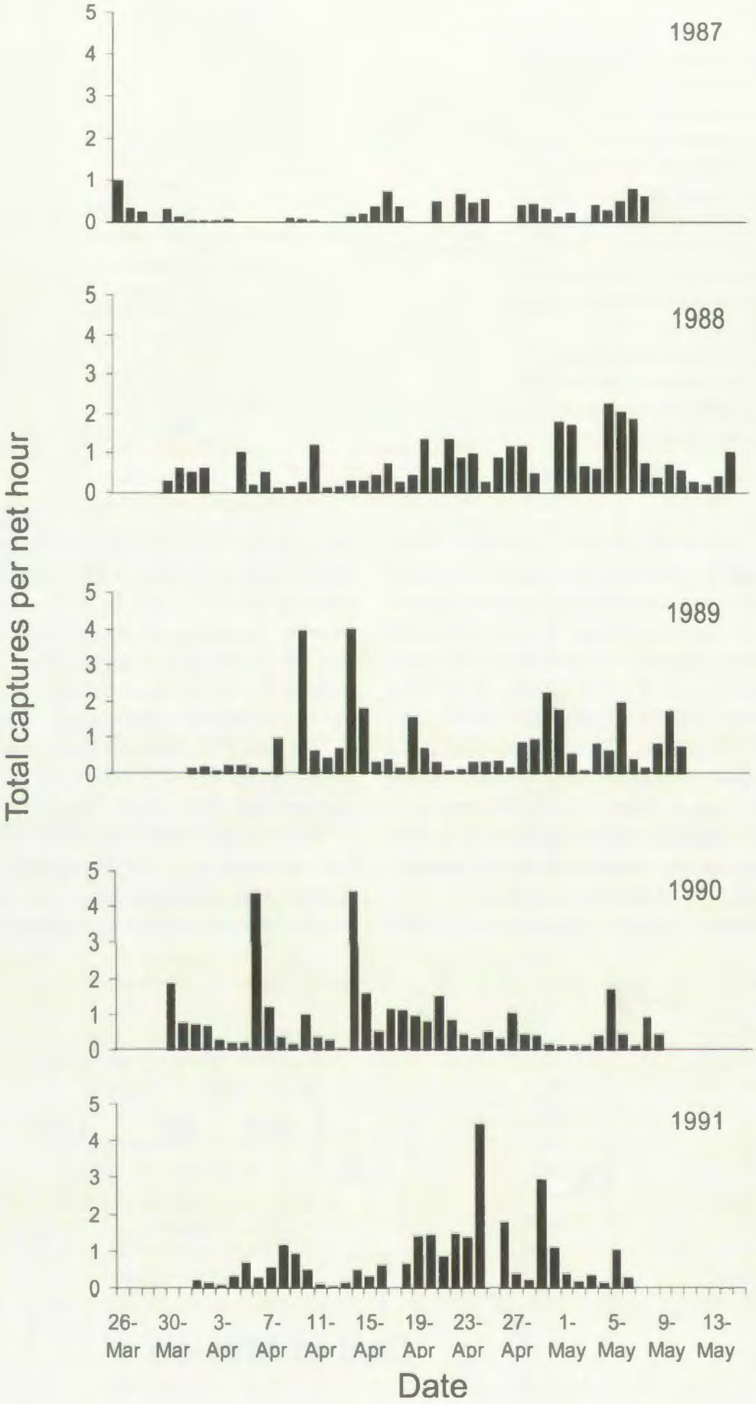

FIGURE 2. Capture rates of trans-Gulf migrants on East Ship Island, 1987–1991.

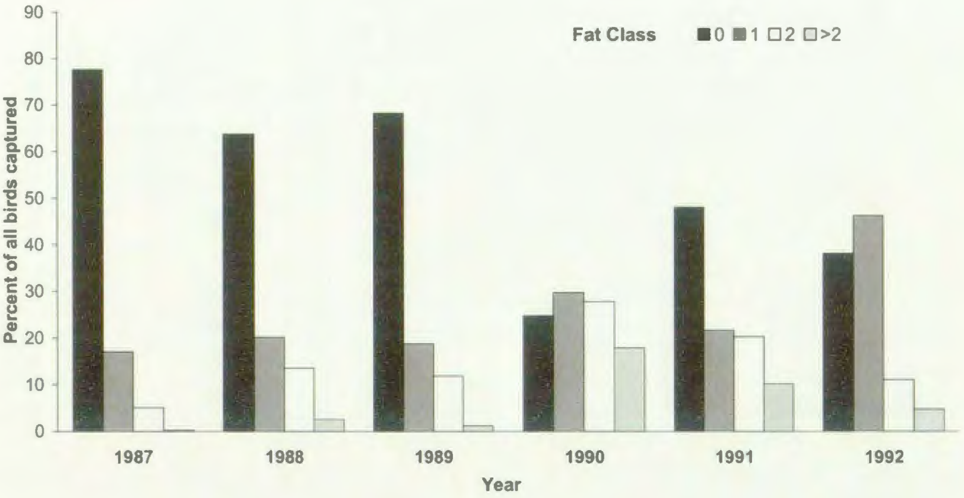

FIGURE 3. Distribution of arrival fat scores of trans-Gulf migrants netted at East Ship Island (1987–1991) and Horn Island (1992), Mississippi.

Birds with no fat reserves were more likely to remain at stopover sites and be recaptured than were birds with higher levels of body fat (Fig. 4). Examination of arrival weight and stopover length for six common species illustrates the pattern. In general, birds arrived at Peveto Beach in better condition (Table 2) and tended to depart sooner (Table 3) than birds at East Ship island. We previously found evidence of differences in habitat quality related to prey availability at the two stations (Moore and Simons 1992, Simons et al. 2000), which may explain why birds at Peveto Beach tended to gain weight more quickly than birds stopping over on East Ship Island (Table 4). Thus, the capture probabilities for individual birds at these two stopover sites appeared to be a function both of the bird's arrival condition and the availability of food at the stopover sites.

We compared mist-netting data from Horn Island in Mississippi Sound with data collected simultaneously from a coastal weather radar site, and from field censuses on mainland habitats (Fig. 5), to evaluate the stopover habitat requirements of trans-Gulf migrants at broader geographic scales. Results provide some indication of the extent to which mist-net data from a single station reflect conditions at a broader scale (Fig. 6). Over the course of the entire

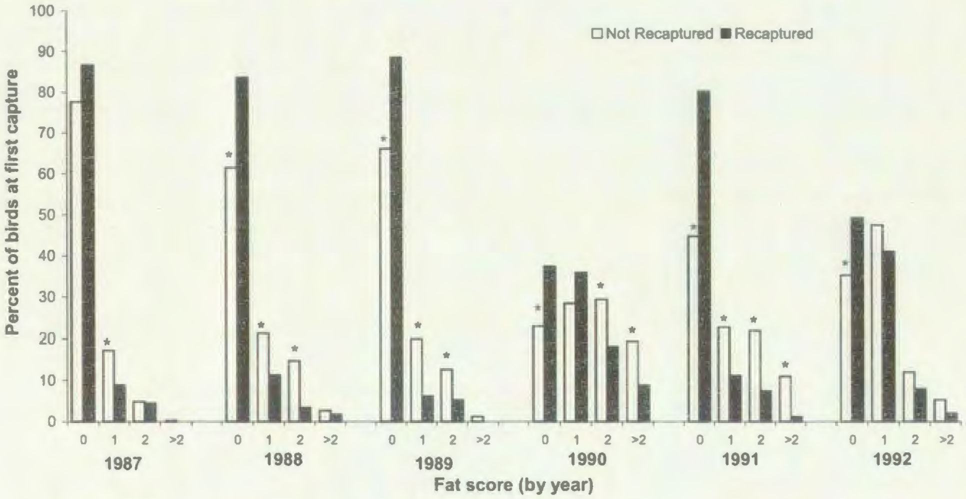

FIGURE 4. Fat score vs. recapture status of trans-Gulf migrants netted on East Ship Island (1987–1991) and Horn Island (1992), Mississippi. * indicates difference between percents (t-test, $P < 0.05$).

TABLE 2. AVERAGE ARRIVAL WEIGHT (GRAMS) OF TRANS-GULF MIGRANTS AT COASTAL STOPOVER SITES

Species	Site	1987	1988	1990	1991
Hooded Warbler	PEV	9.67 ± 0.86 (273) *	9.57 ± 0.90 (288)	9.84 ± 0.85 (134) **	9.62 ± 0.88 (58)
	ESI	9.40 ± 0.90 (31)	9.80 ± 0.90 (32)	9.30 ± 1.10 (152)	9.70 ± 1.00 (94)
Red-eyed Vireo	PEV	15.65 ± 0.16 (199) **	15.79 ± 1.59 (574) **	15.82 ± 1.53 (80)	16.26 ± 2.10 (25)
	ESI	15.00 ± 1.70 (170)	15.5 ± 1.60 (883)	15.70 ± 1.70 (280)	16.40 ± 1.90 (370)
Indigo Bunting	PEV	12.25 (1)	12.80 ± 1.38 (372) **	12.88 ± 1.21 (49)	13.08 ± 1.43 (85)
	ESI	12.70 ± 1.50 (50)	13.60 ± 1.80 (360)	12.80 ± 1.70 (101)	12.80 ± 1.40 (105)
Black-and-white Warbler	PEV	9.53 ± 0.89 (33)	9.56 ± 0.90 (147) **	9.62 ± 1.15 (31) **	9.30 ± 0.75 (27)
	ESI	9.30 ± 0.80 (29)	8.80 ± 1.00 (65)	8.60 ± 0.80 (62)	9.20 ± 0.90 (62)
Summer Tanager	PEV	27.17 ± 2.38 (56) *	27.63 ± 2.47 (154) **	28.60 ± 3.50 (73) *	27.77 ± 2.81 (37)
	ESI	26.10 ± 2.30 (45)	26.30 ± 2.30 (93)	27.30 ± 3.30 (73)	28.80 ± 3.10 (43)
White-eyed Vireo	PEV	11.15 ± 0.92 (41) **	11.42 ± 1.12 (138) **	11.27 ± 1.22 (81) **	11.27 ± 1.05 (17)
	ESI	10.60 ± 1.00 (73)	10.60 ± 0.90 (91)	10.60 ± 1.00 (536)	11.00 ± 1.20 (228)

Notes: PEV = Peveto Beach, Louisiana, ESI = East Ship Island, Mississippi. Data are reported as mean ± one SE (N). Two sample t-test for differences between sites, one-tailed P values reported as * ($0.01 < P < 0.05$), ** ($P < 0.01$).

TABLE 3. AVERAGE DAYS OF STOPOVER BY TRANS-GULF MIGRANTS AT COASTAL STOPOVER SITES (MOORE AND KERLINGER 1987)

Species	Site	1987	1988	1990	1991
Hooded Warbler	PEV	1.43 ± 0.74 (41)	3.15 ± 2.67 (106)	1.85 ± 1.66 (33) *	2.61 ± 1.75 (23)
	ESI	4.50 ± 4.95 (2)	1.00 (1)	2.97 ± 2.37 (30)	2.20 ± 1.48 (9)
Red-eyed Vireo	PEV	2.00 ± 1.00 (4)	2.00 ± 1.80 (36)	2.92 ± 2.23 (12)	2.00 (1)
	ESI	2.33 ± 1.53 (3)	1.97 ± 1.90 (29)	2.57 ± 1.90 (7)	1.80 ± 1.30 (5)
Indigo Bunting	PEV	–	3.10 ± 4.36 (11)	–	2.00 ± 2.00 (2)
	ESI	2.00 ± 1.00 (3)	3.52 ± 3.67 (31)	7.18 ± 9.81 (17)	2.20 ± 1.10 (5)
Black-and-white Warbler	PEV	1.33 ± 0.58 (3)	2.50 ± 2.00 (19) **	2.50 ± 2.12 (2)	2.00 ± 1.00 (3)
	ESI	1.50 ± 0.71 (2)	1.50 ± 0.65 (14)	3.41 ± 2.69 (17)	2.60 ± 3.72 (10)
Summer Tanager	PEV	1.75 ± 0.95 (4)	1.80 ± 0.87 (19)	2.22 ± 1.72 (9)	13.00 (1)
	ESI	3.00 ± 2.83 (2)	1.75 ± 1.49 (8)	3.80 ± 4.09 (5)	3.67 ± 3.06 (3)
White-eyed Vireo	PEV	1.83 ± 1.17 (6)	3.40 ± 3.45 (33)	2.18 ± 1.47 (11) **	2.00 ± 1.73 (3) **
	ESI	2.67 ± 1.63 (6)	2.90 ± 2.71 (30)	5.11 ± 5.71 (75)	4.84 ± 5.62 (37)

Notes: PEV = Peveto Beach, Louisiana, ESI = East Ship Island, Mississippi. Data are reported as mean ± one SE (N). Two sample t-test for differences between sites, one-tailed P values reported as * ($0.01 < P < 0.05$), ** ($P < 0.01$).

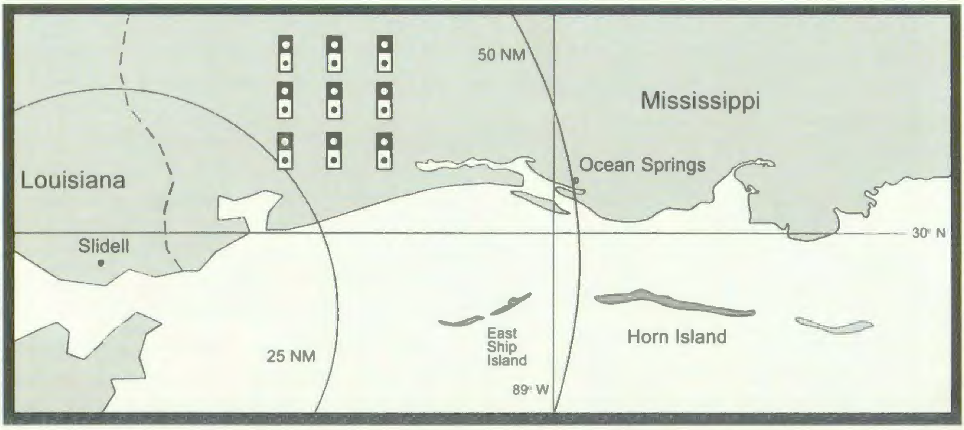

FIGURE 5. Study sites used for comparison of data on migratory bird activity collected using mist nets (Horn Island, Mississippi), field censuses (9 paired study sites in pine uplands and riparian habitats, coastal Mississippi; shown by paired squares with circles in them), and radar imagery (WSR-57 weather radar, Slidell, Louisiana).

season, mist-net capture rates, migratory activity indicated by radar echoes, and the number of migrants detected on field censuses were correlated within a geographic radius of 100 km. Peaks in coastal migratory bird activity evident in mist-net and radar data around 30 March, 7 April, 20 April, and 1 May were generally followed by peaks in number of passage migrants detected by field censuses on the mainland (Fig 6; Kendall's rank correlation analysis, $W = 0.643$, $\chi^2 = 32.793$, $0.01 < P < 0.025$).

DISCUSSION

Data collected by netting birds at coastal stopover sites are useful for answering a variety of questions related to the ecology and habitat requirements of

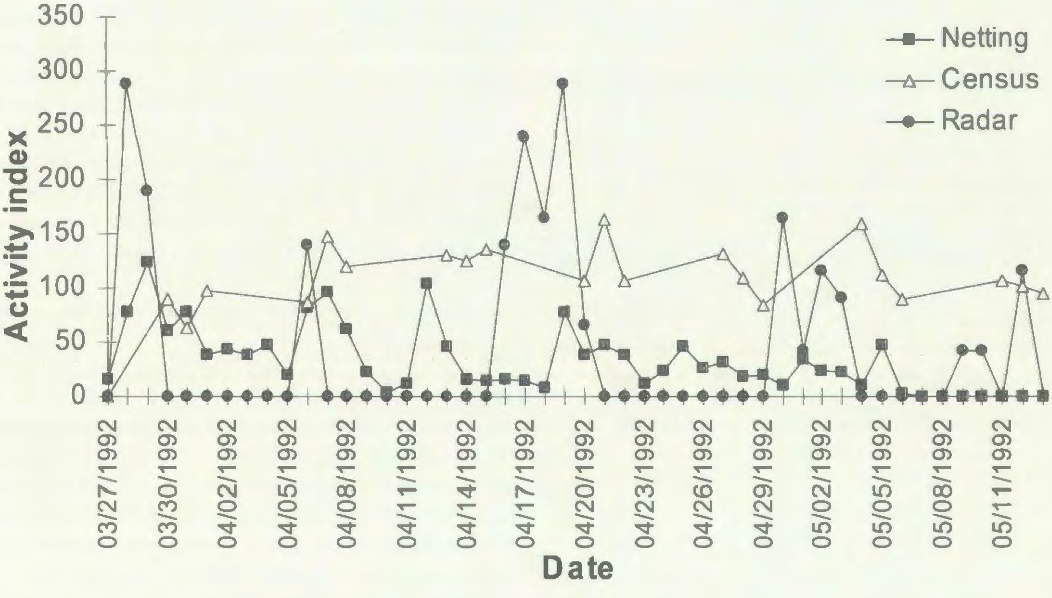

FIGURE 6. Comparison of migratory bird activity based on data from mist netting, field censuses, and WSR-57 radar imagery. Netting data (dark squares) are reported as number of birds captured/50 net-h. Census data (white triangles) are reported as total number of migrants counted in morning censuses. Radar data (dark circles) are reported as the mean number of flocks per 20^0 sector of the WSR-57 radar image (Gauthreaux 1994).

TABLE 4. AVERAGE MASS CHANGE (G/D, SEE KUENZI ET AL. 1991) OF TRANS-GULF MIGRANTS AT COASTAL STOPOVER SITES

Species	Site	1987	1988	1990	1991
Hooded Warbler	PEV	0.16 ± 0.69 (41)	0.18 ± 0.39 (106)	0.003 ± 0.43 (33)	0.22 ± 0.25 (23)
	ESI	0.38 ± 1.59 (2)	–	-0.42 ± 1.78 (30)	-0.25 ± 0.95 (9)
Red-eyed Vireo	PEV	0.10 ± 0.56 (11)	-0.19 ± 0.78 (36) **	0.18 ± 0.40 (12) **	0.18 (1)
	ESI	–	-1.25 ± 0.73 (29)	-1.23 ± 1.13 (7)	-0.23 ± 0.91 (5)
Indigo Bunting	PEV	–	0.12 ± 0.47 (29)	–0.21 ± 0.10 (2)	
	ESI	-0.17 ± 0.63 (3)	0.03 ± 0.95 (31)	0.48 ± 1.00 (17)	0.09 ± 0.65 (5)
Black-and-white Warbler	PEV	0.34 ± 0.26 (3)	0.15 ± 0.42 (33) *	0.19 ± 0.01 (2)	0.14 ± 0.60 (3)
	ESI	-0.50 ± 0.71 (2)	0.09 ± 1.24 (14)	0.21 ± 0.84 (17)	0.54 ± 0.71 (110)
Summer Tanager	PEV	0.60 ± 0.55 (4)	0.22 ± 2.27 (19) *	0.33 ± 1.00 (9) **	0.47 (1)
	ESI	1.25 ± 1.41 (2)	-1.64 ± 1.54 (8)	2.83 ± 1.47 (5)	0.72 ± 1.41 (3)
White-eyed Vireo	PEV	0.20 ± 0.65 (6)	0.33 ± 0.47 (33) *	0.16 ± 0.32 (11) **	0.27 ± 0.25 (3)
	ESI	-0.17 ± 0.70 (6)	0.08 ± 0.84 (30)	-0.43 ± 1.01 (75)	-0.07 ± 0.79 (37)

Notes: PEV = Peveto Beach, Louisiana, ESI = East Ship Island, Mississippi. Data are reported as mean ± one SE (N). Two sample t-test for differences between sites, one-tailed P values reported as * $(0.01 < P < 0.05)$, ** $(P < 0.01)$.

migratory birds. However, population indices, such as mist-net captures from stopover sites along the Gulf Coast, may not provide data suitable for monitoring population levels if capture probabilities vary over time or space (Pollock et al. 2002).

Analysis of the arrival condition of birds at stopover sites suggests that birds with sufficient energy reserves continue migration, or move to alternate habitats more quickly than lean birds, or that they may simply over-fly some coastal stopover sites entirely. Confirmation of this phenomena is provided during a typical bird "fallout," which occurs when birds encounter late cold fronts or local thunderstorms. Under these conditions, it is common to capture birds with large fat reserves that, under favorable weather conditions, would have simply over-flown these coastal sites (Moore et al. 1990). In 1990, when fallout conditions occurred on East Ship Island in early and mid-April (Fig. 2), birds were fatter on average than in years when fallout events were less common (Fig. 3).

Weather is clearly a dominant factor influencing the total number of birds captured per net-hour at an individual station (Buskirk 1980, Moore and Kerlinger 1987). Weather conditions favorable for migration will reduce the proportion of a population stopping at a migratory stopover site. Favorable weather also increases the likelihood that birds visiting stopover sites will be in better condition. We have shown that recapture rates are lower for migrants in better energetic condition. The average energetic condition of birds (determined by their condition on departure from the wintering grounds, distances flown, or wind conditions encountered enroute) will all influence capture probabilities at stopover sites. It is usually not possible to distinguish whether differences in capture rates at stopover sites reflect differences in the average energetic condition of migrants or actual differences in population levels. For long-term trends to be unbiased it has to be assumed that variation in mean annual energetic condition occurs randomly among years.

Finally, variability of habitat quality at stopover sites will also influence the likelihood and duration of stopover, and therefore capture probabilities. Both the yearly succession of vegetation and the temporary abundance of prey within years influence capture probabilities at stopover sites, which is why recommendations for migration monitoring emphasize the need for maintaining uniform habitat (Hussell and Ralph 1998). Thus, differences in seasonal and annual weather patterns, the arrival condition of migrants, and habitat quality at stopover sites all influence the probability of capturing birds with mist-nets at stopover sites along the northern Gulf coast.

Abundance estimates based on mist-net based count indices can be adjusted by modeling date, weather, moon phase and year as covariables (Dunn and Hussell 1995, Dunn et al. 1997, Hussell et al. 1992, Pyle et al. 1993). These approaches may be most suitable for inland sites adjacent to breeding areas where the energetic condition of migrants, habitat conditions, and migratory pathways are less variable. At sites with high daily turnover rates, modeling covariates may provide unbiased indices of population size if the assumption that only newly arrived birds are included in analyses can be met (Dunn and Hussell 1995). When recapture rates are low (<10%) this assumptions may be valid. Higher recapture rates (up to 20%) at our study sites along the Gulf Coast may make it difficult to meet the assumptions of this approach. Modeling covariables may not be sufficient to control for the variability in capture probabilities inherent to populations migrating across large ecological barriers such as the Gulf of Mexico.

Not surprisingly, differences in the factors affecting mist-net capture probabilities appear to increase with the distance between study sites. Differences in the arrival condition of birds at Peveto Beach and East Ship Island (400 km apart) suggest that these sites are sampling populations following different migratory routes. In contrast, local WSR 57 radar, field census results, and mist-net data were correlated on a scale of 50–100 km at our study sites in Mississippi. Williams et al. (2001) observed a similar local scale correspondence between observations of migrants in New Hampshire using portable marine radar, ceilometer, and ground census data.

Presumably, sampling at a fairly fine geographic scale across the northern Gulf would be necessary to understand population level patterns of trans-Gulf migration. Nevertheless, establishing a network of sampling sites along the Gulf Coast would probably prove to be an inefficient approach to population monitoring, because while migration can be viewed as a broad-front phenomena on decadal or longer time scales, annual patterns of arrival tend to be quite localized. In any single year only a small percentage of sites would be expected to collect data sufficient to assess population trends. Thus the sampling frame required to adequately track population trends would be very large and expensive.

Recent advances in the application of WSR-88D Doppler weather radar to bird migration hold the promise that it may one day be feasible to implement a sampling frame sufficient to monitor bird population trends through migration monitoring (Gauthreaux and Belser 1998, Gauthreaux and Russell 1998), although individual species can not be identified. On-going validation studies employing ground truthing of radar imagery with mist-net and census based field data will determine the potential of this new technology.

ACKNOWLEDGMENTS

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

JOHN FAABORG, WAYNE J. ARENDT, AND KATIE M. DUGGER

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

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

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

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

METHODS

STUDY SITE

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

NETTING PROTOCOL

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

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

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

POINT COUNT METHODS

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

RESULTS

SPECIES COMPOSITION

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

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

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

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

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

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

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

** Black-and-white Warbler and American Redstart

CAPTURE RATES WITHIN THREE-DAY NETTING SESSIONS

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

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

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

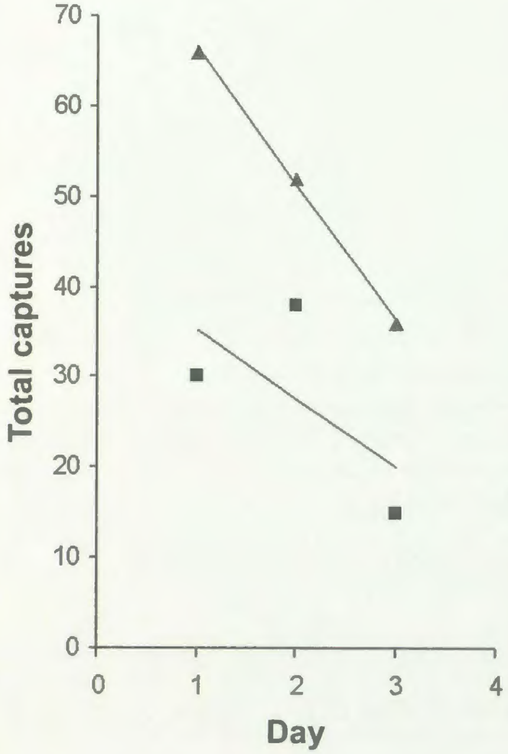

FIGURE 1. Daily capture rates of birds over three-day samples on the original Guanica net line, showing a particularly linear sample (triangles: 1973 sample, $r^2 = 0.99$) and a less linear sample (squares: 1987 sample, $r^2 = 0.41$).

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

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

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

NET AVOIDANCE

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

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

RATES OF CAPTURE THROUGH THE DAY

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

ANNUAL CAPTURE AND RECAPTURE RATES

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

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

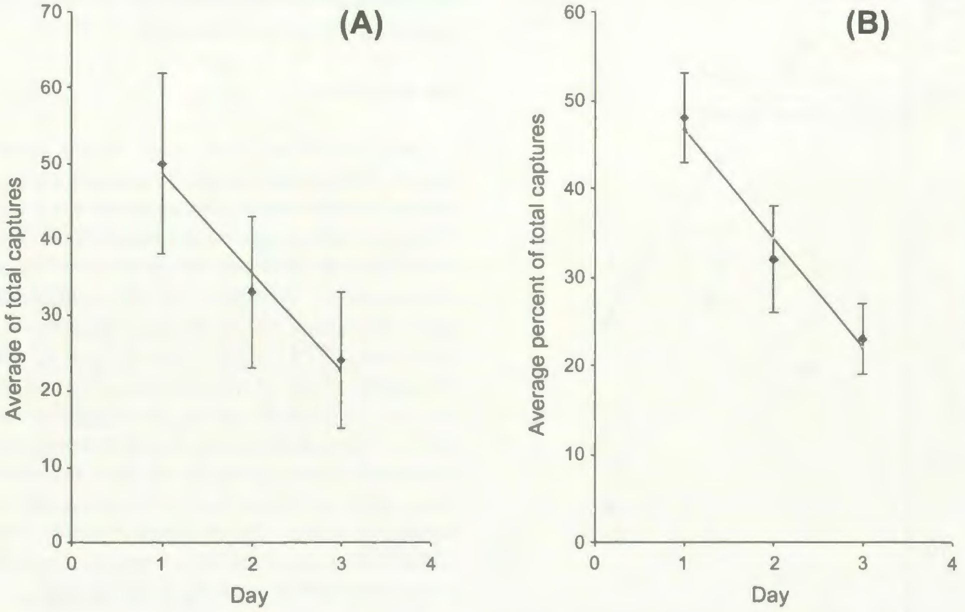

FIGURE 2. (A) Pattern of three-day capture rates by mean of total daily captures (A; $r^2 = 0.972$), or (B) by mean of the percent of total captures caught on each day of the sample ($r^2 = 0.974$) for 18 samples of the original Guanica net line run 1973–1993. Error bars show ±SE.

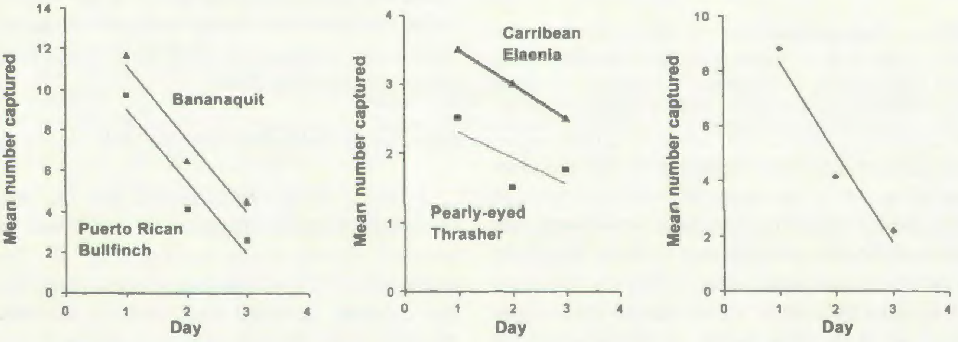

FIGURE 3. Capture rates of species and species groups during the three days of sampling, showing: (A) abundant species with steep declines in capture rates (Puerto Rican Bullfinch [$r^2 = 0.906$] and Bananaquit [$r^2 = 0.945$]); (B) species that have lower and more gradual capture rates (Caribbean Elaenia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

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

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

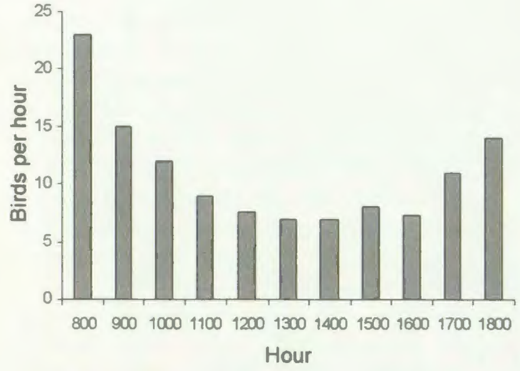

FIGURE 4. Capture rates of birds at the original Guanica net line through the day, averaged for 1990–1995 samples. Birds/hour was computed by counting total captures for the 60-min period ending on the hour (e.g., 0800 hours). First and last hourly periods may include a few birds caught before 0700 hours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

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

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

DISCUSSION

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

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

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

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

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

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

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

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

ACKNOWLEDGMENTS

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

ELIZABETH P. MALLORY, NICHOLAS BROKAW, AND STEVEN C. HESS

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, birds, canopy height, capture rates, experimental design, mist net, multivariate statis-

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 confound 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 low 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 principle, 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 multifactor 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 once during the first wet season, that is, in the third or 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 hourly 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

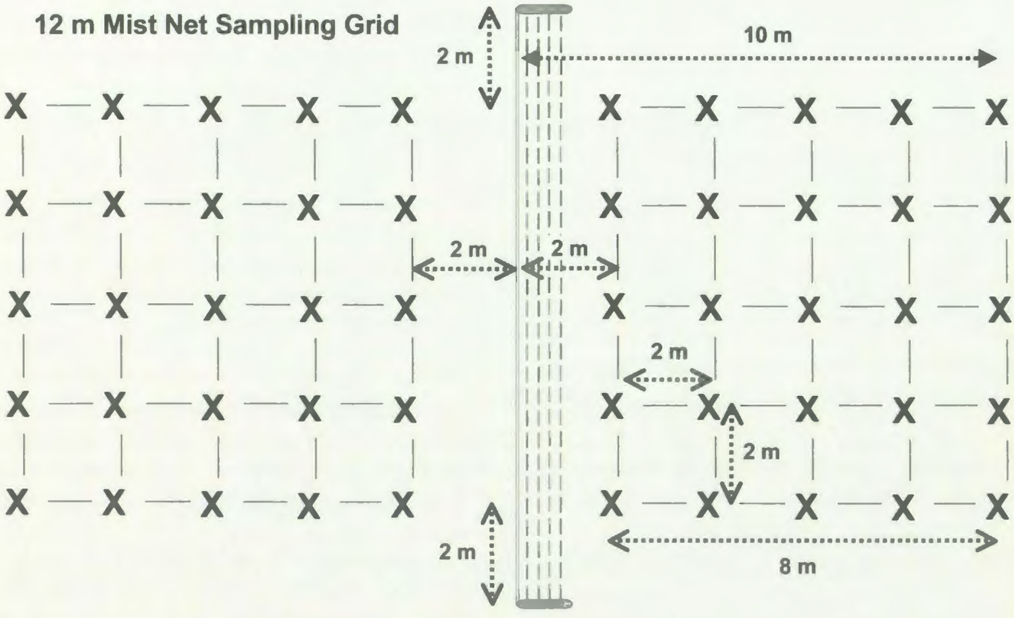

FIGURE 1. Layout of canopy height sample points (X's) at each net.

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

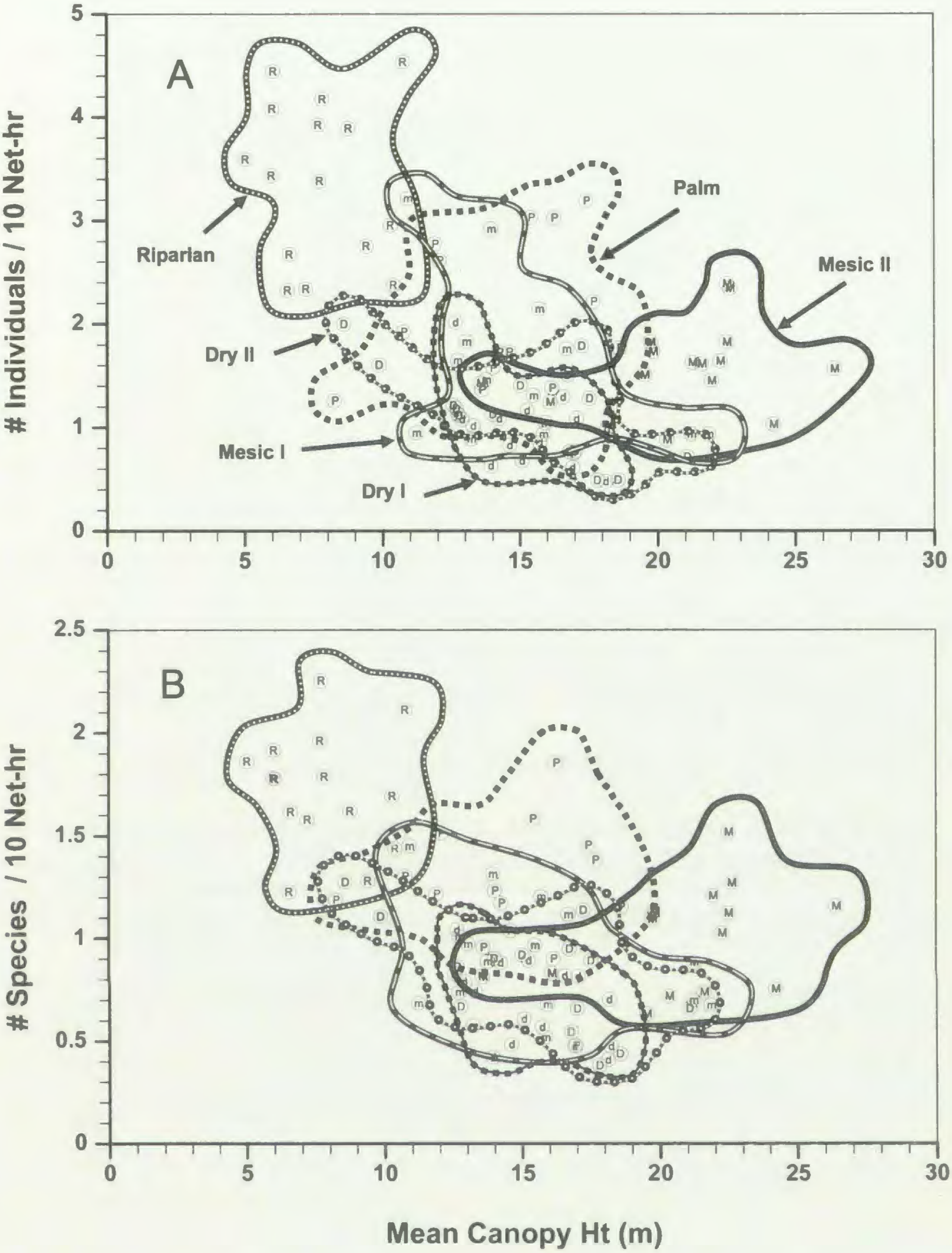

FIGURE 2. Capture rates versus mean canopy height (m) around each mist net (N = 90) at six forest stations in the Rio Bravo Conservation and Management Area, Belize (plotted on untransformed axes). (A) Total number of individuals from all species combined /10 net-h; (B) Total number of species/10 net-h. 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 1, 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					
		All species	Residents	Migrants	Individuals	Recaptures	Species/ session
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	F	9.06**	7.63**	1.19 ns	5.63*	1.51 ns	0.49 ns
TEMPERATURE	F	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.

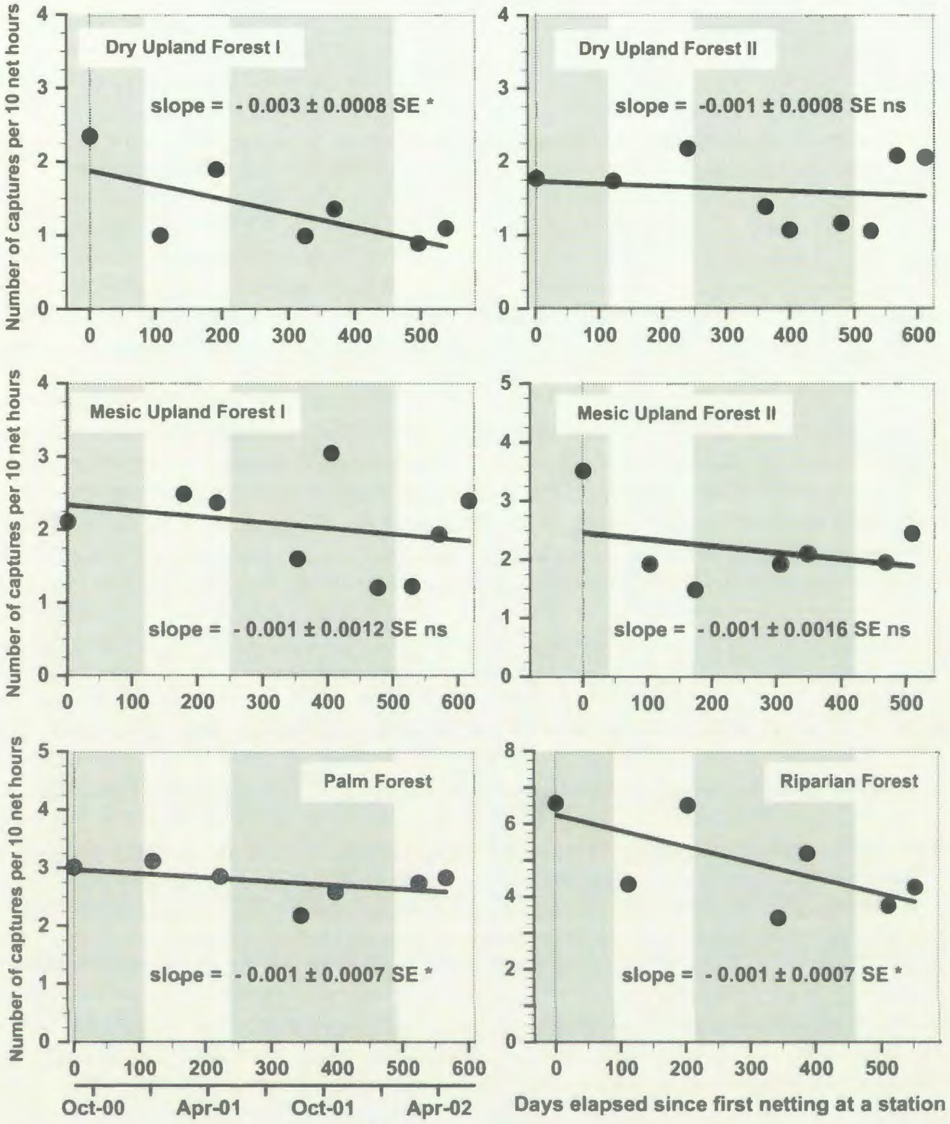

FIGURE 3. Mean capture rates (total captures, all species combined) for 46 sessions among six stations, in four forest types, netted from September 1990 to May 1992 in the Rio Bravo Conservation and Management Area, Belize. Sessions are in chronological order by the number of days elapsed since netting 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 disproportionately more often 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 statistically 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 reduce factors that may contribute to net shyness during set up and operation of nets by minimizing disturbance and net visibility. When we first established the net sites we cleared as little as needed to avoid net tangling and removed vegetation from sites. We did not cut net poles, but used tent poles. Following establishment, net sites needed little further maintenance. 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. 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 after net establishment. A number of migrant warblers first banded in the fall 1990 and not recaptured during that over-wintering 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 1982a, b; 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 versus 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 some 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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USE OF MIST NETS FOR STUDY OF NEOTROPICAL BIRD COMMUNITIES

ANDREW A. WHITMAN

Abstract. I reviewed mist-netting protocols of 43 recent Neotropical bird inventory studies. Most studies had multiple objectives, which likely contributed to a broad range of protocols being used. Most studies used 36 mm mesh, 12 × 2.5 m nets set singly, ~25 m apart. Netting typically took place within the first 8 h of the day starting at sunrise, and was conducted for three consecutive days, but there was much protocol variation within and among studies. Tall forest and agricultural areas were the most frequently studied habitats. Number of captures is affected by effort, net type and distribution, number of net-hours per day, number of days netting at a station, and number of visits to a station within a season. Variation in protocols therefore makes it difficult to compare results among studies, although there are a few techniques for doing so. Inventory by mist nets of a large proportion of species may require an effort of 1,000 net-h, more than in most of the studies reviewed. Any inventory should include aural surveys as well.

Key Words: inventory methods, mist netting, Neotropical birds, Neotropical forest, survey methods.

Mist netting has been commonly used to study bird communities in the Neotropics (Karr 1981b). Because protocols often differ among studies, comparisons of results among mist-netting studies usually involve standardization of effort by expressing captures as birds per net-hour (1 net-h being one net open for 1 h; Ralph 1976). However, variation in other aspects of mist-netting protocols can also preclude direct comparison (e.g., Bierregaard 1990, Pardieck and Waide 1992, Ralph 1976, Remsen and Good 1996, Robbins et al. 1992). Here I review 43 Neotropical mist-netting studies that had species inventory as one of the objectives to illustrate the range of variation in mist-netting protocols and to indicate which factors influence capture rates.

METHODS

DATA SET

Studies reviewed here (Appendix) were selected from Keast and Morton (1980), Hagan and Johnston (1992), Gentry (1990), Wilson and Sader (1995), and from journals over the 16-year period 1986–2002 (including *Auk*, *Condor*, *Biotropica*, *Ecology*, *Ibis*, *Journal of Field Ornithology*, and *Wilson Bulletin*). I excluded studies with undefined mist-netting protocols, or that focused on migrating birds or food habits. The review included 43 Neotropical studies covering 194 sample locations. Studies resulting in multiple publications were included only once. When possible, I used data only from the period from December to March, because many Neotropical mist net studies take place in this period to survey residents and Neotropical migrants simultaneously. Most studies conducted surveys within one season or year. The seasonal restriction also reduced the effect of variation in capture rates caused by migration, or by seasonal shifts in the height strata used by different species (Karr 1981a,b).

For each study, I noted objectives, latitude, habitat (old field, scrub, secondary forest, tall forest, agricultural), canopy height (m), net mesh size (mm), net size (m), meters of mist net run per day, number of nets per net line (a net line being one or more adjacent nets set within 10 m of each other), distance between net lines (m), number of consecutive netting days, number of netting hours per day, use of other census techniques, total net-hours, number of species and of individuals caught, number of visits (periods of consecutive netting days), number of days between visits, and number of stations. "Stations," for the purposes of this paper, are defined as net arrays separated by habitat differences or >500 m. Habitats with canopy heights less than 15 m tall were classified as scrub habitat (including scrub forest).

ANALYSES

To determine which factors affected the number of species and of individuals captured in inventory studies, I used simple pairwise Pearson correlation of number of species and of individuals captured during the entire course of the study with the following as independent variables (Wilkinson 1990): distance between net lines, total net-hours, number of net lines surveyed, number of visits, latitude, number of consecutive days of mist netting during visits, canopy height (m), mesh size of net, meters of net per day, nets per net line, and hours of mist netting per day. I estimated correlations separately for forest stations (secondary and tall forest) and non-forest (old field, scrub, and agricultural) stations, because a preliminary analysis with habitat as a covariate indicated that capture rates may be differently affected by these variables in different habitats. Given the large number of tests (N = 52) and probable multi-collinearity of variables, it is likely that some significant results were spurious. Moreover, this statistical approach did not consider possible non-linear relationships. Nonetheless, results can be used as a preliminary indicator of the factors that affect numbers and kinds of species captured.

RESULTS

STUDY CHARACTERISTICS AND PROTOCOLS

Of the 43 studies reviewed (Appendix), 12 had the sole objective of inventory (i.e., characterization of a community by numbers of species or individuals, proportion of migrants, or relative abundance of individual species). About three-quarters (31 of 43) had one or more additional objectives, including habitat use (measuring relative abundance of several species in more than one habitat), mark–recapture (estimating site fidelity, survival, or population size), and population trends (change in abundance at the same location across years). In only about one-third of the papers (15 of 43) did authors discuss biases associated with mist netting. Only one study was based on a pilot study (Robbins et al. 1992), and only four papers cited methodological studies that verified whether mist netting was the best technique to achieve the stated research goals. About one-quarter of the studies (12 of 43) also included aural censuses.

In most studies, researchers used nets of with a mesh size of 36 mm (Fig. 1A) and used nets of only a single mesh size (Fig. 1B). Nets were typically 2.5 m tall × 12 m long (Figs. 1C, 1D). Nets were set in lines ranging from 1 to 30 nets (Fig. 1E). Lines of nets were spread widely (median = 25 to 50 m; Fig. 1F). In most studies researchers netted between 5 and 12 h/day starting at sunrise (Fig. 1G), and netted for one to three days at a location (Fig. 1H).

Tall forest and second growth forest were the most frequently surveyed habitats (Fig. 2A). Most stations were visited only once (Fig. 2B). Most stations were sampled for greater than 500 net-h (Fig. 2C), usually with over 100 m of mist net (Fig. 2D). At 47 inventory stations with net-hour data, however, only about 25% (11) were netted for >1,000 net-h. Inventory stations were netted for a mean of 2,012 net-h (SD = 3,268). Stations commonly captured between 20 and 39 species (Fig. 2E) and up to 400 individuals (Fig. 2F).

FACTORS RELATED TO NUMBER OF CAPTURES

The protocol parameters affecting number of species and number of individuals captured differed between habitats (Table 1). In non-forest habitats, there were only two significant correlations: number of species captured increased with greater distance between net lines, and number of individuals captured decreased with increasing latitude.

Number of species captured in forested habitats was significantly correlated with many parameters. These included effort variables (total net-hours), equipment (mesh size), sample area (distance between net lines and number of net lines surveyed), amount of continuous effort at a station (number of visits and number of consecutive days of netting at each visit), and habitat structure (canopy height). In forest habitats, the number of species captured was not correlated with latitude or with amount of daily netting effort (meters of net per day, number of nets per net line, or hours of netting per day).

In forested habitats, several parameters were also correlated with number of individuals captured. These included parameters related to effort (total net-hours), sample area (distance between net lines and number of net lines surveyed), and amount of continuous effort at a station (number of visits). The number of individuals captured in forest habitats was not correlated with number of consecutive days mist netting, vegetation structure (canopy height), mesh size, amount of daily mist netting (meters of net per day, number of nets per net line, or hours of mist netting per day), or latitude.

PROTOCOL VARIATION

Sampling protocols varied significantly within individual inventory studies. Two-thirds (25 of 43) of the studies did not use the same sampling protocol at each station, and only 17% (7) used the same protocols for all locations sampled (variation in the protocols of the remaining 11 studies was not reported). Two-thirds of the studies sampled different sized areas at some stations (N = 12), or used different net densities (N = 10).

DISCUSSION

Results in this paper indicated a high variability of mist-netting methods in the Neotropics both among and within inventory studies. Variation of this magnitude makes it very difficult to directly compare results among studies (Magurran 1988). Here I discuss some of the effects of that variation on inventory results.

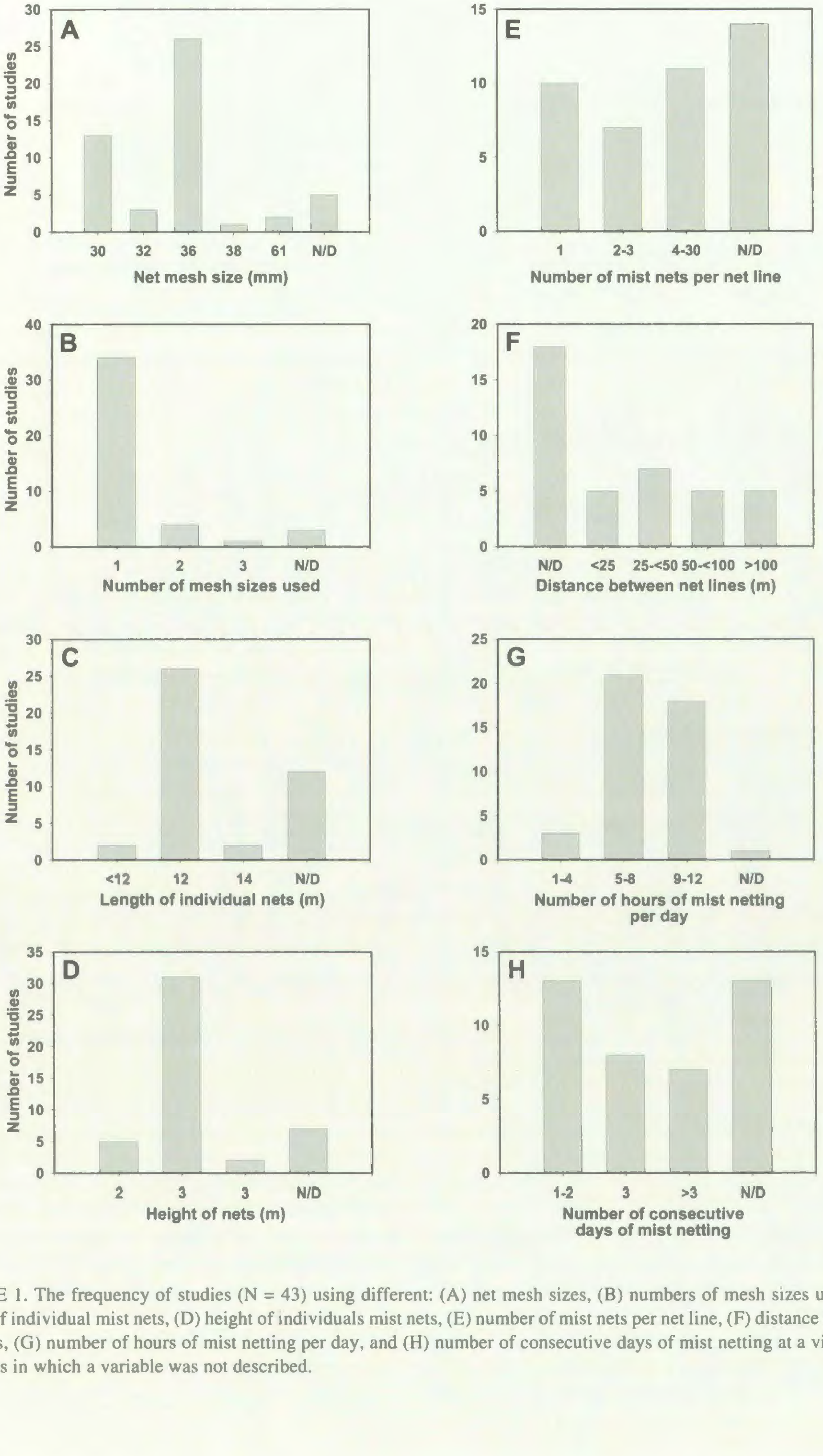

FIGURE 1. The frequency of studies (N = 43) using different: (A) net mesh sizes, (B) numbers of mesh sizes used, (C) length of individual mist nets, (D) height of individuals mist nets, (E) number of mist nets per net line, (F) distance between net lines, (G) number of hours of mist netting per day, and (H) number of consecutive days of mist netting at a visit. N/D = studies in which a variable was not described.

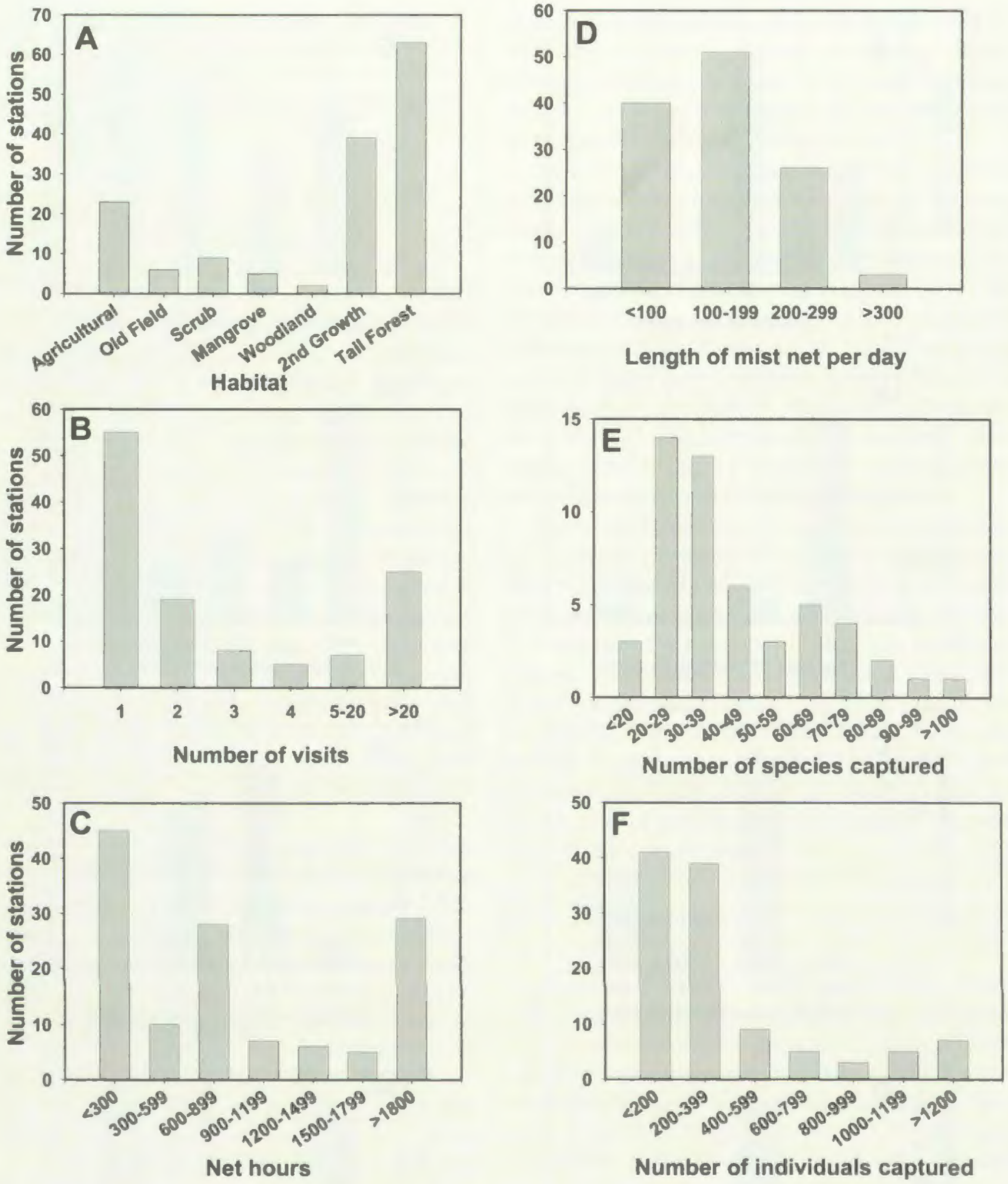

FIGURE 2. The frequency of stations (N = 194) with different: (A) habitats, (B) numbers of visits (netting sessions of one or more consecutive days), (C) net hours, (D) length of mist net operated per day, (E) numbers of species captured, and (F) number of individuals captured.

Overall Effort

Karr (1981a) concluded that for the purposes of species inventory, capture of 100 individuals was an adequate compromise between effort and quality of results. Most studies reviewed here met that objective (Fig. 2C). However, it should be recognized that such studies may not yield accurate assessment of species evenness (Bierregaard 1990), or reveal the presence of uncommon species. In agricultural and shrub habitats, a sample of 700 net-h may be needed to detect most individuals and species (Petit et al. 1992, Borges and Stouffer 1999), whereas in forest habitats, a sample of 1,000 net-h may be needed (Blake and Loiselle 2001, Petit et al. 1992, Lopez de Casenave et al. 1998). Most studies in this review had <1,000 net-h (Fig. 2C).

Another way of evaluating the effort required

TABLE 1. PEARSON CORRELATION COEFFICIENTS BETWEEN THE NUMBER OF SPECIES OR OF INDIVIDUALS CAPTURED AND VARIOUS INVENTORY PROTOCOL PARAMETERS, IN NON-FOREST AND FOREST HABITATS

	Non-forest habitat			Forest habitat		
	Number of species	Number of individuals	Number of studies	Number of species	Number of individuals	Number of studies
Distance between net lines (m)	**0.598**	0.437	12	**0.918**	**0.990**	9
Total net-hours	0.337	0.325	22	**0.830**	**0.925**	13
Number of net lines surveyed	0.233	0.147	17	**0.717**	**0.801**	12
Number of visits	-0.007	0.364	25	**0.544**	**0.760**	17
Latitude (°)	-0.132	**-0.568**	26	-0.098	-0.396	18
Consecutive days of netting	-0.251	-0.127	25	**0.506**	0.442	14
Canopy height (m)	-0.190	-0.006	16	**0.574**	0.263	15
Mesh size of net (mm)	0.329	-0.275	26	**0.597**	0.221	15
Meters of net per day	0.241	0.022	17	0.433	0.385	12
Nets per net line	0.314	-0.007	26	0.302	0.480	15
Hours netted per day	-0.084	0.055	23	-0.013	0.172	16

Notes: Correlation coefficients in boldface were significant ($P < 0.05$).

for useful species inventory is to look at number of individuals captured. A high proportion of species was detected after capture of at least 500 individuals, whether in forest (Lynch 1989) or non-forest habitats (Borges and Stouffer 1999, Lynch 1989, Mallory and Brokaw 1993). However few studies included this many individuals (Fig. 2F), and an essentially complete survey in forest habitats may require a sample of 1,000 individuals (Blake and Loiselle 2001, Karr et al. 1990b). Although capture of more than 500 individuals usually does not detect many additional species, the new species will be ones that are rare. Thus, samples comprised of few captures will have low proportions of rare species and greater species evenness, as compared to samples with many captures.

Aural surveys detect many species better than mist netting (and hence more species and individuals; Blake and Loiselle 2001, Lynch 1989, Rappole et al. 1998, Wallace et al. 1996), but they are affected by observer bias (Faanes and Bystrak 1981, Levey 1988, Verner 1985). Mist netting, on the other hand, detects a few common bird species better than aural surveys, is not affected by observer bias, and may yield greater counts of individuals for some species (Blake and Loiselle 2001, Rappole et al. 1993, 1998, Wallace et al. 1996, Whitman et al. 1995). Therefore, thorough studies of Neotropical bird communities may require both aural surveys and mist netting.

NETTING PROTOCOL

Increasing mesh size correlates with increasing capture rates for larger species, so restriction of mesh-size biases inventory results (Heimerdinger and Leberman 1966, Pardieck and Waide 1992). In this review, 36-mm mesh nets were by far the most commonly used, and few studies used more than one size. Karr (1981a) suggested using 36-mm mesh nets as a good general mesh size for catching most species 8 to 100 g. However, 36-mm nets will catch up to 50% fewer individuals of small (<20g) species than will 30-mm mesh nets (Heimerdinger and Leberman 1966, Pardieck and Waide 1992).

Most researchers preferred distributing their nets uniformly within a study plot to eliminate observer bias in station selection. Some researchers argue for maximizing capture rates by placing nets at "good" locations that have many species, but this introduces observer bias, especially in the capture rates of individual species (Karr 1979, Whitacre et al. 1993), and may make statistical comparisons among stations inappropriate.

Spacing nets >50 m apart may maximize the numbers of unique individuals and species captured (e.g., Karr 1981a). However, for a fixed sample area, nets placed along a transect will cross more microhabitats and bird territories than nets placed in a grid, and therefore will capture more species and new individuals.

In Neotropical studies, number of sequential days of netting at a station has been shown to strongly influence capture rates (Robbins et al. 1992, Faaborg et al. *this volume*). The number of birds caught declines after the first day because the proportion of the population captured increases with each passing day, and captured birds avoid mist nets after being caught (Bierregaard 1990, Robbins et al. 1992, Terborgh and Faaborg 1973). Thus, a mist-netting study conducted on a single day may not be comparable to a study conducted on several days, unless the raw data are available and the analyses are restricted to data in common.

In tall forest, additional visits may increase the number of species and individuals captured as long as there are at least three weeks between visits. A three-week interval may sufficient to minimize net shyness (Bierregaard 1990), although other researchers suggests that much longer intervals may be necessary (J. Faaborg, pers. comm.).

ADDRESSING VARIATION IN PROTOCOLS

When mist nets are used to conduct inventories and accomplish other objectives as well, more than one sampling protocol may be necessary. For example, the chief goal of an inventory is to catch as many different species as possible, which includes minimizing effort spent on recapture. Mark–recapture studies have the opposite goal, that is, to maximize the number of recaptures. Simple comparisons of species richness among locations can be accomplished by using species accumulation curves from each station (Herzog et al. 2002) even when different protocols were used. If the original data are available and protocols do not differ significantly, bootstrap analysis can be an effective technique for eliminating the effect of unequal sampling effort on results (Karr et al. 1990b). However, use of standardized protocols whenever possible should help make results of mist netting studies more comparable.

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APPENDIX. LOCATION, HABITAT, NUMBER OF SURVEY STATIONS, AND OBJECTIVES OF REVIEWED STUDIES

Study	Country(s)	Habitats[a]	Number of stations	Objectives[b]
Bierregaard 1990	Brazil	Tall forest	1	I, M, P
Blake 1989	Panama	Tall forest	3	I
Blake and Loiselle 1992	Costa Rica	Secondary and tall forest	5	H, I M
Borges and Stouffer 1999	Brazil	Old field	6	H, I
Lopez de Casenave et al. 1998	Argentina	Tall forest	1	H, I
Gonzalez-Alonso et al. 1992	Cuba	Shrub	1	I
Greenberg 1992	Mexico	Tall forest	5	H, I M
Karr 1990	Panama	Tall forest	1	I, M
Kricher and Davis 1992	Belize	Secondary and tall forest	3	H, I
	Belize	Old field	3	H, I
Lefebvre et al. 1992, 1994	Venezuela	Mangrove	1	I, M
Lopez de Casenave et al. 1998	Argentina	Tall forest	2	I
Lynch 1992	Mexico	Old field, scrub	2	H, I, P
Malizia 2001	Argentina	Tall forest	2	H, I
Mason 1996	Venezuela	Tall forest	14	H, I
Martin and Karr 1986	Panama	Secondary forest	1	I, M
Machado and Da Fonseca 2000	Brazil	Tall forest	4	I
Mills and Rogers 1992	Belize	Agricultural	5	I
Murphy et al. 1988	Bahamas	Low secondary forest	3	I
	Bahamas	Mangrove	2	I
	Bahamas	Old field, scrub	5	I
Poulin et al. 1993	Venezuela	Scrub, woodland	3	H, I
	Venezuela	Tall forest	3	H,I
Rappole et al. 1998	Mexico	Tall forest	10	H, I
	Mexico	Secondary forest	10	H, I
	Mexico	Agricultural/old field	10	H, I
Robbins et al. 1992	Puerto Rico	Agricultural	8	H, I
	Jamaica	Tall forest	8	H, I
	Belize	Tall forest	8	H, I
	Costa Rica	Tall forest	8	H, I
Robinson and Terborgh 1990	Peru	Tall forest	1	I, M, H
Stouffer and Bierregaard 1995	Brazil	Tall forest	9	I

APPENDIX. CONTINUED

Study	Country(s)	Habitats[a]	Number of stations	Objectives[b]
Thiollay 1994	French Guiana	Tall forest	1	I
Waide 1980	Mexico	Old field, tall forest	5	H, I
Waide 1991	Puerto Rico	Tall forest	1	I, P
Wallace et al. 1996	Cuba	Secondary forest	6	H, I
		Low secondary forest	9	H, I
		Scrub	2	H, I
		Mangrove	1	H, I
Whitman et al. 1995	Belize	Tall forest	1	I, H
Will 1991	Nicaragua	Tall forest	1	I
Wunderle 1995	Puerto Rico	Tall forest	1	H, I, P
Young et al. 1998	Costa Rica	Tall forest	20	I

[a] Tree crops include citrus, coffee, cacao, mango.

[b] H = habitat use, I = inventory, M = mark–recapture, P = population monitoring.

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SOME CONSEQUENCES OF USING COUNTS OF BIRDS BANDED AS INDICES TO POPULATIONS

JOHN R. SAUER AND WILLIAM A. LINK

Abstract. In mist-net studies, it is often difficult to use capture–recapture methods to estimate number of birds present. Many investigators use number of birds captured as an index of population size. We investigate the consequences of using indices of bird abundance as surrogates for population size in hypothesis tests. Unless all of the birds present are captured, indices are biased estimates of local population size, and the amount of bias depends on the proportion of birds captured. We demonstrate the potential effects of bias on hypothesis tests based on indices. The bias generally causes type I error rates to be inflated. Investigators should either estimate the proportion of animals captured using capture–recapture methods or demonstrate that results of hypothesis tests based on indices are not consequences of bias in the indices.

Key Words: abundance estimation, banding, bias, capture–recapture, counts, index, population size

Banding data provide the only source of information regarding many interesting questions about bird populations. Data from mist-net studies are presently used to estimate population trends of passerine birds (Dawson 1990, Hussell et al. 1992), to examine survival and population sizes of birds (e.g., Faaborg and Arendt 1992b), and to evaluate productivity of passerines (DeSante 1992). Large-scale banding programs such as MAPS (DeSante 1992) and the British Constant Effort Sites (Peach 1993) provide the opportunity for monitoring trends and demographic characteristics at regional geographic scales.

Unfortunately, in mist-net studies, relatively few individuals of the target species are typically encountered. Because mist nets have a limited height, the probability of capturing a bird that does not forage in the understory is relatively small. Also, after being captured, birds may become aware of the location of nets, leading to low recapture rates (DeSante 1992). Consequently, most bird species are represented by small sample sizes from any study site.

Small sample sizes pose many challenges for analysts of mist-net data. The most important problem relates to use of capture-recapture methods with small samples. These methods provide many interesting opportunities for estimation of demographic parameters (Kendall et al. *this volume*), but small samples can preclude estimation from individual sites or greatly lower the power of tests for differences in parameters over time or between sites. Many investigators choose to avoid the problems inherent in small-sample capture–recapture analyses by using indices in their population analyses. For example, the total number of birds captured at a site is used as an index to total population size, trends are estimated based on changes in the total capture indices, total numbers of recaptures are used as an index of return (or survival) rates, and the ratio of number of young to adults captured is used as an index of productivity.

In this paper, we explore the consequences of using indices in analysis. We develop a conceptual framework for analyzing indices and relating them to possible changes in the underlying populations. Finally, we demonstrate how indices should be considered in terms of underlying capture–recapture models.

WHAT IS AN INDEX?

An index count is often defined as any kind of count that reflects the presence of animals, but not their absolute number. This definition is inadequate, in that it makes no statement about the relationship between the count C and the unknown population size N. To be an adequate reflection of N, C must have some consistent relationship with N. This relationship is sometimes defined by noting that C must be positively correlated with N. For an index C to be useful, however, C must be a reasonable surrogate for N, both in hypothesis tests and in its association with covariates.

Consider the count of birds captured (or recaptured) at a mist-netting site as a possible index to the population size. The relationship of captured birds at a mist-net site to the actual population size can be expressed as

$$\mathbf{E}(C|p,N) = pN$$

where $\mathbf{E}(C|p,N)$ denotes the expected value of C conditional on the actual population size N, and p is the proportion of animals encountered. In general, if p is not related to N, and is not 0, then C is a reasonable index of N. However, the correlation between C and N will depend on the variation of p, and any analysis of count data relies on some assumptions about either the magnitude of p or its consistency over any comparisons of populations that use counts. This has led to two major philosophical approaches to the analysis of index data.

Proponents of the first approach have said that "Using just the count of birds detected (per unit effort) as an index [of] abundance is neither scientifically sound or reliable" (Burnham 1981:324), and that "It is imperative in designing the preliminary survey to build in the capability...of testing homogeneity of the proportionality factor values..." (Skalski and Robson 1992:29). To apply this approach, an experimenter explicitly estimates p and tests for differences in p that can be confounded with the comparison of interest. For mist-nets, capture–recapture methods are used to estimate p (Kendall et al. *this volume*). If no differences in p are found, then the indices are used in analyses. However, without estimating p as a routine component of a study, these tests cannot be conducted, and the study will have little credibility (a point forcefully made by Anderson 2001).

In the second approach, indices are used in analyses without estimation of p. Instead, it is assumed that standardization and covariate analysis can be used to control variation in p that might invalidate hypothesis tests (e.g., differences in p might be confounded with treatments). Proponents of the second approach feel that it is impossible to design extensive studies to estimate p due to the practical constraints of low recapture rates and small sample sizes for most species in mist-net studies. In fact, many large-scale monitoring programs (such as the North American Breeding Bird Survey [BBS], Peterjohn and Sauer 1993) do not allow for estimation of p.

The first approach (in which p is estimated) should be considered in design of any field study, and the ornithological community increasingly attempts to estimate detectability in studies that count birds (e.g., Rosenstock et al. 2002). However, mist-netting samples are often too small to allow proper estimation, or the hypothesis tests based on the data have too low power to ever be able to test whether detection probabilities differ. In practice, many analyses are conducted on unadjusted counts of captured (or observed) birds.

ALTERNATIVE ESTIMATES OF POPULATION SIZE

Three distinct quantities are commonly referred to as the population size: first, N, the parameter (found only by censusing, which is almost never accomplished in bird monitoring); second, $\hat{N}$, the capture-recapture estimate, found by estimating p and defining

$$\hat{N}_i = \frac{C_i}{\hat{p}_i},$$

(Lancia et al. 1994); and third, C, the index. To investigators, it is not always clear how these quantities differ, and when it is appropriate to use $\hat{N}$ or C as a surrogate for N in hypothesis tests. To understand the consequences of this choice, we must consider two characteristics of the estimates, bias and precision.

Bias

The bias of an estimate is the difference between the expected value of the estimate and the parameter. For the capture–recapture estimate, the expected value of $\hat{N}$ is $E(\hat{N}|N) \approx N$ (the estimator is slightly biased; Skalski and Robson 1992). In contrast, the bias of C is $E(C|N) - N = pN - N = N(p - 1)$; hence C is always biased unless $p \equiv 1$.

Bias can be an extremely serious deficiency in an estimator, if it is not taken into account in hypothesis tests. The possibility that bias can differ among treatments should be considered in any hypothesis test that uses counts, and obviously invalidates use of the index as an estimate of population size. An additional consequence of the bias in C is that comparative tests of population size based on the counts may also be invalid. For example, suppose that we have replicate counts from sites 1 and 2. We are interested in testing a null hypothesis:

$$H_0: N_1 = N_2,$$

by comparing mean counts. Counts should only be used in this analysis if $p_1 = p_2$. Of course, this condition of equal p's is also necessary for any comparative test (e.g., a ratio analysis of productivity, where groups 1 and 2 would denote different age classes).

Bias is therefore a critical consideration for any analysis of count data. Unfortunately, after counts are collected, most statistical tests do not directly include an assessment of possible bias, so investigators do not become aware of these difficulties in the analysis.

PRECISION

At a single site, sampling error is the variance of the estimate conditional on the population parameter. Sampling error for a population estimate $\hat{N}$ is denoted by $V(\hat{N}|N)$. In a capture–recapture study, $V(\hat{N}|N)$ is estimated by assuming N and p are unknown but fixed, and estimating p from observed counts of marked and unmarked animals (Skalski and Robson 1992). If multiple sites are sampled, an additional factor, the among-site variance $V(N)$, is also a component of error, and the variance calculated among site estimates i, $V(\hat{N})$, is

$$\mathrm{V}(\hat{N}) = \mathrm{V}(N) + \mathbf{E}(\mathrm{V}(\hat{N}_i|N_i)),$$

where $\mathbf{E}(V(\hat{N}_i|N_i))$ is the expected value (average) of the within-site sampling errors. In most studies, $V(N)$ is the variance component of interest (Skalski and Robson 1992, Link and Nichols 1994).

If only counts are collected, this partitioning of sampling error and among-site variance cannot be conducted unless p is assumed fixed among sites, and known (Skalski and Robson 1992). Consequently, estimation of p is essential for studies in which estimation of variance components are of interest. Unfortunately, most studies of temporal variation in bird populations do not do this, and may provide incorrect results (Link and Nichols 1994).

Estimation of p still allows for use of C in hypothesis tests when p does not differ among populations to be compared. Skalski and Robson (1992) note that, unless $p = 1$, coefficients of variation of C will be smaller than coefficients of variation of $\hat{N}$ for a site. Hence, use of C in hypothesis tests will lead to higher power relative to tests based on $\hat{N}$, but only when p can be documented to be constant. Of course, if p is not constant the increased precision will only lead to an increased chance of a false rejection of the null hypothesis.

DEVELOPING A STRUCTURE FOR ANALYSIS OF COUNT DATA

The foregoing discussion provides a general view of the statistical properties of indices and capture–recapture-based estimates. However, investigators need specific methods for evaluation of the performance of indices and adjusted counts. Capture–recapture models provide a convenient framework for this evaluation. We can develop models for sampling the population, and see how counts and capture–recapture estimates differ in the context of the models. We provide an example of this based on the Lincoln index, as defined by Skalski and Robson (1992:63–64).

In the model, banding occurs in two periods ($j = 1,2$) at a single site. We use this notation:

N = number of animals
n_j = number of animals captured in period j
p_j = probability of capture in period j
q_j = 1 - probability of capture in period j
m = number of marked animals from period 1 recaptured in period 2.
$C = n_1 + n_2 - m$ = number of distinct captures

Under this model, the estimates of population size are

$$\hat{N} = \frac{n_1 n_2}{m} \approx \frac{(n_1+1)(n_2+1)}{(m+1)} - 1,$$

with sampling variance

$$\hat{\mathrm{V}}(\hat{N} \mid N) \approx \frac{N q_1 q_2}{p_1 p_2}.$$

The number of distinct animals counted is

$$C = n_1 + n_2 - m$$

with mean and variance

$$\mathrm{E}(C \mid N) = N(1 - q_1 q_2)$$
$$\mathrm{V}(C \mid N) = N q_1 q_2 (1 - q_1 q_2).$$

Under this model, we can directly estimate the bias and precision of counts and the capture–recapture population estimates.

Suppose that there are two sites, and a Lincoln experiment has been done on each. To test the null hypothesis that

$$\mathrm{H}_0: \mathrm{N}_1 = \mathrm{N}_2,$$

two alternative statistics can be used. The first is based on the capture–recapture-based estimate, using the statistic

$$z_{\hat{N}} = \frac{\hat{N}_1 \bullet \hat{N}_2}{\sqrt{\mathrm{V}(\hat{N}_1 | N_1) + \mathrm{V}(\hat{N}_2 | N_2)}}$$

The second is based on the counts of animals captured, using the statistic

$$z_C = \frac{C_1 \bullet C_2}{\sqrt{\mathrm{V}(C_1 | N_1) + V(C_2 | N_2)}}$$

Note that $z_{\hat{N}}$ and z_C do not test the same hypothesis. For $z_{\hat{N}}$, the null hypothesis is: H_o: $N_1 = N_2$, but for z_C it is: H_o: $\mu_{C1} = \mu_{C2}$ (where μ_{Ci} = mean count for i). These hypotheses are only the same when $p_1 \equiv p_2$.

To show the consequences of using z_C as a surrogate for $z_{\hat{N}}$, use the expected values given above in formulas for the z statistics, setting $N = N_1 = N_2$, $p_1 = p_{11} = p_{12}$, $p_2 = p_{21} = p_{22}$, and $p_1 \neq p_2$, to simplify the discussion. We can assess the differences in the tests for differing values of p_1 and p_2. For $z_{\hat{N}}$,

$$E(z_{\hat{N}}) = \frac{N - N(\pm \text{small bias})}{\sqrt{N\left(\frac{q_1^2}{p_1^2} + \frac{q_2^2}{p_2^2}\right)}} \approx 0;$$

and for z_C,

$$\mathrm{E}(z_C) = \frac{N(q_2^2 - q_1^2)}{\sqrt{N(q_1^2 + q_2^2 - q_1^4 - q_2^4)}}.$$

In other words, $\mathbf{E}(z) \neq 0$ for a z statistic based on the C's, but $\mathbf{E}(z) = 0$ for the statistic based on the N's, thus tests based on z_C will have an inflated probability of a type I error rate (α) level. Using the expected values, we can quantify the inflation for a fixed N, p_1, and p_2 as

$$\alpha_{N,p_1p_2} = \overline{\Phi}[z_{\alpha/2} - \mathrm{E}(z_C)] + \Phi[-z_{\alpha/2} - \mathrm{E}(z_C)]$$

where Φ signifies the cumulative normal probability, and $\overline{\Phi} = 1 - \Phi$. Calculating these as a function of N with $\alpha = 0.05$, it is evident that the inflation of α increases both as a function of N, p_1, and p_2 (Table 1). When the total population size is moderately large (e.g., $N > 100$), the inflation in α is quite large for even small (5%) changes in p.

We conclude that minor changes in p between treatments can lead to large increases in type I error rates. When hypothesis tests are based on counts, differences in detection rates are confounded with differences in the actual population sizes; significant differences found in the test of equality of counts between populations may be entirely due to differences in p. Changes in p do not appear anywhere in the count-based analysis, and would be interpreted as rejections of null hypotheses by the investigator.

The changes in detection probabilities affect all aspects of hypothesis testing. For example, power (the probability of rejecting a "false" null hypothesis) is a function of the difference between the estimate and a hypothesized value of the parameter, and increases as the variance of the estimate decreases. Because variances decrease as sample sizes increase, test power increases with sample size. Consequently, increasing the observed power of a test when the estimate is biased leads to greater probability of error. Standard sample allocation procedures are therefore invalid, and lead to higher than nominal type I error rates.

A MORE GENERAL CASE

Suppose we have a study that only collects count data from $j = 2$ treatments, where C_{i1}, $i = 1,\ldots,I$, and C_{l2}, $l = 1,\ldots,L$ represent the counts for I replicate sites in treatment 1 and L replicates in treatment 2. Further, assume that for each treatment the counts are indices to population size, and that $p_1 \neq p_2$ (i.e., the detection probability is constant within treatments but differs between treatments).

To test whether H_o: $N_1 = N_2$, we use

$$z_C = \frac{\overline{C}_1 - \overline{C}_2}{\sqrt{\hat{V}(\overline{C}_1) + \hat{V}(\overline{C}_2)}}$$

which actually tests H_o: $\mu_{C1} = \mu_{C2}$.

The numerator of the test has expected value

$$p_1N_1 - p_2N_2$$

which, when the null hypothesis is true, equals

$$N(p_1 - p_2).$$

TABLE 1. THE ACTUAL ALPHA (α') ASSOCIATED WITH HYPOTHESIS TESTS ON COUNT DATA WHEN THE PROPORTION OF ANIMALS DETECTED CHANGES, FOR A FIXED TOTAL POPULATION SIZE

N	$\alpha'(\Delta p = 0.5$–$0.55)$	$\alpha'(\Delta p = 0.5$–$0.6)$	$\alpha'(\Delta p = 0.4$–$0.6)$
10	0.0574	0.0793	0.1820
50	0.0878	0.2020	0.6486
100	0.1267	0.3545	0.9117
150	0.1663	0.4932	0.9819
200	0.2063	0.6116	0.9968

We can use the argument given above to demonstrate the effect of differences in p between treatments on the hypothesis tests. Specifically, for any observed difference in counts (C_1 - C_2), the numerator of the test, we can ask whether, given that the mean population is of size N at both sites, what differences in proportion detected between treatments (denoted by Δp) would be expected to produce the observed z value.

For fixed N between treatments, Δp is

$$\Delta p = \left(\frac{E(C_1)}{N} - \frac{E(C_2)}{N} \right)$$

If these Δp values are small, the tests have little credibility. For example, Hanowski et al. (1993) presented data on mean counts of Downy Woodpeckers (*Picoides pubescens*) on two treatments, each based on 40 point-count sites. The estimates for the two treatments were 0.35 ± 0.09 (SE) and 0.17 ± 0.08. For fixed values of N, we calculate values of Δp that would produce the observed difference in means, given that both treatments have the same N ($N_1 = N_2 = N$). For example, if N equals 1.0 in both treatments, a Δp of 0.18 would be needed to produce the observed difference in counts, but if $N = 2.0$, a Δp of 0.09 will produce the observed difference in counts. If the counts are similar in magnitude to the actual population size (e.g., p is close to 1.0), then it is unlikely that changes in p are causing the observed differences in counts. However, if the p_m is much less than 1.0 (i.e., N is much greater than C), then relatively small differences in proportions detected between treatments will explain the differences between the observed counts. In this case, and in any analysis involving counts as surrogates for population size, it is informative to play "what if" games to evaluate whether the analysis is likely to be affected by differences in detection probabilities between treatments. To do this, postulate the detection probabilities and evaluate the consequences for the analysis. A similar procedure can be developed for any hypothesis test based on counts, such as testing for change over time or for ratios of counts.

CONCLUSIONS

In this paper, we have provided a framework for the analysis of count data, and identified some of the fundamental attributes of counts of birds captured as surrogates of population parameters.

- Counts are always biased unless $p = 1$. This means that counts do not estimate population size, but estimate population size times p.
- Counts are always more precise than adjusted population estimates. This is due to the bias in the estimate ($p < 1$), and the additional error associated with estimating p that occurs in the adjusted estimates. Counts are most precise when $p = 0$, which demonstrates that the increased precision of counts is not useful for hypothesis testing unless differences in p are accommodated in the analysis.
- Sample allocations based on C are not appropriate, because increased samples lead to more precise estimates of $\mathbf{E}(C)$ rather than of N. This amplifies the bias in statistical tests.
- Simple analyses of C omit discussion of bias. Hypothesis tests do not accommodate the possibility of differences in p, and will produce inflated α levels with even moderate differences in p.
- We can use mark–recapture structure to incorporate bias into the analysis, and simulate the effects of changes in p between treatments. If no estimate of p is available, we can model possible effects of variation in p on analysis.
- It is wrong to eliminate p from analyses of count data. The best way of incorporating p in the analysis is to estimate p for each treatment, test for differences in p between treatments, and if necessary incorporate the ps in the hypothesis tests (e.g., Skalski and Robson 1992). If p cannot be estimated, then it must be demonstrated that the hypothesis test is likely to be valid for moderate differences in p between treatments. However, ignoring the possibility of differences in p will lead to analyses with low credibility.

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ON THE USE OF CAPTURE–RECAPTURE MODELS IN MIST-NET STUDIES

WILLIAM L. KENDALL, JOHN R. SAUER, JAMES D. NICHOLS, ROGER PRADEL, AND JAMES E. HINES

Abstract. Capture–recapture models provide a statistical framework for estimating population parameters from mist-net data. Although Cormack-Jolly-Seber and related models have recently been used to estimate survival rates of birds sampled with mist nets, we believe that the full potential for use of capture–recapture models has not been realized by many researchers involved in mist-net studies. We present a brief discussion of the overall framework for estimation using capture–recapture methods, and review several areas in which recent statistical methods can be, but generally have not yet been, applied to mist-net studies. These areas include estimation of (1) rates of movement among areas; (2) survival rates in the presence of transients; (3) population sizes of migrating birds; (4) proportion of birds alive but not present at a breeding site (one definition of proportion of nonbreeding birds in a population); (5) population change and recruitment; and (6) species richness. Using these models will avoid the possible bias associated with use of indices, and provide statistically valid variance estimates and inference.

Key Words: Capture–recapture, estimation, population size, species richness, survival rate, statistics, transients.

Recent publications that document population changes in migratory birds (Robbins et al. 1989, Hagen and Johnston 1992) have led to great public interest in the population status of birds. Partners in Flight and conservation organizations have attempted to focus this interest into programs for monitoring the status of bird populations and conducting research into the causes of population change in birds. Several monitoring programs, such as Monitoring Avian Productivity and Survival (MAPS; DeSante 1992), use banding data to address questions about population change at both local and regional scales. We believe that banding studies provide the only realistic way of addressing many questions of interest to population ecologists, and careful design of programs will allow estimation of many relevant parameters.

Monitoring and research programs frequently share a common goal: estimation of some demographic parameter for some pre-defined population. Clearly, the initial step in any banding program is definition of the parameter to be estimated and specification of a goal for precision of the estimate. Parameters of interest for both monitoring and research programs include population size, survival, recruitment, species richness, and movement probabilities among multiple study locations. Historically, monitoring programs tended to emphasize estimation of changes in these parameters over time, whereas research programs tended to evaluate differences in these parameters among predefined treatments. However, modern approaches to management require that information from monitoring be nested within a modeling framework, in which the monitoring is used to evaluate the validity of predictions (from models) of the consequences of management actions. The additional rigor associated with adaptive management and modeling exercises provides a strong impetus for designing monitoring programs that can be used to evaluate population responses to management.

There has recently been a great deal of statistical research regarding estimation of demographic parameters from banding studies (Seber 1982; Brownie et al. 1985; Burnham et al. 1987; Pollock et al. 1990; Lebreton et al. 1992; Nichols 1992, 1994; Schwarz and Seber 1999; Williams et al. 2002). Application of these procedures to mist-netting studies will greatly enhance the validity and credibility of the results. In this paper, we discuss methods and designs for estimating population parameters from banding studies. We emphasize capture–recapture methods because they are commonly used for passerine birds.

WHY NOT USE INDICES?

Naïve users of data from mist-net studies often draw inferences about the parameters mentioned above using capture indices. For example, the total number of animals captured is an index to total population size, and the return rate of birds to a location between years is an index to survival rate. The expected values of these indices differ from the actual population values by some unknown proportion, and any hypothesis test must make assumptions about the constancy of the proportions. In general, these constancy assumptions are not tested, and the proportions of animals detected may differ among treatments or over time, invalidating hypothesis tests.

This difficulty with the use of indices is easily documented in any hypothesis test. If the differences between group means can be explained by differences in detection probabilities, then the rejection of the null hypothesis cannot be attributed to the treatment (Sauer and Link *this volume*). For example, if mean captures from two treatments are 11.5 and 14.0, it cannot be established that the 2.5 more birds in one treatment are due to higher capture rates or a larger population in the treatment. In fact, a "better" study in terms of a larger number of replicates will lead to a higher chance of a false result, if the difference in counts is due to differences in capture rates (Barker and Sauer 1995).

We will not discuss the statistical properties of these indices (see Sauer and Link *this volume*), but we note that the methods we discuss here provide a means for testing the assumptions implicit in the use of indices for comparative purposes (Skalski and Robson 1992, MacKenzie and Kendall 2002, Sauer and Link *this volume*). Capture–recapture methods allow us to estimate the proportions of animals detected and test whether the proportions are constant over time or treatments. If the assumption of constancy is concluded to be reasonable, then inferences may be based on the index statistics in some cases (Skalski and Robson 1992, MacKenzie and Kendall 2002). However, if the hypothesis of constant sampling proportions is rejected, then inferences should be based on the capture–recapture model estimates. Interestingly, the use of indices relative to detectability-adjusted estimates continues to be a topic of discussion in the literature. However, we believe that it is time to move past this topic, and we agree with Anderson et al. (2003) that index-based designs are limiting the value of wildlife studies.

A SIMPLE INTRODUCTION TO CAPTURE–RECAPTURE PROCEDURES

All capture–recapture methods require that there are trapping occasions in which animals are captured, previously marked animals are recorded as recaptures, new animals are marked, and animals are released. If there are *k* of these occasions, we can define a capture history for each animal in which a 1 indicates a capture in occasion *i* and a 0 represents no capture of the individual in occasion *i*, as

	Trapping occasion (*i*)				
Animal number	1	2	3	4	.. *k*
9999	0	1	1	0	.. 1

The capture history of animal 9999 reflects that it was not captured in occasions 1 and 4 but was captured in occasions 2, 3, and *k*. The capture history is a fundamental format used in capture–recapture estimation and modeling.

There are two major categories of capture–recapture models (e.g., Seber 1982, White et al. 1982, Pollock et al. 1990, Nichols 1992, Williams et al. 2002). The population is "open" when sufficient time exists between capture occasions to allow animals to leave (via death or movement) or enter (via birth or movement) the population, and open-population estimation procedures estimate parameters such as survival between occasions and population size at trapping occasions. On the other hand, the population is "closed" when little time occurs between capture occasions, and it is assumed that population size is not changing among the occasions. Closed-population estimation procedures are used to estimate population size or density during the trapping occasions. Finally, some studies employ a "robust design" (Pollock 1982, Pollock et al. 1990, Kendall et al. 1995, Schwarz and Stobo 1997, Kendall and Bjorkland 2001), in which an investigator will conduct several trapping occasions during a short period of time, and then repeat the sampling at a future time. The data from the short period of time are usually used with closed-population models to estimate detection probability and population size, and data from the repeated samples are used with open-population models to estimate survival and movement in and out of the study area (Kendall et al. 1997). In addition, the robust design can permit (1) estimation of population size, survival, and recruitment for more periods than standard open population analyses; (2) estimation of components of recruitment; and (3) estimation that is robust to unequal catchability. This design is quite similar to the design employed by MAPS and other constant-effort programs.

Statistical procedures for all of these designs share a common approach. Parameters are defined and used to model the events giving rise to specific capture histories. These parameters are typically defined as probabilities, and are associated with both sampling (e.g., detection probability) and demographic (e.g., survival probability) processes. The events giving rise to a particular capture history are thus used to develop a probability model for that history. The probability models for the different capture histories, together with the numbers of animals observed to exhibit each history (the data), are used to obtain estimates of the model parameters and their variances.

As with all statistical procedures, there are assumptions that must be met for the estimates to be completely valid. There are several basic assumptions, such as the banded sample must be representative of the population and bands must not be lost or misread, that apply to all models (Seber 1982). Then, each model has a specific set of assumptions about how the parameters of interest are defined. For example, survival might be time specific, requiring a separate estimate for each year, or constant over time, requiring only a single estimate. Generally, tests and model selection statistics are available to allow users to assess the validity of the assumptions and determine whether models with different sets of parameters might be more appropriate for the data.

STATISTICAL METHODS AND MODELS

Open Population Capture–recapture Models

For open populations, the basic model, called the Cormack-Jolly-Seber (CJS) model after the individuals who first developed it, considers capture histories in terms of two sets of parameters:

ϕ_i: Probability(survive from trapping occasion i to $i+1$ | alive and present at time i)

p_i: Probability(captured at trapping occasion i | alive and present at time i)

Note that the vertical bar indicates that the probabilities are conditional, and reflect the probabilities of the event described before the vertical bar given that the event described after the bar occurred. Capture histories can be described in terms of products of these parameters. For example, for animals captured in period 1 and subsequently released, a capture history of 1 0 1 would have associated probability $\phi_1(1 - p_2)\,\phi_2 p_3$. Of course, there will be many different capture histories in any study, and each history can be written in terms of the underlying probabilities. These probabilities form cells in a multinomial distribution, and this multinomial model can be used as a basis for estimating ϕ_i, p_i, and their variances. Due to technical issues of estimation, some of the parameters cannot be separately estimated, and therefore we cannot always estimate survival and capture probabilities for all periods. See Lebreton et al. (1992) for an excellent explanation of the estimation procedure.

This modeling structure, in conjunction with appropriate software such as Program MARK (White and Burnham 1999; www.cnr.colostate.edu/~gwhite/software.html) is extraordinarily flexible. Beginning with the basic CJS model, any number of variations can be implemented. For example, survival or detection probabilities can be modeled as time dependent or constant. Age dependence in parameters can be implemented. In addition, data for groups of animals (e.g., males vs. females or birds found in mature vs. early successional woodlands) can be separately but simultaneously analyzed, to permit comparison of parameters (e.g., Peach 1993, Hilton and Miller 2003, Miller et al. 2003, Peach et al. *this volume*). Finally, survival and capture probabilities can be modeled as functions of covariates. For example, if winter temperature is thought to influence survival, it can be incorporated into the analysis by modeling survival as a function of temperature.

Estimation of population size from capture–recapture data requires a more stringent assumption than is required to estimate survival rate, because both marked and unmarked birds must have similar capture probabilities. Although population size can be estimated directly using program MARK, the Jolly-Seber population size estimation feature in the program is subject to numerical problems. Programs JOLLY (www.mbr-pwrc.usgs.gov/software.html) and POPAN (www.cs.umanitoba.ca/~popan/) provide direct estimates of population size. Alternatively, one could estimate population size indirectly from the number of birds caught in a given time period (n_i) and the estimate of detection probability ($\hat{p}_i$) as $n_i/\hat{p}_i$ (e.g., Williams et al. 2002).

The flexibility of the model structure and the relatively user-friendly nature of software such as MARK can lead to "data snooping," as it is tempting to model parameters as a function of an inordinate number of factors. Given the limited sample sizes that often result from mist-net studies, consideration of too many factors increases the risk of spurious results (i.e., good fit but not repeatable and with little predictive ability). Therefore one is better off taking the time *a priori* to formulate hypotheses about the key causal factors that drive the survival process.

Once an *a priori* set of models (e.g., constant survival, time-dependent survival, survival that is age-dependent and influenced by temperature) is chosen, the significance of these factors (relative to the amount of data available) can be evaluated for certain cases through direct tests (i.e., likelihood-ratio tests when models are nested). Alternatively, information theory criteria like AIC (Burnham and Anderson 1998) can be used to choose the most appropriate of the candidate models, or to average parameter estimates across all candidate models, using relative model selection metrics as weights (Burnham and Anderson 1998).

CLOSED POPULATION CAPTURE–RECAPTURE MODELS

In closed population studies, the goal is to estimate population size (*N*). Because the population size, although unknown, is assumed to be constant over the trapping occasions, the modeling procedure fits alternative models that differ with regard to assumptions about temporal, behavioral, and individual heterogeneity in capture probabilities. Otis et al. (1978) and White et al. (1982) reviewed models for closed populations and developed program CAPTURE (Otis et al. 1978, Rexstad and Burnham 1991) to fit four models: (1) M_0: Probabilities of capture are the same for all individuals at all capture occasions; (2) M_h: Probabilities of capture differ among individuals, but do not change over capture occasions; (3) M_t: Probabilities of capture differ over capture occasions, but not among individuals; (4) M_b: Probabilities of capture do not change over capture occasions or individuals, but change the first time an animal is captured (behavioral response), so all unmarked animals have one capture probability and all marked animals a different probability. An extreme case of the latter occurs when individuals are only seen once, then they are never seen again (a "removal" model). Models combining these assumptions also exist, including M_{tb}, M_{th}, M_{bh}, and M_{tbh}. Population size can be estimated under all of these models (Chao 2001). In general, individual heterogeneity in detection probability causes difficulties, unless that heterogeneity is small or can be described completely in terms of covariates. Program CAPTURE can be accessed within program MARK. In addition, MARK itself provides the ability to model closed population data for models M_0, M_t, M_b, and M_{tb}, and model M_h, where heterogeneity consists of two unspecified groups with different capture probabilities between them, but homogeneity within group (Pledger 2000).

For those models where program MARK can be used directly, model selection can be conducted using likelihood-ratio tests or AIC, as described above. Program CAPTURE uses a different model selection procedure based on multivariate statistics, which is not always considered reliable. Stanley and Burnham (1998) were unable to develop a satisfactory model selection algorithm and recommended use of an estimator averaging approach.

TOPICS IN CAPTURE–RECAPTURE ANALYSIS

Developments in capture–recapture analysis over the last decade provide some interesting possibilities for analysis of mist-net data. In this section, we briefly discuss some of these developments and their relevance to mist-net studies of passerine birds.

ESTIMATION OF MOVEMENT RATES

Large-scale banding projects tend to have multiple netting stations scattered over large areas. Sometimes, it is of interest to estimate probabilities of moving among stations. The movement can be seasonal, as occurs when moving from breeding to wintering ranges, or can be between years among locations located on the breeding or wintering grounds, or among stopover sites. In fact, many interesting hypotheses about age-specific site fidelity of passerine birds can be phrased in terms of a movement probability study. Models for estimating movement probabilities have been developed by Arnason (1972, 1973), Hestbeck et al. (1991), Nichols et al. (1993), Schwarz (1993), Schwarz et al. (1993), and Brownie et al. (1993).

Movement probabilities have been estimated for birds using resighting data (e.g., Hestbeck et al. 1991, Nichols et al. 1993), band recovery data (Schwarz 1993), and recapture data (Spendelow et al. 1995, Blums et al. 2003). These models have been used with passerines (Senar et al. 2002), but such uses are relatively rare. The almost complete absence of recapture information of birds banded as juveniles poses a particular challenge for capture–recapture studies of passerine birds.

To estimate movement probabilities among locations, the experimental design requires multiple capture stations, and multiple capture occasions at each station. This design yields data on the locations of captured animals at the various sampling periods at the different stations (c.f. Hestbeck et al. 1991). From these fates, we can define capture histories in which stations are indexed by characters (A = at station A, B = at station B) and these characters replace the "1" in the capture history. For example, a capture history for six periods at two stations could be 0A0BBA. Probabilistic models are developed for such data using the following parameters:

ϕ_i^{rs} = transition probability that an animal alive and at station r at time i is alive and at station s at time $i + 1$.

p_i^s = probability of capture for an animal at station s at time i.

The parameters ϕ^{rs} and p_i^s can be estimated from these data using the multinomial-based statistical models. Because ϕ_i^{rs} is a parameter that includes two interesting events, survival and movement, it is sometimes useful to decompose the transition probabilities. If survival from i to $i + 1$ depends only on location at i, and not on location at $i + 1$, then we can write the transition probabilities as:

$$\phi_i^{rs} = S_i^r \ \psi_i^{rs}$$

where S_i^r = probability that an animal in location r at time i survives until $i + 1$, and $\psi0_i^{rs}$ = conditional probability that an animal in location r at time i, is present in location s at $i + 1$, given that it is alive at $i + 1$.

Many interesting ecological hypotheses can be tested using these models (Nichols and Kendall 1995). One elaboration is that sometimes these movement probabilities are not simply a consequence of the location of animals at the most recent time period. Instead, animals may retain memories of where they were in earlier periods and the memories can modify their movements. We can develop a test to see whether transition probabilities depend only on location at time i (a Markovian model), or are influenced by location from earlier time periods (a memory model; see Hestbeck et al. 1991, Brownie et al. 1993). To do this, we add additional parameter subscripts, conditioning on releases at i for which locations at time i-1 are known.

Markovian models can be implemented using programs MARK (White and Burnham 1999) and MSSURVIV (Hines 1994). These programs provide estimates (and associated variances) of location-specific survival, capture, and movement probabilities. Memory models can be implemented in program MSSURVIV. It has been difficult to assess fit of multistate models, but a new goodness-of-fit test has been developed by Pradel et al. (2003) for this purpose.

An example of multistate modeling is provided in Hestbeck et al. (1991) using an extensive mark–resighting study of Canada Geese (*Branta canadensis*). Geese were neck-collared at several locations in eastern North America, and resighted in winter for several years in the Mid-Atlantic states, the Chesapeake Bay region, and the Carolinas. The goal of the study was to look at location changes between years in wintering populations. Estimates of mean annual movement probabilities (Table 1) showed that probability of remaining in the same wintering area was lowest for the Carolina population, and that movement probabilities differed among study areas.

ACCOUNTING FOR TRANSIENTS

One enduring problem in the analysis of capture–recapture data from mist-net studies has been the separation of resident birds from transients in analysis. Because migration periods are difficult to define, and because they may change yearly, many breeding-season banding programs experience transients early and late in the season, and the presence of these birds can greatly influence the results of the capture–recapture analysis. Several approaches have been taken to minimize the effects of transients in the analysis, such as only analyzing data from the period of greatest population stability, eliminating birds from the analysis if they are never recaptured, and eliminating initial captures of all birds. Unfortunately, these approaches either bias survival rate estimates (if all birds seen only once are eliminated from the analysis) or use data inefficiently (if all initial captures are eliminated). Pradel et al. (1997) have developed a model that avoids these problems by incorporating the proportion of transients among newly released birds as a parameter in the model. Let γ_i = proportion of transients in the sample of unmarked birds at period i. In the model, the survival probability for first-captured animals is a sum of survival rates for transients (ϕ_i^t) and residents (ϕ_i^r), each weighted by its proportion, or:

$$\gamma_i \phi_i^t + (1 - \gamma_i) \phi_i^r$$

The "survival" rate (that is, the chance of surviving and returning to the study location) of transients is 0 by definition. Information exists on the survival rate of residents from previously marked animals in the population. This survival probability (ϕ_i^r) can be estimated from animals seen in at least one previous period, permitting estimation of γ_i in the standard multinomial framework. Pradel et al. (1997) illustrate this method with data from Lazuli Buntings (*Passerina amoena*). Their estimates of resident survival rates are substantially higher with this model than with the standard CJS model. This model is implemented in program TMSURVIV (www.mbr-pwrc.usgs.gov/software.html) and can be implemented in MARK (White and Burnham 1999) as a model with trap response in survival.

Peach (1993) describes two alternative procedures for eliminating transient birds from survival analysis of resident birds, and suggests that defining a group of birds recaptured at least 10 days after initial marking will provide sufficient information for separating the cohort into transients and residents. Hines et al. (2003) formalized the suggestion of

TABLE 1. Mean annual movement probabilities with associated standard errors for Canada Geese in three wintering locations in the eastern United States (Hestbeck et al. 1991)

	Location year *i*+1		
Location year *i*	Mid-Atlantic	Chesapeake	Carolinas
Mid-Atlantic	0.71 (0.02)	0.29 (0.02)	0.009 (0.001)
Chesapeake	0.10 (0.01)	0.89 (0.01)	0.02 (0.002)
Carolinas	0.07 (0.01)	0.37 (0.02)	0.56 (0.03)

Peach (1993) as an extension of the model of Pradel et al. (1997). A bird first captured in period *i*, which would normally be assigned to the release cohort of unknown resident status, is instead reassigned to the cohort of known residents if it is recaptured at least *x* days after initial release in the season of release. Nott and DeSante (2002) applied this approach to data for several species from the MAPS program.

Estimating the Proportion of Birds Alive but Not Breeding (Present) at a Study Location

The proportion of animals in a population that are active breeders is an important demographic parameter, but is extremely difficult to estimate. However, there are several possible approaches to estimation of this proportion, if we are willing to assume that presence of a breeding-age animal in a breeding area is evidence of breeding. This assumption, although not generally appropriate, may be acceptable for some bird species. The expected value of the capture probability estimate from an open population model can be written as $E(\hat{p}_i) = \alpha_i p_i^*$, where α_i = probability that the animal is in the sample area (equivalent to breeding probability), p_i^* = conditional probability that the animal is caught, given that it is in the sample area. Recently, two approaches have been developed to estimate the parameter α_i. Both approaches depend on the ability to estimate p_i^*.

Clobert et al. (1990, 1993, 1994) suggested that if we assume that $\alpha_i = 1$ for adult birds, then $E(\hat{p}_i) = p_i^*$ for all *i* for adults. Thus, we can estimate α_i for other age classes based on the ratio of $\hat{p}_i$ for the class of interest to $\hat{p}_i$ for adults. Pradel and Lebreton (1999) suggest using a multi-state approach to the same model, which permits the use of program MARK or MSSURVIV for maximum-likelihood estimation (Spendelow et al. 2002, Lebreton et al. 2003).

Alternatively, we can use the robust design to estimate α_i (Kendall et al. 1997). Within a season, closed population models can be used to directly estimate p_i^*. Between seasons, CJS models are used to estimate p_i. The ratio of these estimates can be used as an estimate of α_i in cases where all birds at time *i* have the same probability of being a breeder. Kendall et al. (1997) also consider a more complicated model in which the probability of an individual breeding at time *i* depends on whether it bred at time *i* - 1. Programs MARK and RDSURVIV permit estimation of α_i for robust design data. Fujiwara and Caswell (2002), and Kendall and Nichols (2002) consider the estimation of α_i when robust design data are not available or possible, but their results confirm that the robust design should be used if at all possible.

Estimation of Recruitment and Population Change

One of the most interesting new developments in capture–recapture methods is the possibility that the Jolly-Seber approach can be reparameterized to directly estimate the demographic parameters of recruitment rate and finite rate of population change. In the original J-S model, survival and capture probabilities are the primary parameters to be estimated. Population size and recruitment do not appear as model parameters, but can only be estimated as functions of capture and survival rates. However, Pradel (1996) has shown that the model can be reformulated to include any one of these parameters:

$1 - \gamma_i$ = proportion of birds in the population at *i* that are new (i.e., that entered the population between periods *i* - 1 and *i*; this can be viewed as a turnover statistic).

f_i = number of new animals present at *i* + 1, per animal present at *i* (this can be viewed as a per capita recruitment rate).

λ_i = finite rate of population increase (N_{i+1}/N_i).

Under some circumstances, γ_i and $1 - \gamma_i$ represent the proportional contributions of survival and recruitment to population growth, an interpretation analogous to elasticities for asymptotic population projection modeling (Nichols et al. 2000).

Uses of the new parameterizations include (1) direct modeling of γ_i or f_i as functions of other study data (e.g., estimates of nest success) or of environmental covariates, which can help provide a mechanistic understanding of the recruitment process; (2) direct incorporation of recruitment rate estimates into population projection models; and (3) use of the λ-parameterization to provide a canonical framework for estimation of population change from capture–recapture and other sources of data. Under situation 3, if another formal estimation method (e.g., variable circular plot, line transect) is used on the mist-net study site, then a joint likelihood can be constructed and λ_i estimated using both data sources. If count data (e.g., point counts) are obtained on the study area, then λ_i can be modeled as a function of these data permitting (1) a test of the hypothesis that the count data really do provide a good "index" of population change and, if they do, (2) use of these data as covariates to obtain a better estimate of λ (Nichols and Hines 2002).

This modeling is relatively recent (Pradel 1996), and few examples exist of its application to mist-net studies (but see Nichols et al. in press). However, we believe the approach of a canonical framework permitting direct estimation of rate of population change using all relevant data (e.g., capture–recapture and point-count) simultaneously, should be preferable to the approach of obtaining separate estimates of λ_i from different data sources and then attempting to combine them or reconcile differences among them.

CAPTURE–RECAPTURE AND MIGRATION BANDING

Banding of birds during migration occurs at many capture stations throughout North America, and data from these stations provide a sometimes controversial view of population changes in birds that breed in the northern regions of North America. Most investigators who attempt to estimate trends in migrating birds use indices to number of birds passing through a banding station (e.g., total number of individual birds captured), but this index is clearly influenced by many environmental variables (Dawson 1990). Though data can be adjusted for some of these variables (e.g., effects of date, weather, and moon phase; Dunn and Hussell 1995, Dunn et al. 1997, Hussell *this volume*), capture probability may be influenced by other factors not measured or accounted for. Capture–recapture methods provide a reasonable alternative to these index approaches, and use of open-population models permits estimation of both the total number of birds passing through a station and residence times of birds at migration stations (Nichols 1996).

Although not commonly done (but see Brownie and Robson 1983, Pollock et al. 1990), it is possible to estimate residence times ("survival") at migration banding stations using standard CJS models. These analyses would use recapture data from the stations to estimate the proportion of animals missed by the sampling, and "survival" rates (primarily the probability of remaining at the station) of marked birds at the station. From these rates an average residence time can be estimated as $-1/\ln(\hat{\phi})$, where $\hat{\phi}$ is the estimate of average survival rate between sample intervals. The total population passing through the station can be estimated as the sum of the CJS estimates of B_i, the number of new animals entering the population between sampling periods (e.g., Shealer and Kress 1994).

Schaub et al. (2001) further generalized the above approach for estimating total stopover duration. They use the method of Pradel (1996) to estimate stopover duration before or after capture, using "recruitment" and "survival" analyses, respectively. They then combine them into total stopover time. They implement this approach in Program SODA (www.cefe.cnrs-mop.fr/wwwbiom/Dyn-Populations/biom-ftp.htm).

The superpopulation modeling approach of Crosbie and Manly (1985) and Schwarz and Arnason (1996) provides an alternative approach to analyzing migration banding data. Under this approach, parameters reflecting entry of new animals into the population are incorporated directly into the model, and total number of individual birds using the station during the entire sampling period (between the first and last samples) can be estimated. If migration banding as described above is conducted for a series of years, the within- and between-year information can be combined to estimate survival rate, as well as the probability that an individual used that particular stopover site in a given year (Schwarz and Stobo 1997, Kendall and Bjorkland 2001).

Of course, these analyses require recapture or resighting data for survival rate estimation, and hence they will only work well when "sufficient" recaptures or observations exist. Even though limited recapture information exists for most species, we feel that these methods have great potential to improve estimation associated with migration banding programs as they provide a means for investigators to directly evaluate the critical assumption of consistency in proportions of animals captured. Innovative applications of methods to increase the number of recaptures (e.g., through resighting procedures) may increase the feasibility of applying capture–recapture methods to a larger number of species, and provide a means for generally estimating the proportion of birds "missed" in capture indices during migration.

SPECIES RICHNESS ESTIMATION

Information on biodiversity has become of increasing importance to conservation, and surveys of species richness are frequently conducted in the Neotropics. Often, the total number of species captured in mist nets, or identified through other sampling procedures, is used as the estimate of species richness. Unfortunately, this estimate is clearly biased, and the extent of the underestimate is a function of both the probabilities of encountering species and the sampling effort. Capture–recapture methods can be used with replicated species list data to directly estimate the total numbers of species present from mist-net and other samples (Dawson et al. 1995, Nichols and Conroy 1996, Boulinier et al. 1998).

To do this, species are treated as individuals, and capture histories can be developed for each species by (1) observing presence–absence of the species at multiple trapping occasions at a single station; (2) observing presence–absence over multiple stations at a single occasion; or (3) recording number of individuals per species at a single station and occasion. The data from approaches (1) and (2) can be analyzed using the closed population models of Otis et al. (1978); models that allow heterogeneity in capture probabilities among species (such as model M_h) are likely to be most useful. In these models, total number of species is estimated, allowing each species to have a different chance of capture.

If data from only a single trapping period are available (scenario 3), a version of the Burnham and Overton (1979) model, M_h, can still be used to estimate total species richness. For this estimator, data are summarized as number of species for which one bird was caught or seen, the number of species for which two individuals were caught or seen, etc., up to the number of species for which five individuals were seen. J. E. Hines has written a program to estimate species richness using the limiting form of model M_h with capture frequency data (Hines et al. 1999). Application of this approach to mist-net data is shown in Karr et al. (1990b).

We view these species-richness estimation methods as providing a useful way of resolving some of the sampling problems that occur in tropical mist-net studies, in which the mist nets do not sample species with equal probability, and counts encounter a different (but not necessarily independent) subset of the bird species present in an area. For these areas, data can be combined from mist-net captures and point counts to get a composite species richness estimate that is free of the bias associated with total number of species captured (Dawson et al. 1995). These methods also permit estimation of parameters associated with community dynamics, such as rate of change in species richness, local extinction rate, and local colonization or immigration rate (Nichols et al. 1998a,b).

CONCLUSIONS

In this paper we have tried to provide some insights into how capture–recapture estimation can be useful in mist-net studies, and describe some new procedures that should be of use to biologists. We emphasize that capture–recapture models form an appropriate structure for thinking about mist-netting studies, and should be considered in the design of any mist-net study. Indices that are not adjusted for the proportion of birds missed by the sampling procedure involve untested assumptions, and capture–recapture provides a way to test these assumptions (Skalski and Robson 1992, MacKenzie and Kendall 2002).

All of the statistical models discussed in this paper are defined in terms of a series of parameters that are assumed to be of importance. Investigators must collect data and use evidence from the data (such as goodness-of-fit tests) to evaluate whether the set of parameters is reasonable for their data sets. Estimation of some parameters, such as number of transients in the population, requires more restrictive assumptions (equal capture probabilities of transients and residents in the transient model) than does estimation of other parameters (e.g., proportion of transients in the sample of unmarked birds does not require this assumption). Before using these models, investigators should evaluate the underlying biological and statistical assumptions implicit in each model. However, we emphasize that these methods will often be preferable to index-based methods, as the latter frequently require much more restrictive assumptions, although these are often left unspecified.

There have been many exciting advances in capture–recapture work over the last decade, and we have discussed advances in the estimation of movement probabilities, survival rates in the presence of transients, populations at migration stopover sites, temporary emigration (breeding proportions), rate of population change, and species richness. User-friendly computer programs exist for application of most of these procedures. Understanding these methods will allow investigators to (1) define the parameters that they want to estimate using a banding study; (2) develop study designs that will allow them to estimate the parameters; and (3) define needed sample sizes, in terms of capture probabilities and number of animals captured and recaptured, that will be needed to achieve prespecified goals of estimate precision and test power. Studies designed with such a focus should permit stronger inferences about avian population dynamics than have been possible previously.

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EFFECTIVENESS OF INFORMAL BANDING TRAINING AT THREE WESTERN CANADIAN BANDING STATIONS

BRENDA C. DALE

Abstract. Skills of trainee banders from three western Canadian banding stations were assessed in 1993, using minimum performance standards in use at that time. Each trainer–trainee combination independently examined the same birds. Quantitative skills appeared to be learned quickly, but there were few passing scores on aging, sexing, skulling, and fat assessment, and none on overall achievement using the test standards. However, many trainee errors were of a non-critical nature, which was not well reflected in the scoring system. Several individuals did score well if the nature of their errors was taken into account. Time spent with a trainer, experience, and personality may all play a role in trainee performance. Results demonstrate the need for trainers to meet an established standard, and for continued spot-checking of skills after training has been completed.

Key Words: banding techniques, banding test standards, bander training.

Use of data collected at banding stations for such important international programs as Monitoring Avian Productivity and Survival (MAPS) and migration monitoring is predicated on the belief that data are collected accurately. However, standards for obtaining banding permits vary greatly throughout the world. In a few cases, a formal test is administered, but in North America permits are awarded on the basis of letters of recommendation from banders who already have permits.

Recently, the North American Banding Council (NABC) developed detailed guides on banding techniques, a guide for trainers, and specialized manuals for the banding of landbirds, hummingbirds, and raptors (Hull et al. 2001; North American Banding Council 2001a, b, c; Russell et al. 2001). Intensive training courses are increasingly available, and a bander can now undergo testing to earn formal certification. In the last few years the Canadian Bird Banding Office and the U.S. Bird Banding Lab have begun to accept certification as proof of sufficient skill, knowledge, and experience to warrant a permit.

Despite the growth of opportunities for formal training, many North American banders gain their initial skills, knowledge, and experience through informal training, defined here as working in the presence of a trainer until the latter is satisfied with the consistency and correctness of data collection techniques and procedures. The purpose of this study was to investigate the outcomes of informal training, by comparing results to the minimum performance standards in use at the time of the study (1993), prior to development of NABC materials. Although these criteria are now largely outdated, the study demonstrates the importance of both training and evaluation procedures in ensuring accurate and consistent results.

METHODS

Research took place in 1993 at Beaverhill Bird Observatory in Alberta, Last Mountain Bird Observatory in Saskatchewan, and Delta Marsh Bird Observatory in Manitoba. Informal training varied among these stations, but in all cases the trainer did not allow the trainee to collect data alone until the trainee had achieved a high degree of agreement with the trainer. Quantifying length of the training period was often difficult, because checking diminished gradually in most cases. For each trainee, we obtained an estimate of total experience, and an estimate (from the trainer) of the time the trainee had access to the trainer. I chose to define training period as time spent in proximity to the trainer, because this could be most readily quantified.

Each trainer–trainee combination independently examined and collected data on the same birds. Number of birds measured by each trainer–trainee combination varied from 37 to 171. All data were collected in August and September, so participants were not usually able to use cloacal protuberance and brood patches as an indication of the sex or age of the birds. All stations used a five-point fat scale. Two stations used a three-class and one a six-class skull ossification scale. All participants recorded data without input from others (usually out of sight from one another). No discussion of birds being handled was allowed for the entire length of the experiment. For the purposes of this study, it was assumed that the trainer had correctly classified, assessed, and measured the bird.

For measurements, I calculated the average of the absolute deviations of trainee data from those of the trainer, and divided deviation by the average value achieved by the trainer. For categorical scores (fat and skull), I determined the proportions of cases in which a trainee scored the bird the same as the trainer (agreement), differed by one class, or differed by two classes. For age and sex I calculated the proportion of cases in which a trainee scored the bird exactly the same as the trainer (agreement).

Scores were assessed by comparison to minimum performance standards suggested by C. J. Ralph (pers. comm.), which were developed in 1993 for a one-week training course to teach banding skills. These criteria are shown in Table 1. However, some errors are less important than others, and thus I also determined whether errors were "critical" or "non-critical." A trainee classifying a bird as "unknown age" (or sex) when the trainer felt able to classify to an age or sex category was a non-critical error, whereas errors when trainer and trainee assign opposing age or sex classes were critical. For skulling, a class error within the hatch year categories was considered non-critical.

RESULTS

QUANTITATIVE MEASURES

Analysis of quantitative measurement differences were limited to wing chord. One trainee was in the "top" category, using the standards in Table 1, and the rest were comfortably within the "pass" category (Table 2). The bulk of the birds measured were small passerines with wing chords less than 100 mm, so any error was almost sure to put the trainee in the pass rather than top category. Most errors were similar in magnitude to the amount of variation typical of an individual repeatedly measuring the same bird. There was no relationship to the amount of time the trainee had spent in proximity to the trainer or to overall length of experience. Wing measurement appears to be a skill that is learned quickly, and the skill is retained well after contact with the trainer is over.

QUALITATIVE MEASURES

Species

Correct identification of species ranged from 98 to 100%. Two of the four errors committed were transcription errors, with the trainee writing the name of the previous species instead of the species being processed. The other two errors involved confusion between Least (*Empidonax minimus*) and Alder (*E. alnorum*) flycatchers. Examination of measurements collected by the trainer and application of formulas showed that the trainees made the wrong decisions because they did not collect all the necessary data. Using the Table 1 standard of 100% to pass, there were two passing and three failing individuals.

Age

Using 100% as the pass score (Table 1), no trainee achieved a passing score for assigning age (Table 3). One trainer–trainee combination did agree on the age of 99% of the birds. The only disagreement was a bird classed as unknown age by the trainee. Of the remaining four banders, three achieved scores in excess of 80% and one failed by a wide margin. Most errors by these four banders were of a critical nature (an adult bird called hatch year or vice versa), rather than non-critical (an adult or hatching year called unknown age).

Sex

No trainee achieved a perfect score on assigning sex (Table 3), so all failed according to the standards in Table 1. One trainee achieved a score of 98%, three more achieved scores above 80%, and one failed by a wide margin. Most errors were of a non-critical nature, in which the trainee classed the bird as unknown sex while the trainer classified it as known sex. However, every trainee made at least one critical error.

Skull

No individual attained a top score for correct skull classification (Table 4) according to the standards in

TABLE 1. MINIMUM PERFORMANCE STANDARDS FOR BANDERS EXPRESSED AS ACCEPTABLE PERCENT ERRORS OR CONCURRENCE BETWEEN TRAINEE AND TRAINER

	Measurement	Species, age, sex	Qualitative (skull, fat)	
	% error	% agree	% agree	% differ by one class
Top	< 1	100	> 95	< 5
Pass	> 1 to 3	100	80–95	< 20
Marginal/ fail	> 3 to < 5	n/a[a]	50–80	20–40
Definite fail	> 5	< 100	< 50	> 50

Notes: Standards are those suggested by C. J. Ralph (pers. comm.) in 1993. All rates of agreement or error are in reference to answer as determined by the trainer.

[a] Anything less than 100% agreement for these categories was considered a failure so there is no marginal score for these skills.

TABLE 2. TRAINEE SCORES FOR WING MEASUREMENT AND SPECIES IDENTIFICATION

Trainer/Trainee (N)	Wing measurement % deviation	Species identification % agreement[a]
A / B (171)[b]	1.77	**99**
B / C (169)	1.62	**98**
D / E (100)	0.72	**99**
F / G (86)	1.90	100
F / H (37)	1.40	100

[a] Bold marks are failures by standards in Table 1.

[b] Sample size for these two skills for each pairing of personnel appears in parentheses.

Table 1. One passed, two achieved marginal scores, and two failed. With the exception of bander H, most errors were of a non-critical nature (differed in class within bird of the year categories), and these birds would have been aged correctly on the basis of skull. Using critical and non-critical classification for errors produces somewhat different results than does "differences of one class." Judging on the basis of Table 1, the number of serious errors made by G and H would have been underestimated, and the number of serious errors made by B would have been overestimated (Table 4).

Observer H had a high number of errors in skulling (Table 4). According to F (the trainer), H appeared to be skulling well at the end of the training period but had not subsequently asked for confirmation on many birds when trainer and trainee were in proximity. There was some parallel between scores on age and skull for H. This did not hold true for B, C, and E who seemed to have acceptable skulling ability (at least 85% agreement or non-critical errors), but did not assess ossification on some birds, and this is where most of their aging errors occurred. Skulling every bird would probably have improved their age classification performance.

Fat

There was one pass and three marginal scores (Table 5). Almost all errors, even by the failing individual H, were within a class of the trainer's determination.

Training levels

All the trainees had achieved a high degree of agreement with their trainers after initial training

TABLE 3. TRAINEE SCORES FOR AGE AND SEX DETERMINATION

Trainer/	Age			Sex		
Trainee (N)	% agree	% non-critical error	% critical error	% agree	% non-critical error	% critical error
A / B (171)[a]	**84**[b]	1	15	**70**	29	1
B / C (169)	**92**	0	8	**98**	0	2
D / E (100)	**99**	1	0	**85**	11	4
F / G (86)	**93**	1	6	**86**	9	5
F / H (37)	**65**	0	35	**84**	8	8

Notes: Values are expressed as percent of agreement, non-critical, and critical error.

[a] Sample size for these two skills for each pairing of personnel appears in parentheses.

[b] Bold marks are failures by standards in Table 1.

TABLE 4. TRAINEE SCORES FOR SKULL OSSIFICATION

Trainer/Trainee (N)	% agree	% non-critical error	% critical error	% differ by one class	% differ by two classes
A / B (52)[a]	**48**[b]	40	12	37	15
B / C (51)	63	33	4	33	4
D / E (87)	74	26	0	26	0
F / G (76)	80	13	7	19	1
F / H (37)	**46**	24	30	49	5

Notes: Values are expressed as percent agreement and percent by error type.

[a] Sample size for this skill for each pairing of personnel appears in parentheses.

[b] Bold marks are failures by standards in Table 1.

TABLE 5. TRAINEE SCORES FOR FAT ASSESSMENT

Trainer/Trainee (N)	% Agree	% Differ by one class	% Differ by two classes
A/B (171)[a]	79	19	2
B/C (169)	87	12	1
D/E (100)	61	31	8
F/G (86)	56	41	3
F/H ((37)	**40**[b]	49	11

Notes: Values are expressed as percent agreement and percent by error type.

[a] Sample size for this skill for each pairing of personnel appears in parentheses.

[b] Bold marks are failures by standards in Table 1.

(prior to this experiment). Experience gained subsequent to training (as measured by number of birds banded), and the period of long term access to the trainer following training, differed among those tested (Table 6). There was only one trainee (B) who was given a defined period of training and then banded alone thereafter.

It was recognized from the onset that it would be difficult to separate the influences of training and experience, because both are often acquired together and quantifying them in a meaningful way is difficult. The small sample size precludes quantitative analysis. Although data for the first three individuals in Table 6 suggest that access to a trainer beyond the first intensive period may be a factor in long term performance, this was not consistent. For example, bander H had a very long period of access to a trainer, but the worst score.

Results from bander B suggest that practice alone does not increase performance (Table 6). DeSante et al. (*this volume*) also presented data indicating that experience of banders does not necessarily ensure a higher degree of accuracy.

Discussions with F, the trainer of G and H, revealed that personality or temperament may be an important factor in training effectiveness. For example, trainee G was trained for a short time but was extremely cautious. Trainee G frequently asked questions of the trainer and spent a lot of time reading source and reference materials. Trainee H did well in initial training and testing, but rarely asked questions during the extensive period following training when the trainer F was accessible but not actively probing and testing H.

TABLE 6. ACCESS TO TRAINER, EXPERIENCE AND PERFORMANCE OF BANDING TRAINEES

Bander	Access to trainer (days)	Experience (birds banded)	Cumulative score (out of 600)
B	10	>3,000	478
C	65	~1,000	536
E	55	~2,000	518
G	29	~2,000	513
H	60	~2,000	433

DISCUSSION

No individual attained a fully satisfactory performance level based on the standards in Table 1. Several individuals had mainly errors of a non-critical nature, which was not reflected in the Table 1 scoring system that was in use at the time of the study. Current standards for performance assessment are quite different. The NABC does not treat all errors as equal, and although the council sets a high standard, it does not expect performance of 100% in aging and sexing birds. NABC standards also penalize critical errors more harshly than non-critical errors, because classing a bird as unknown age or sex is preferable to categorizing it incorrectly. Determination of age and sex is often based on subtle plumage characteristics, and it is to be expected that trainees will record a greater number of unknowns than trainers. Indeed, a trainee who rarely uses the "unknown" category may be overconfident, and probably should be rechecked for errors (M. McNicholl, pers. comm.). Nonetheless, the NABC does impose some penalty for non-critical errors made during testing, to encourage precision when a true determination is possible.

Despite the improvement of training guides and development of performance standards for certification, results in this paper indicate that individual differences among banders can readily arise and be promulgated. A good example of this is the case of banders B and C in this study. Bander B was given a short period of intensive training and then banded for a summer. The next year, B trained C, and the two worked together for the summer. It appears that because C had constant access to B prior to testing in this study, there was a high degree of agreement with B during the test. In fact, C was the only individual who came close to achieving a passing score. It appears B had done a very good job of passing on information to C, which was the testing criterion in this study. However, B's score indicates that the information passed on to C was incomplete or incorrect.

Results of this study indicate that trainers should achieve a common standard before we rely on agreement of trainer and trainee results as the test of competency for new banders. Without this initial standardization, we will be perpetuating high variability in standards, because trainees reflect their trainer's skills. Moreover, it is important to recognize that learning and evaluation must not cease at the end of the training period. Recommendations to address these issues include the following:

1. More banding stations should undertake evaluations of their training effectiveness. This may clarify which factors most influence performance, and identify weaknesses in training programs. Especially needed is development of a schedule for follow-up spot checking after initial training has been completed.

2. Trainers should attend regional or national workshops so that all trainers teach from a similar standard. Contact and verification among trainers in a region should take place at least annually to maintain consistency.

3. Station personnel (regardless of experience) should periodically compare results, and immediately discuss sources of variation to iron out any problems revealed. For example, as a result of this study, F gave H a refresher course and they began regular comparisons, which showed a much higher level of agreement.

4. The role of trainer and trainee temperament should be given consideration in designing and carrying out training and assessment.

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RECOMMENDATIONS FOR THE USE OF MIST NETS FOR INVENTORY AND MONITORING OF BIRD POPULATIONS

C. John Ralph, Erica H. Dunn, Will J. Peach, and Colleen M. Handel

Abstract. We provide recommendations on the best practices for mist netting for the purposes of monitoring population parameters such as abundance and demography. Studies should be carefully thought out before nets are set up, to ensure that sampling design and estimated sample size will allow study objectives to be met. Station location, number of nets, type of nets, net placement, and schedule of operation should be determined by the goals of the particular project, and we provide guidelines for typical mist-net studies. In the absence of study-specific requirements for novel protocols, commonly used protocols should be used to enable comparison of results among studies. Regardless of the equipment, net layout, or netting schedule selected, it is important for all studies that operations be strictly standardized, and a well-written operation protocol will help in attaining this goal. We provide recommendations for data to be collected on captured birds, and emphasize the need for good training of project personnel.

Key Words: mist net, monitoring, recommendations, standards, technique.

Mist netting is a valuable tool for monitoring bird populations (Dunn and Ralph *this volume*). Since becoming widely available over the last half of the 20th century, mist nets have been employed in a wide variety of studies, often using very different protocols. Information has gradually accumulated about the effects on capture rates of netting equipment, spatial arrangement of nets, and netting protocol. We are now in a position to make recommendations on the best practices. It is important to use methods that are effective and efficient, because mist netting requires specialized training and intense effort. Standardization is crucial to preventing spurious variation in capture rates. Finally, using widely accepted and tested protocols whenever possible will facilitate comparison of results across studies, and pooling of data for common analysis.

This paper contains recommendations for mist netting that are appropriate for a wide variety of inventory and monitoring purposes, taking into consideration the welfare of captured birds. The paper integrates the latest information contained in this volume and prior literature, and represents a general consensus of the authors contributing to this volume and of other participants in the workshop giving rise to it (see Preface). All recommendations apply to all seasons, unless specifically noted otherwise, and are summarized in Table 1.

PRIOR TO SETTING UP A NETTING STATION

Study Design

The number and type of nets used, their placement, target levels of netting effort, and data to be collected, all should be chosen to address the study objectives most effectively. Therefore, prior to selecting station locations and setting up nets, it is important to clearly define goals for population parameters to be measured, geographic scope, temporal frames of interest, and targets for species and sample size. For example, species inventory projects may require netting in a wide variety of habitats, as opposed to a study whose objective is to compare population parameters among particular habitats. Long-term monitoring will require a location that is likely to remain accessible over the life of the study, and for some purposes it will be important that habitat also remain relatively unchanged. A desire to capture particular target species will influence the habitats and vegetation structure where netting should take place, and may require use of special net types or capture techniques (such as canopy nets, or lures such as water drip traps or tape recordings; e.g., Whitaker 1972, Wilson and Allan 1996, Sogge et al. 2001). For some habitats or species (including certain grassland birds), netting may not be the best means of obtaining population data, and other methods should be considered.

Objectives of the study should consider the most appropriate geographic scale, which in turn affects the number of netting stations to be established. Is the intention to compare results among several stations to contrast distinct habitats or management practices, or are data to be pooled from multiple stations and habitats to represent a region as a whole? Adding effort at a single station can enlarge sample size, which is particularly important for estimation of survivorship (Nur et al. 2000, *this volume*; Ballard

TABLE 1. SUMMARY OF RECOMMENDED PROCEDURES FOR MIST-NETTING STUDIES

Parameter	Season	Recommendations
Station location(s)	All	Stations likely to be accessible for life of study
		Study-specific requirements are addressed
		Capture rates are sufficient to meet study objectives
Number of nets	All	Sufficient for sample size objectives to be met
		Matched to number of personnel available, at effort level sustainable for life of study
Mesh size of nets	All	Most suitable size for target species, or use range of sizes for species inventory
Net placement	All	Convenient and fast to check
		Study-specific criteria are met (nets placed to sample target species or habitats, or systematically sample several habitats)
	Breeding and wintering	Grid arrays to maximize territorial individuals captured and increase recapture probability, although lines may be better for sampling territorial birds when size of individual ranges are unknown or are variable among target species
Net density	All	1–5 nets/ha to sample as many territories or home ranges as possible
		>1–5 nets/ha, if desired, when birds are not territorial
Distribution of sampling periods[a]	All	Equal sampling periods throughout season
Number of sampling periods	Breeding	Demography: 10 to 12 consecutive 10-day periods, covering whole breeding season
		Abundance/site fidelity: minimum of 3 sampling periods per season, but more is better
	Wintering	1–3 sampling periods per season is a common protocol, but more frequent sampling is likely to provide better information
	Migration	Annual abundance indices and long-term trends: near-daily sampling, either at a single station or spread among a cluster of stations[b]
		Comparison of abundance among stations within years: 5–10 sampling periods (with simultaneous netting sessions)
Length of netting session[c]	Breeding	One day/10-day period (multiple stations pooling data), or up to 7/10-day period (single station studies where greater sample sizes are required, capture rates remain high enough for continued netting to be efficient, or sampling periods are relatively few)
	Wintering	1–2 days, or longer if capture rates remain high enough for continued netting to be efficient
	Migration	Annual indices of abundance or age ratio: near-daily netting through season
		Comparison of abundance among stations within a year: one or more days per netting session (preferably with simultaneous sampling at stations to be compared)
Hours of operation	All	At least 4 h, starting at dawn (unless peak activity of target species occurs at a different time)
		Effort level should be sustainable over life of study
Standardization	All	Standardize all equipment, net placement, and effort parameters within stations
		Standard protocol can differ among stations if direction and magnitude of temporal changes is being studied, but not if capture rates are being directly compared
		Maintain stable vegetation height and density at net sites to extent possible.
	Breeding and wintering	Mark–recapture studies require less strict adherence to constant effort than studies relying on indices, but equipment, net placement, and vegetation at net sites should still be standardized
Training	All	Ensure that all participants are trained to standards of the North American Banding Council
		Train all participants to follow a standard protocol that is detailed in a written document
Data	All	Develop field recording and data management procedures to ensure uniformity in collection of all relevant data, and to enable rapid analysis
		Collect metadata relevant to station (including protocols and at least basic habitat description)
		Record daily effort data

[a] Period within which a netting session of 1+ consecutive days will take place.

[b] Effect on results of pooling less than daily data from each of several stations has not been tested (Dunn and Ralph *this volume*).

[c] Period of consecutive days of netting within a sampling period.

et al. *this volume*). However, increased netting within a site can sometimes lead to net avoidance, and may not sample a directly proportional increased number of territories. Increasing number of stations may often enlarge sample size more than increasing effort within a site, and sampling at multiple stations allows estimation of sample variance at the same time that overall sample size is increased (Burton and DeSante *this volume*). Sometimes, the sample size needed for a good measure of annual survival can often be obtained only by combining results from a network of stations (Hilton and Miller 2003). Single stations are poor at tracking annual changes in regional productivity for at least some species (Nur et al. 2000), but as few as 3–10 stations may be sufficient to produce representative regional results (Bart et al. 1999, Ralph et al. *this volume b*). Of course, pooling data among stations can obscure important differences among sites.

Once a decision has been made to establish multiple stations, further decisions are needed on how many, how far apart, and in what habitats they should be placed. The number of stations to be established should be based on target sample size (see below), as well as on availability of funding and personnel. If there is a likelihood of high turnover in the set of stations contributing data for pooled analysis, the effect of such turnover on quality of results also should be considered. Optimal spacing of stations will depend on study objectives (e.g., study of juvenile dispersal or adult emigration may require stations to be clustered). For the greatest power to represent an entire region, stations should be distributed according to geographic or habitat strata.

Before beginning the study, an investigator should decide upon the desired precision of an estimate or the effect size to be detected, which will help determine the minimum sample size required (number of mist-net stations and nets, number of birds captured and recaptured, or both). For survival analyses, the minimum sample size will be determined primarily by the number of birds recaptured. For comparisons of productivity, the number of mist-net stations and number of birds captured will be considerations. A preliminary estimate of sample size required to meet study objectives can be made through review of published papers on similar studies, or consultation with a statistical expert. Because of variability of capture rates among species, plans should be made for a pilot study and power analysis of preliminary data to allow for adjustment of effort.

Researchers should be well aware that mist-net captures are indices of the population being monitored, and that the proportion of the true population that is captured is unknown and variable (Nur et al. *this volume*). Much variation in capture proportion can be avoided through good study design and standardizing protocols, but capture proportion is not necessarily constant over time or space, thereby introducing potential bias into comparisons among indices (Sauer and Link *this volume*). Whenever feasible, the parameter of interest (e.g., adult population size) should be studied using mark–recapture techniques or other means of estimating capture probability (Dunn and Ralph *this volume*, Peach and Baillie *this volume*, Nur et al. *this volume*, Kendall et al. *this volume*).

Monitoring of population size and demography nearly always benefits from standardized netting. It is therefore recommended that alternative net placements be tested in a pilot study, such that a standardized array can be maintained without further change throughout the actual study period. Pilot work should also test the most appropriate distribution and length of sampling periods for a particular study. Careful thought should be given to the likelihood that the proposed netting schedule (daily hours of operation as well as duration and frequency of netting sessions) can be sustained over the intended life of the project, after station operators' initial flush of enthusiasm has waned.

TRAINING

All personnel should be well trained before beginning a study that involves use of mist nets. Such training should include the operation and care of nets, safe and ethical handling of birds, procedures for obtaining permits, and record keeping. Hands-on training should be done under the tutelage of a bander experienced in the use of mist nets and adept at training, and can be arranged by contacting a certified trainer, a local bird banding organization, or bird observatory. Such resources can be found by searching the Internet or by contacting the U.S. or Canadian banding offices.

All prospective participants in a mist-netting study should follow the guidelines in the appropriate North American Banding Council training guide (Hull et al. 2001; North American Banding Council 2001a, b; Russell et al. 2001). These guides are very detailed, so here we need only to emphasize the importance of appropriately training all project personnel. Joint training sessions for all participants in a particular study, regardless of experience level, is particularly desirable to ensure uniformity of technique (Dale *this volume*) and familiarity with the specific study protocols.

NETS

SELECTING A STATION LOCATION

Locations for mist-netting stations should be selected in accordance with the geographic scope of the study and question being addressed, but the choice should be tempered by accessibility, security from disturbance, and availability of personnel and support facilities. Often, station locations will be chosen to sample a pre-selected group of locations or habitats, perhaps employing a stratified or other sampling design. Depending on the study objective, it may also be very important to select specific locations with high capture probabilities (e.g., for studies involving mark–recapture). Capture rates are usually higher in riparian and shrubby habitats than in forest, in part because many birds fly above net level when vegetation is taller than the nets. If multiple stations are being established and study of dispersal is not a research objective, stations should be at least 1–5 km apart to ensure that most individuals will not be caught at more than one location (Ralph et al. *this volume b*).

For migrating birds, the most suitable study locations for long-term trend monitoring are ones from which birds are likely to move on as quickly as possible (i.e., locations that are not especially attractive for stopover), because some current methods for trend analysis assume that each day's count is an independent sample of the population (Dunn and Hussell 1995). By contrast, if the monitoring questions involve interest in stopover ecology, suitability of habitat, resident birds, and similar questions, then it may be preferable to find locations that have large populations of birds overall, including migrants with more lengthy stopovers. Locations for abundance monitoring during migration should be selected where overall habitat change will be minimal (Kaiser and Berthold *this volume*). Otherwise, change in use of the area by migrants could be interpreted as a change in the size of the breeding population in the region from which the migrants came (Ballard et al. 2003). Suitable locations with relatively stable habitat include those kept at an early successional stage by natural processes (such as regular flooding), or locations where the station operator has permission to cut vegetation regularly throughout the study area to maintain habitat structure and vegetation height at relatively stable levels.

NUMBER OF NETS

The number of nets used at each station should be defined both by the target sample size (related to the study questions) and by the ability of available personnel to handle the normal rate of capture. The North American Banding Council (2001a) gives detailed guidelines on the balance between bird numbers and the number of personnel. In general, most well-trained people can handle 5 birds/h. We suggest that if capture rates at a two-person station regularly exceed 50 birds in a 5-h period, consideration should be given to adding personnel, or reducing the number of nets. If the capture rate is consistently less than 3 birds/person-h, consideration should be given to increasing the number of nets (if higher numbers are needed to meet study objectives), or to having a single person operate the station and sending other personnel to operate additional stations.

Sometimes the number of nets that can safely be operated varies widely from day to day, for example, during migration seasons, or at locations where high winds often make certain nets unusable. In such cases, a core group of nets can be designated that includes nets opened on essentially all days that netting takes place. One or two additional groups can then be defined, of nets that will be closed first (as a unit) when some nets must be closed. A variable representing the net groups opened each day can then be added to analyses to model the effect of variable effort.

NET PLACEMENT

Several factors should be considered in deciding how to place nets within the study area.

Ease of checking nets.—A person should be able to complete a net round within about 15 min or less, if no birds are captured. Rounds can be longer if one person can patrol nets constantly and someone else processes the birds, as long as birds are never left in a net for much more than 30 min (North American Banding Council 2001a). If the study design allows, it is efficient to place nets in an array that brings the observer back to the starting point at the end of the net round (e.g., circular or grid array, rather than linear).

Habitat.—Many studies require sampling of particular habitats, species, or locations. If there are no such constraints, nets should be placed where (a) capture rates will be reasonably high, (b) nets are sheltered from prevailing winds, and (c) vegetation at net sites can be manipulated to maintain it at a relatively constant stage for the duration of the study. For relatively random sampling, making no prior assumptions about movements of birds or relative use of habitat, nets should be placed systematically across a study area or with some element of randomization in placement and orientation.

Net density.—The optimal distance between nets varies widely with research question. Number of species inventoried will increase with low net density and sampling of a large area. For studies of adult population size and survival rates, obtaining large sample sizes and having high capture and recapture probabilities will increase precision of estimates (Pollock et al. 1990). As net density is increased, capture probability of individual adults will increase but effective population size sampled will decrease to a certain threshold, which will be related to size of home range or territory.

If territorial birds are being captured, then nets should be spaced at distances appropriate to sampling as many territories as possible (DeSante et al. *this volume*). Nur et al. (*this volume*) and Ballard et al. (*this volume*) found that resident birds >200 m from nets had a very low probability of capture, and Remsen and Good (1996) indicated that species with typically short flight distance would be captured with lower probability than species making longer flights. DeSante et al. (*this volume*) suggested a net density of 1–1.5 nets/ha as a good starting point for breeding season studies for studies of North American breeding birds, whereas 5 nets/ha is the recommendation of the French STOC monitoring program (Suivi Temporel des Oiseaux Communs; C. Vansteenwegen, pers. comm.).

Faaborg et al. (*this volume*) used linear arrays of nets set end to end for winter sampling in the Neotropics. This design is less efficient for sampling many territories (either breeding or wintering) than is a more dispersed array of nets, because several nets may fall within the territory of a single bird when they are set end to end. Moreover, relatively small shifts in territory location between years can have a large effect on recapture probability. However, this design should increase capture probability for birds whose territories are being sampled, which could be important if netting effort at a station is very limited. Moreover, a linear array of nets should sample species with a wide range of territory sizes, whereas dispersed nets could be less efficient in this circumstance.

For capture of migrating birds, nets can be placed much closer together than if territorial birds are the target.

TYPE OF NETS

Mesh size should be appropriate to the target species (Heimerdinger and Leberman 1966, Pardieck and Waide 1992, Jenni et al. 1996). Small birds become unduly tangled in large-mesh nets, whereas large birds often bounce out of small-mesh nets. Capture rate and ease of using nets also depends on net material and fullness. For most passerines, capture rates are highest using 30- or 36-mm-mesh nets (as measured by the maximum stretch), but certain study objectives (e.g., species inventory) might well require use of a variety of mesh sizes. Nets of standard dimension (12 m long, with four panels) are recommended because they are easier to handle than very long or very high nets, and non-standard nets or novel placements should be used only if especially needed (e.g., Whitaker 1972, Wilson and Allan 1996). See North American Banding Council (2001a) for additional information on net types.

SCHEDULE OF OPERATION

CHOICE OF SEASONS

Netting across seasons can provide valuable data on within- and between-season movements that could be missed by more limited efforts (e.g., Ralph and Hollinger 2003). However, limiting netting to specific seasons may be important for certain studies. Species-specific migration seasons can be defined as the period in which 95% of the individuals of the target species pass through a particular area, as in Hussell et al. (1992). It can be useful to define species-specific breeding seasons in a similar way, as the period in which 95% of individuals in an area confine their breeding activities, from territorial establishment until post-breeding dispersal of juveniles. Using these definitions, post-breeding dispersal is that period between the breeding season and fall migration, and "wintering" season is the period between fall and spring migration. Because the timing of these seasons, particularly the periods of dispersal and migration, can vary markedly with species, age, sex, location, and year, the best dates for study will have to be determined individually for each locale.

For some studies, netting across the boundaries of seasons can cause problems for analyses because of misclassification of transients. For example, inclusion of late migrants in a study of survival rates of local breeders may bias results because one cannot distinguish mortality from emigration through netting alone (Pollock et al. 1990). Even though transients can be dealt with to some degree with mark–recapture analyses (Brownie and Robson 1983; Pradel et al. 1997; Nur et al. 2000, *this volume*), it may be best for survival studies to avoid such complications to the extent possible, through judicious choice of netting dates (DeSante et al. *this volume*).

It has been suggested that capture of local residents during the migration season could lower the chances of recapturing those individuals during the breeding season due to net avoidance. This, in turn, could bias certain kinds of population studies, although statistical methods exist for reducing such bias. No reduction in capture probability across seasons was found by Nur et al. (*this volume*), but only one species has been investigated. If studies are being carried out both in the migration and the breeding season, consideration can be given to using a different study area for each season. On the other hand, if capture of late-migrating individuals will not bias results of a particular breeding season study, it will be most efficient to use a single study area, and to define the breeding season as beginning when the first summer residents arrive, even though migrants may still be passing through.

Number and Length of Sampling Periods

The number and length of sampling periods (each containing a netting session of one to several consecutive days) should be selected on the basis of study objectives, tempered by availability of personnel and accessibility of the station. Multiple and evenly spaced sampling periods are important, both to increase sample size and to ensure that annual samples are not biased by within- and between-year variation in abundance or capture probability of age and sex groups. Optimum length of sampling periods will depend upon the selected length of netting sessions within these periods (see below), and the desired length of gaps between netting sessions.

The MAPS protocol calls for dividing the breeding season into 10-day sampling periods, which we recommend as the standard unless there is need for more frequent sampling. Wintering season studies frequently sample only 1-3 times/season (e.g., Faaborg et al. *this volume*). Although this may be sufficient for detecting site fidelity and long-term changes in use of a location (e.g., Latta and Faaborg 2002), monthly or more frequent sampling should offer better opportunities for detecting intra-seasonal variation in movements of age and sex classes, and for greatly increasing precision of population parameter estimates.

For monitoring population change of migrating populations, it is best if sampling is conducted daily or near daily, to allow modeling of the effects of date and weather on number of migrants present, and to increase precision of parameter estimates (Dunn et al. *this volume a*, Hussell *this volume*, Thomas et al. *this volume*).

Length of Netting Sessions

Depending on the length of the gaps between successive netting sessions, personnel may be able to rotate among stations and sample several locations within a single sampling period. Moreover, gaps allow birds to lose net shyness between sampling periods (see below), and can decrease the chance of recapturing transients within seasons, making it easier to identify transients in mark–recapture models (Pradel et al. 1997). Regardless of the number of days in each netting session, we recommend that nets be operated for the same number of days in each session so that capture effort will be the same in each sampling period.

The MAPS protocol calls for 1 day of netting per 10-day sampling period, which produces a sufficient sample size when data are pooled among many stations. In other studies, especially where stations are visited infrequently and may be quite inaccessible, or when larger sample sizes are needed to determine local (rather than regional) metrics, it may be desirable to net for two, three, or more days in a row to catch the maximum number of birds possible. It is often found that netting for more than 3 days in a row becomes unproductive because of net avoidance, so that few naïve birds remain to be captured (Burton and DeSante *this volume*, Faaborg *this volume*). Even birds stopping over during migration may show net avoidance after first capture (Dorsch 1998). Some evidence suggests that recapture probability may be depressed for as much as a month after capture or even longer, based on tropical wintering birds (Faaborg et al. *this volume*; J. Faaborg, pers. comm.). However, DeSante et al. (*this volume*) suggested that in temperate breeding birds, net avoidance may last only a week or less, and in some species there is no evidence of any net avoidance (Nur and Geupel 1993a, Ballard et al. *this volume*). Whenever feasible, the presence and duration of net avoidance should be studied for each target species to determine the most efficient netting schedule for a particular study (Burton and DeSante *this volume*).

Despite the possibility of net avoidance, near-daily netting effort may be necessary during the breeding season to capture representative numbers of breeding adults or locally produced young birds, which may be present on the study plot for only a few days after fledging (Ballard et al. *this volume*). Optimal length of netting sessions therefore varies with study species and objectives.

During seasons when birds are relatively resident, abundance is assumed not to vary systematically from day to day, such that samples collected from a variety of locations on different days will give the same results as if all samples had been collected simultaneously. However, temporal change can be rapid, even during the breeding season, and species differ in the timing of breeding activities (Ralph and Hollinger 2003, Ballard et al. *this volume*). For within-year comparisons among locations, therefore, netting sessions should be paired temporally to the extent possible.

During migration, abundance and species composition of migrants present at any given station are very likely to differ from day to day, depending largely on weather and date in the season. Studies aimed at comparing habitat use by species or age classes during migration should therefore sample all stations on the same days, especially if relatively few netting sessions can be undertaken. Over a period of years, however, a network of stations operated on different days should provide similar information, although with greater variance.

DAILY TIMING OF OPERATIONS

Netting normally should take place early in the morning, because capture rates are usually highest in the first 4-6 h after dawn when birds are most active. To obtain a good sample of the birds present, nets should be open for at least 4 h (weather permitting), as is the norm at the vast majority of stations. Depending on objectives of the study, and on predictable availability of personnel, nets can be run for a longer period, even for the entire day (e.g., Kaiser and Berthold *this volume*). This may be the preferred option in situations where birds are known to be active throughout the day (Faaborg et al. *this volume*; E. Mallory, unpubl. data), or when logistics make it more efficient to increase effort within a netting session than to add visits to the station. Whatever the choice of daily hours of operation, that level should be sustainable throughout the expected life of the study to maintain standardization of data collection (see below).

DATA TO BE COLLECTED

BIRD DATA

There is broad agreement on basic data that should be collected for every bird captured, but ongoing discussion on how much extra data should be taken that banders have no plans to use in their own analyses (e.g., time of day that a bird was weighed, fat score, or molt). However, these data can be of great value when pooled with those from other study locations (e.g., Dunn 2002), and in some cases only pooled data can provide samples large enough for analysis. As long as the data can be collected without stress to birds (i.e., holding and handling times are not too great), we recommend that banders collect all data listed in Table 2. Physical samples, such as blood for genetic study or feather samples for genetic or isotopic analysis, should only be collected as part of a specifically designed project for which necessary permits have been obtained.

Methods used for taking measurements and for recording skull pneumatization should follow the recommendations of the North American Banding Council (2001a, b). Pyle (1997) provided detail on aging and sexing birds by plumage characteristics.

We recommend that a camera be kept on hand at every netting station to document characteristics of birds that are unusual (as well as to document habitat at net sites; see below).

OTHER DATA

We recommend that information on station operation be recorded at a level of detail that would allow others to reconstruct the study if desired. These metadata should include at the minimum: definition of the boundaries of the study area, number and type of nets, individual net locations (carefully mapped with compass orientation and preferably GPS documented), and schedule of operation.

Depending on the goal of the study, it may be necessary to collect detailed data on vegetation in and around the study area, including the type, density, and height of each vegetation type at each net site. Even if not part of the study, we recommend that a simple, broad habitat classification be done each year, as described in Ralph et al. (1993). Annual photographs of net sites can also aid in documenting habitat. This material will provide important evidence for interpreting the factors responsible for capture rates at each net site over the course of the study. A brief description of the landscape in which the study area is embedded can also help in interpreting results, and can be helpful when comparing results among different projects. Plotting net locations onto a topographic map or aerial photograph is a good way to document landscape and land use characteristics of the surrounding area.

In addition, banders should record daily effort data, including date, hours of opening and closing nets, which nets were open (if not all), and names of personnel participating. We recommend also that a daily narrative be written, covering any events that may have affected results (e.g., presence of

TABLE 2. RECOMMENDATIONS FOR COLLECTION OF DATA ON CAPTURED BIRDS.

Data type	Comments
Mandatory	
Data required by Banding Offices	Date, location, band number, auxiliary marking status, species, age, sex
	Age, sex, or both should be recorded as "unknown" unless designation is at least 95% certain
Retrap status	First capture vs. retrap
Recommended	
Subspecies	If difficult to distinguish or unusual, record characters used to identify
Tail length	If needed to identify subspecies
Bill dimensions	If needed to identify subspecies
Tarsus length	If needed to identify subspecies
Skull pneumatization	Record score in appropriate season, and use routinely in combination with plumage characters that are not known to be at least 95% accurate
Breeding condition	Record condition code in appropriate season
How aged and sexed	Record codes for how aged and sexed (e.g., codes used by MAPS; http://www.birdpop.org/DownloadDocuments/manual/Newband.PDF), recording presence of brood patch or cloacal protuberance, eye color, molt limits, tail shape, or other criteria on which aging and sexing is based
Wing length	Banders in the Western Hemisphere are advised to measure unflattened wing chord (the norm in North America), which is thought by some to be most reproducible and which allows most opportunity for direct comparison and pooling of data; Europeans usually measure flattened wing chord (or length, or both, of the eighth primary; Kaiser and Berthold *this volume*)
Weight	Specify weighing equipment in station protocol
Fat score	Ralph et al. (1993) is widely used in North America, but use of Kaiser (1993a) may lead to less variation in scoring among observers (Dunn 2003)
Time of handling	Select time of start or end of net round, or time of weighing (for standard use; record time to nearest 10 min)
Net of capture	Useful in assessing factors affecting capture rates (habitat, distance from nest); some people also record side of net and net panel in which individuals are captured
Molt	In appropriate season, record details or, at a minimum, the presence or absence of wing and body molt
Notes	E.g., on aberrant plumage, disease or parasites, deformities, or to note that photos were taken; record extent of juvenile plumage; record probable age and sex if designation was <95% certain

predators, windstorm, or other disturbance). Records should be kept as well of factors that could affect year-to-year results (such as insect epidemics or presence of heavy fruit crops in the study area). If weather variables are to be used in analyses, it often may be easier to obtain computerized data from a nearby weather station than to record it in great detail at the netting station. Nonetheless, weather conditions on site may differ from weather office records (particularly wind speed and occurrence of local showers), so keeping simple local records can be worthwhile, and will aid in interpretation of daily capture rates. Automated weather stations can be purchased relatively inexpensively.

STANDARDIZATION

Most monitoring studies are intended to detect temporal and spatial variation in bird abundance or demographic parameters. It is therefore crucial that capture operations be standardized as much as possible over time and space. Without standardization, ascribing variation in capture rates to test variables can be criticized, because it always can be argued that the variation may have resulted from changes in capture protocol. Standardization will help minimize variation in capture probability and allow use of more powerful yet parsimonious statistical models in estimation of survival and population size (Peach and Baillie *this volume*, Sauer and Link *this volume*). If a change in protocol is required (such as new net locations or different hours of operation), we recommend that the old and new protocols be used on alternate dates for a year or two so that the effect of the change can be appropriately modeled in analysis. This approach, however, is cumbersome and expensive in time and effort. It is far preferable to conduct a pilot study to determine the optimal equipment, net placement, and operation protocol, and then follow that protocol strictly throughout the life of the project.

NETS

We strongly recommend that net number and placement be held constant when abundance monitoring is a study objective. It is often tempting to open more nets when extra personnel are available or to add or alter net sites during the course of a study. However, this can bias results, because net sites are not equal in the number and types (species, age, sex) of birds captured. For example, birds captured per net-hour could differ between years simply because in one year nets were placed where they were particularly efficient at catching the target species.

Type of net (length, height, and mesh size) also should remain constant if at all possible, and if several types of net are used, the different types either should be placed always at the same location, or rotated frequently and on a regular schedule among all possible locations. Net characteristics such as the relative fullness of nets between trammel lines, whether or not nets are tethered, and material of construction (nylon vs. polyester) also may affect capture rates (North American Banding Council 2001a), but their effects have not been rigorously tested. The rule of thumb is to use exactly the same type of net (from the same maker if possible) in each location throughout the life of the study.

Finally, height of the net affects capture rates. Nets should be set such that a bird captured in the lowest panel just clears the ground (North American Banding Council 2001a), unless the study goals require otherwise (e.g., inventory studies in which ground-hugging species could be missed using normal settings). Some netting stations mark poles with tape showing where each net loop should go to ensure uniformity among personnel in the way nets are set each day. Thibodeau (1999) felt this unnecessary because he found that most birds were captured in middle panels of nets at his station. However, Jenni et al. (1996) found a higher capture rate in upper panels, suggesting that variation in the height of the top of the net could indeed affect overall capture rate.

Any use of lures (bait, water drip traps, tape recordings) should normally be avoided, because it difficult to use them in a standardized manner. In some monitoring studies, however, their use is important (e.g., Sogge et al. 2001; or for nocturnal netting of owls, Erdman and Brinker 1997). Lures should be used on a regular schedule and either should be placed in the same location at each use or rotated regularly among placements. Sound lures should use the same recordings throughout the study and should be broadcast on standard equipment at a specified volume. Digital recordings (solid state or CD) are less subject to degrading than are tape recordings.

SCHEDULE OF OPERATION

Just as net locations are not equal in number and kinds of birds (species, age, sex) that are captured per net-hour, neither are time periods equal (hour in day, day in season). If the schedule of operation changes in a systematic way during the study (e.g., running nets in the morning in one year, but all day in another), then birds captured per net-hour will likely differ between temporal samples solely because of the change in schedule. If nets are operated longer on some days than others, we recommend that analysis be limited to the time period in which nets are always open, as with MAPS (see DeSante et al. *this volume*). Capturing a bird during non-standard hours, however, may result in net avoidance during subsequent standard netting hours, such that excluding data from these non-standard periods from analysis might result in biased estimates of population parameters. Although the likelihood of this happening probably varies seasonally, it may be advisable to avoid non-standard netting within study areas where standardized protocols are in place and net avoidance is suspected to occur.

It is not critical that dates of netting sessions within each sampling period be exactly the same year after year, but they should be paired as closely as practicable. Length of the netting session (consecutive netting days) also should be standardized to the extent possible, to ensure that effects of net-avoidance are the same in every sampling period.

Habitat

Even if netting is completely standardized, changes in vegetation around nets can cause changes in the numbers and kinds of birds captured, independently of changes in local bird populations (Ballard et al. 2003). More birds fly over nets as vegetation becomes taller and fuller, and more (or fewer, depending upon the species) may be captured if understory vegetation fills in gaps next to net lanes. It is therefore important either to choose net sites at which vegetation is likely to remain relatively unchanged for the life of the study, to control vegetation at the net site through regular trimming and thinning, or to use mark–recapture methods to track changes in capture probability over time (Kendall et al. *this volume*). As noted above, we recommend that photography and vegetation assessment be undertaken each year at each net site to document vegetation height and density, and to serve as a reference for vegetation management.

Written Protocol

An important aspect of maintaining standardization is to prepare a formal operating protocol for the project. This requires clearly defining the standards, serves as a reference for future personnel, and also serves as a record of metadata that are relevant to the use and interpretation of results. The protocol should describe the exact net locations, type of net to be used at each net site (with full detail on maker, material, mesh size, dimensions, etc.), schedule of operation, instructions on keeping habitat around nets at a clearly defined constant height, methods used for measuring birds or taking fat scores, and all other operational details. The protocol should be sufficiently detailed so that a person experienced in mist netting, but without experience of the study or study location, could continue the study without any guidance beyond the written protocol. While ensuring standardization of operations and quality of data, a protocol also will contribute to safety of birds (e.g., by providing instructions on frequency of net checks and procedures to use in case of bad weather).

CONCLUSION

All people using mist nets should use methods that are ethical and ensure safety of birds that are captured. Beyond that, it is important to select netting methods that will best meet the specific objectives of each study. Whenever possible, however, researchers should use the recommended and commonly used protocols described here, to provide the most opportunity for direct comparison of results among independent studies.

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