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Evaluation of Mist-net Sampling as an Index to Productivity in Kirtland's Warblers

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Many applied and theoretical investigations require information on how productivity varies in time and space (Temple and Wiens 1989, DeSante 1995). Examples include studies of habitat quality, population trends, life-history tactics, and metapopulation dynamics. From a demographic perspective, productivity is the number of young, counted at a given time of year, produced per adult (e.g. Caswell 1989). Various measures have been used to estimate productivity. One of the most attractive is mist netting during the summer after young have left the nest, but ideally before they have left the study area. Several programs use this approach, including the Constant Effort Sites Scheme of the British Trust for Ornithology (Baillie et al. 1986, Bibby et al. 1992) and the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante et al. 1993) in North America.

Hatching-year (HY) and after-hatching-year (AHY) birds are widely believed to have different susceptibilities to netting (DeSante et al. 1995, Peach et al. 1996), so the ratio of HYs to AHYs obtained from netting is not used as an estimate of productivity. Instead, investigators hope that the relative susceptibility to capture is about the same among the samples being compared so that the age ratios in mist-net samples provide a reliable index to productivity (DeSante 1995, DeSante et al. 1995).

Because numerous factors can affect mist-net captures, the reliability of productivity indices based on mist netting needs to be evaluated using independently derived productivity estimates. Feu and McMeeking (1991) found that age ratios in mist-net samples were correlated with nesting success in Eurasian Blackbirds (*Turdus merula*) but not in Song Thrushes (*T. philomelos*). Similarly, Nur and Geupel (1993) found a correlation between mist-netting results and nesting success in Song Sparrows (*Melospiza melodia*) but not in Wrentits (*Chamaea fasciata*).

Studies of this sort have convinced specialists in avian monitoring that mist netting at a single location does not provide a valid index to productivity, either at that site or across a larger region (e.g. DeSante 1995, Peach et al. 1996). It remains uncertain, however, whether mist netting at several locations yields a reliable index of average productivity for the region in which the sites are located. It is possible that annual variation in relative susceptibility of HY and AHY birds to capture in mist nets might obscure trends in productivity across time or space.

Here, we report on the correlation between mist-net indices and productivity in Kirtland's Warblers (*Dendroica kirtlandii*). Our study is unusual because we had good estimates of population-wide productivity, and our mist netting also sampled most of the population. Thus, we had an opportunity to study mist-net indices without the confounding influence of immigration and emigration.

Our primary objective was to determine whether mist netting at several sites provided a useful index to population-wide productivity. Our data also allowed a comparison of capture rates for HY and AHY birds and thus supplement the results presented by Feu and McMeeking (1991) and Nur and Geupel (1993) on the validity of mist netting at a single

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site as a measure of site-specific or regional productivity.

Methods.—Kirtland's Warblers nest in stands of jack pine (*Pinus banksiana*) on sandy soil in scattered but well-known locations in 13 contiguous counties in Michigan (Mayfield 1992). The sex ratio is believed to be approximately equal, and most of the adult males are territorial (Mayfield 1992). The population is surveyed each spring by 30 to 50 experienced observers who work in small groups at all known nesting sites. The goal is to count all singing males, and the results are widely regarded as a virtual census of the population (Mayfield 1992).

Our study was carried out during 1986 to 1992. Population size had been declining for several years when the study began, reaching a low of 167 birds in 1987. Thereafter, much new habitat became available, and population growth was rapid (ca. 20% per year) in most years until the end of the study (Mayfield 1992).

Mist netting was conducted from early July to mid-September on seven sites that were well distributed across the breeding range (Damon, McKinley, Bald Hill, Muskrat Lake, Mack Lake, Saint Helen's, and Ogemaw Management Unit). All but two sites (Bald Hill and Mack Lake) became suitable or unsuitable during the study period owing to habitat changes. Three or four of the seven sites were sampled in each year of the study. The proportion of the population (as determined during spring censuses) that occupied sites where mist netting occurred increased from 0.36 and 0.49 in 1986 and 1987 to more than 0.80 in 1990, 1991, and 1992.

Each site was sampled by placing permanent net lanes in loops or arrays. The density of nets and netting effort were approximately constant among sites. The size of sites, and thus the number of nets per site, varied substantially (from 10 nets in 1 array to 154 nets in 11 arrays). Nets were 12 m long with 36-mm black nylon mesh and were placed over 12-m sections of black roofing felt (see Sykes 1989). Nets were open from approximately 0630 to 1130, weather permitting, and were checked every 20 min. Netting at sites, and lanes within sites, were rotated systematically. Individual nets were opened for a single morning and then rested for three to six days. Our index of productivity was the number of HY birds captured divided by the number of AHY birds captured.

Estimates of actual population-wide productivity were obtained from estimates of change in population size and survival rates. For any two consecutive Junes, we may write:

$$N_2 = N_1S + N_1BS_o, \quad (1)$$

where N_1 and N_2 are the numbers of males alive in June in the two years, S is the proportion of males alive at the start of the year that survive until the end of the year, B is the number of young males produced (i.e. alive in August) per adult male, and S_o is the proportion of those young that survive until the following June. Rearranging equation 1,

$$B = [(N_2/N_1) - S]/S_o. \quad (2)$$

Note that actual productivity, B, is based solely on males (because only males are counted on spring censuses), whereas our index to productivity is based on both sexes (because both sexes are captured and resighted). The number of males produced per adult male, however, is equal to the number of young produced per adult if the sex ratio is equal, as is believed to be approximately true for Kirtland's Warblers (Mayfield 1992). The difference in definitions thus should have little (if any) influence on our analyses.

Estimates (indicated by lowercase letters) of N_1 and N_2 were obtained from the annual spring census of singing males. Estimates of survival rates were obtained from a mark-recapture study carried out during each summer. Each Kirtland's Warbler captured during mist netting was uniquely marked with a USFWS aluminum band and three colored plastic bands. Resightings were obtained from observations made separately during each summer, and resighting effort was distributed evenly across the entire population. Thus, although captures were not random and independent (because net locations were constant), resightings within age and sex cohorts were random.

Survival estimates were obtained using the capture-recapture program SURGE (Lebreton et al. 1992) and will be reported elsewhere. We investigated numerous models specifying how survival and resighting rates varied and selected the most parsimonious model supported by statistical analysis. The model-selection process resulted in a single estimate of survival during the first year (August to June; $S_o = 0.4470$) and a single estimate for subsequent years (June to April; $S = 0.6415$). Equation 2 thus became $B = 2.237(N_2/N_1) - 1.435$. The standard error of the productivity estimate, b, was estimated by expanding equation 2 for B in a Taylor series, which led to:

$$V(b) \cong \frac{1}{S_o^2}\left[V(r) + V(s) + \left(\frac{R - S}{S_o}\right)^2 V(s_o) + \text{cov terms}\right], \quad (3)$$

where $r = n_2/n_1$, and n_1 and n_2 are the estimates of N_1 and N_2 provided by the spring census.

Methods used to estimate each component of $V(b)$ are discussed briefly below. Estimating $V(r)$ required an assumption about what fraction of the birds was detected on the spring census. Although attempts are made to find all singing males, some males undoubtedly are missed. Other studies (Bart and Schoultz 1984) have shown that on multispecies sur-

TABLE 1. Kirtland's Warbler population size, productivity, and age ratio in mist-net samples collected in mid- to late summer.

Variable	1986	1987	1988	1989	1990	1991	1992
Population size[a]	210	167	207	212	265	347	397
No. of nets	71	146	207	234	284	260	238
No. of net hours	1,536	8,921	13,139	11,546	10,038	9,563	14,890
No. of HYs caught	12	46	54	105	112	71	123
No. of AHYs caught	15	34	41	40	38	39	52
HYs per 1,000 net h	7.81	5.16	4.11	9.09	11.16	7.42	8.26
HYs per AHY	0.80	1.35	1.32	2.63	2.95	1.82	2.37
Productivity[b]	0.35	1.34	0.86	1.37	1.50	1.13	1.30

[a] Population size in 1993 was 485.

[b] Calculated with equation 2 with $S_o = 0.4470$ and $S = 0.6415$.

veys, trained observers record about 70% of the audible birds, including many that are audible only (i.e. not seen). On the Kirtland's Warbler census, surveyors record only one species, and they pass close enough to all locations that singing males are readily detectable. Thus, it seems likely that nearly all singing males are recorded. Furthermore, Kirtland's Warblers sing persistently during the census period (Mayfield 1992), so the overall proportion of birds detected is probably 90% or more. We conservatively assumed that actual detection was 85% and that counts in consecutive years were independent. These assumptions led to:

$$V(r) \cong 0.15\left(\frac{n_2}{n_1}\right)^2\left(\frac{1}{n_2} + \frac{1}{n_1}\right) \quad (4)$$

Estimates of $V(s)$ and $V(s_o)$ were obtained from the SURGE output. The covariance terms involved cov(r, s), cov(r, s_o), cov(s, s_o), and multiplicative terms. Cov(r, s) and cov(r, s_o) were assumed to be zero because the estimates of r and the survival rates were obtained from completely separate efforts and analyses. The estimate of cov(s, s_o) was obtained from the SURGE output.

Results and discussion.—In most years, approximately 40 to 50 AHY birds and 50 to 120 HY birds were captured during 9,000 to 15,000 net hours (Table 1). The resighting rate for marked birds was approximately 75%. Estimates of actual productivity, calculated using equation 2, were reasonably precise; coefficients of variation ($SE(b)/b$) were 10 to 12% in each year except 1986, when sample sizes were small and the estimated CV was 22%. Actual productivity, and the index of productivity, each varied about three-fold during the study period.

The sample age ratio derived from mist netting exceeded the estimate of actual productivity in every year, indicating that HY birds were more susceptible to capture than were AHY birds (sign test, $P < 0.01$, $n = 7$). The average estimate of actual productivity during the seven-year study was 1.12 young per adult, and the average age ratio (HY : AHY) of birds caught in mist nets was 1.89. This indicates that on average, HY birds were about 1.7 times more susceptible to capture than were AHY birds.

The index, HY : AHY, was strongly related to productivity (Fig. 1). The correlation (r^2) was 0.82, and the P-value for a test of $R^2 = 0$ was 0.02. The sample r^2 was not significantly different from 1.0. There were no outliers or indications of a nonlinear trend in the data. Thus, in our study, the age ratio in the population-wide mist-net sample provided a good index to productivity, although it was not useful as an estimate of actual productivity owing to HY birds being much more susceptible to capture in the nets.

The number of HY birds captured per net hour was not significantly related to productivity ($r^2 = 0.13$, $P = 0.422$), a result that was not surprising. If population size changes (as was true in our study), then the number of HY birds caught per net hour presumably would tend to change even if productivity per adult did not change. Also, any annual changes in net efficiency caused by weather or other factors could cause changes in the number of HY birds captured. Finally, the susceptibility of HY birds to netting may vary spatially (Nur and Geupel 1993), which would further compromise the use of capture rates of HY birds as a productivity index.

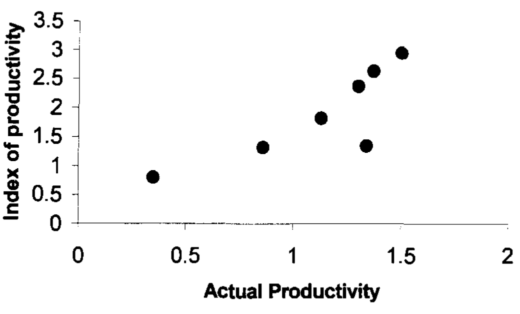

FIG. 1. Relationship between actual productivity for Kirtland's Warblers during 1986 to 1992, calculated using a demographic equation (see text), and the age ratio in a mist-net sample used as an index of productivity ($r^2 = 0.82$, $P = 0.02$).

TABLE 2. Number of Kirtland's Warblers captured in mist nets at two sites on the breeding grounds in Michigan.

	1986	1987	1988	1989	1990	1991	1992
			Bald Hill				
HY	11	46	29	52	22	12	9
AHY	15	24	18	16	7	1	4
HY : AHY	0.7	1.9	1.6	3.3	3.1	12.0	2.3
			Mack Lake				
HY	0	4	24	36	48	35	86
AHY	0	6	23	14	16	28	37
HY : AHY	—	0.7	1.0	2.6	3.0	1.3	2.3

Age ratios at the two sites where netting continued throughout the study (Bald Hill, Mack Lake) were not strongly related to population-wide productivity ($r^2 = 0.05$ and 0.41, $P = 0.64$ and 0.17, respectively; Table 2). The primary reason for this appeared to be that movements differed significantly between HY and AHY birds. At Bald Hill, habitat suitability declined during our study. As this occurred, numbers of HY and AHY birds declined, but the number of AHY birds declined faster, and thus the ratio of HY : AHY birds increased (Table 2). For example, combining data, the ratio was 1.4 for 1986 to 1988 and 3.7 for 1990 to 1992. At Mack Lake, habitat improved during the study. Both HY and AHY birds became more common, but the number of HY birds increased faster such that the ratio of HY : AHY birds tended to increase through time (Table 2). For example, combining data, the ratio was 1.0 for 1986 to 1988 and 2.1 for 1990 to 1992. With site-specific dynamics exerting such a strong effect on age ratios, it is not surprising that the age-ratio index at individual sites did not reflect population-wide productivity very well. These results support the view of DeSante (1995) that multiple sites must be surveyed for mist netting to provide a valid index to population productivity.

The number of sites needed to obtain a reliable estimate of regional productivity presumably will vary among studies depending on numerous factors such as the similarity among sites of trends in habitat quality. If data from a pilot study are available, precision and power can be estimated using standard formulas, with the number of sites as the sample size. In ecological studies, samples of fewer than six or eight rarely provide useful estimates, and we see no reason that this generalization would not apply to studies of productivity. Thus, at least six to eight sites (or more) will probably be needed in most cases.

In summary, in our study (1) capture rates (number of HY birds / number of AHY birds) were not useful as a direct measure of productivity in Kirtland's Warblers because HY birds were about 1.7 times more likely than AHY birds to be captured in mist nets; (2) capture rates varied substantially among sites, presumably because of changes in habitat that affected movements during late summer (thus, capture rates at a single site did not provide a useful index to population-wide productivity); and (3) population-wide capture rates provided useful indices to population-wide productivity. As noted previously, the first two conclusions are already accepted by specialists in the use of mist netting to index productivity. Our study presents the first evidence that annual variation in relative capture rates is sufficiently small that mist netting at multiple sites in a region can provide a useful index to region-wide productivity. The region must be large relative to late-summer movements by the study species, which means that obtaining habitat-specific productivity rates will be possible only within large patches of habitat. It should also be recognized that many species will move much farther than Kirtland's Warblers (owing to their limited breeding distribution). Our results suggest that mist-netting programs like MAPS and the Constant Effort Sites used in Britain can provide useful measures of temporal patterns, large-scale spatial patterns, and year-specific patterns in avian productivity. Furthermore, unlike most nest-monitoring studies, mist netting in late summer measures season-long productivity, the quantity of greatest use in most demographic analyses. Late-summer mist netting thus appears to be a useful method for studying avian productivity provided that investigators realize that results from at least six to eight sites that are well distributed across a large region must be combined to obtain a valid index, and that results obtained in this manner describe relative region-wide productivity, not absolute or local productivity.

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