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AN INVESTIGATION OF PRODUCTIVITY INDICES DERIVED FROM BANDING OF FALL MIGRANTS

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Abstract. Indices of productivity were estimated for seven species of birds captured during fall migration at two mist-netting stations less than 1 km apart, in Kalamazoo, Michigan, where those species occur only as migrants. The indices were proportion of hatch-year birds in the fall migration catch, and abundance of hatch-year birds. These values were positively correlated. Within species, mean annual hatch-year abundance often differed in magnitude between the two stations, and in some species annual abundance indices showed long-term trends in opposite directions. Nonetheless, there was evidence of parallel annual fluctuation of both productivity indices, both within and between stations. Fall migration productivity indices will rarely be useful for tracking reproductive success of specific breeding populations, because the areas from which fall migrants originate are large and poorly delineated, but such indices should be useful for other purposes (e.g., comparing regional productivity in wet and dry years). More work is needed to test the effect on fall productivity indices of habitat, net location, and frequency of sampling. Also needed are more comparisons of productivity indices among a larger number of stations, and better validation through comparison with independently derived productivity estimates.

Key Words: age ratio, banding, migration, productivity indices, validation.

Annual productivity is a key component of integrated monitoring (Baillie 1990). At local scales, intensive nest searching can provide data on reproductive success, but most such studies focus on a single species and station, often for just a few years. At slightly broader scales, constant-effort mist netting spanning the post-fledging, pre-migration period has been shown to give estimates of breeding success that correspond well with nest studies, at least in some species (du Feu and McMeeking 1991, Nur and Geupel 1992). Cooperative programs such as the Monitoring Avian Productivity and Survival program (MAPS) in North America (DeSante et al. 1995) and Constant Effort Sites (CES) in Great Britain (Peach et al. 1996) depend on many contributors to track productivity on regional scales. These programs have provided further evidence that summer mist netting reflects true levels of productivity: productivity indices may fluctuate in parallel among stations (Baillie et al. 1986), long runs of data sometimes show patterns and periodic anomalies that correspond well to suspected causal events (e.g., DeSante and Geupel 1987), and large drops in productivity indices may precede declines in breeding populations the next year (DeSante et al. 1998).

Data on birds captured during migration may provide another valuable source of productivity data. In particular, productivity measures from migrants could provide information on species whose breeding ranges are largely inaccessible for other kinds of survey, such as boreal-nesting songbirds. Migrants captured at a single station can come from broad areas of breeding range (Brewer et al. 2000, Wassenaar and Hobson 2001), so it may take only a few stations to provide results representative of a broad geographic area. Finally, fall banding produces relatively large sample sizes compared to MAPS and CES, which may contribute to making productivity indices more robust. However, although there is widespread belief that age data from the migration season reflect annual reproductive success (e.g., Ralph et al. 1993), there are no studies comparable to those for MAPS and CES that have attempted to demonstrate the validity of fall migration productivity indices.

Here we examine two productivity indices for fall migrants captured at two neighboring stations in southern Michigan: the proportion of young birds in the total sample, and an index representing abundance of young birds. Although abundance of young will vary with population size, a portion of the annual fluctuation in numbers of young should reflect variation in productivity. We compare the two indices with each other both within and between stations and to data from the Breeding Bird Survey, and outline needs for further validation.

METHODS

We analyzed age data for 1979–1991 from two banding stations that are about 0.75 km apart, located at Kalamazoo, in southern Michigan. The "River" station had 30–35 12 m, 30 mm-mesh nets in second growth, open riparian woodland, and marsh shrub. The "Marsh" station had 15–20 similar nets in shrub vegetation bordering a marsh and woodland. Mist nets were operated daily (weather permitting) from early August to mid-November, from shortly after dawn until early afternoon. More than 80% of days in the fall migration period were covered annually.

Species chosen for analysis were Gray-cheeked Thrush (*Catharus minimus*), Hermit Thrush (*C. guttatus*), Swainson's Thrush (*C. ustulatus*), Magnolia Warbler (*Dendroica magnolia*), Yellow-rumped Warbler (*D. coronata*), Dark-eyed Junco (*Junco hyemalis*), and White-throated Sparrow (*Zonotrichia albicollis*). None of these species breeds as far south as the study station, so capture of local residents and dispersing juveniles was not a complicating factor in the analyses.

Data were restricted to first captures only, in species-specific migration "windows" (as defined at Long Point, Ontario, 650 km east of Kalamazoo; Hussell et al. 1992). A species was analyzed only if at least 0.2 adult birds/day were captured (on average) within the appropriate migration window, so that results would not be affected by chance variation in low numbers of adults. All birds were aged by the degree of skull pneumatization, and all species chosen for analysis can be aged by this method through the entire migration period. Unaged birds were excluded from the study, and did not exceed 0.3% of the totals for any species analyzed.

We constructed three indices of annual productivity from the number of birds captured, which we term "Raw HY Proportion" (where HY = hatching year birds), "HY Abundance," and "Adjusted HY Proportion." The first index was calculated for each species for each area as (N of HY birds)/(total of HY + AHY birds). To construct the other two indices, annual estimates of abundance for all birds, and for HY birds alone, were calculated from multiple regressions designed to assign variability in daily numbers to date, weather, moon phase, and year. Analysis was identical to that detailed in Dunn et al. (1997). These abundance indices represent the number of all birds, or of HY birds alone, that would be expected in a given year on an average date, under average conditions of moon phase and weather. HY Abundance was simply the abundance index for HY birds estimated from the regressions. Adjusted HY Proportion was HY Abundance divided by the abundance of all birds, as estimated from the regressions. This figure differed from the Raw HY Proportion in that it was corrected for any variation that may have been caused by weather, moon phase, or date in the season.

Trends in breeding populations for Ontario and Michigan, according to the Breeding Bird Survey (BBS), were obtained from Sauer et al. (2000). Other evidence suggests that migrants at the study stations come from both these areas (Dunn et al. 1997). Trends in HY Abundance were calculated as the slope of the log-transformed annual indices regressed on year, producing an estimated annual percent rate of change that is directly comparable to BBS trends. Trends in HY Proportion were calculated as the slope of the regression on year of the arcsine of the square root of the original indices. Detrended indices (residuals from regression of indices on year) were derived from regression of indices transformed as described above. All other statistics involving HY Proportion were also performed on transformed indices, which normalized their distribution. Results were considered significant if $P < 0.05$.

RESULTS

In all species, annual Raw HY Proportion indices were significantly correlated with annual indices of Adjusted HY Proportion from the same station (r ranged from 0.71 to 0.96, $P < 0.01$ in all cases). However, Adjusted HY Proportion was higher than Raw HY Proportion, and usually had lower variance (Table 1). All remaining analyses were run with both indices, and each produced similar results. In the remainder of this paper, unless noted otherwise, results and discussion are limited to Adjusted HY Proportion (hereafter referred to simply as HY Proportion).

The HY Proportion at both stations averaged about 0.73 (Table 1), which is typical of other inland banding stations in North America (Dunn and Nol 1980). Values were always slightly higher at the River station (Table 1), significantly (or nearly) so

TABLE 1. MEAN RAW AND ADJUSTED HY PROPORTION FOR TWO STATIONS, 1979–1991

	River			Marsh		
Species	Raw	Adjusted	N	Raw	Adjusted	N
Gray-cheeked Thrush	0.64 ± 0.09	0.68 ± 0.08	469	0.54 ± 0.10	0.57+0.11	321
Hermit Thrush	0.82 ± 0.08	0.85 ± 0.07	803	0.75 ± 0.06	0.80+0.07	1,260
Swainson's Thrush	0.82 ± 0.06	0.86 ± 0.08	2,638	0.72 ± 0.13	0.74+0.11	654
Magnolia Warbler	0.71 ± 0.13	0.73 ± 0.07	1,506	0.69 ± 0.13	0.69+0.10	1,101
Yellow-rumped Warbler	0.76 ± 0.09	0.83 ± 0.05	6,862	0.74 ± 0.11	0.79+0.07	754
Dark-eyed Junco	–	–	116	0.65 ± 0.11	0.68+0.09	1,057
White-throated Sparrow	0.64 ± 0.12	0.66 ± 0.08	1,243	0.60 ± 0.10	0.65+0.08	1,348

Notes: Values shown are mean ± SD of indices averaged across years.

for all species except White-throated Sparrow. HY Abundance also differed between stations in six of seven species (Table 2), but there was no consistency in which station had higher mean numbers.

There were no significant long-term trends in HY Proportion, but a few in HY Abundance (Table 3). Direction of trend in HY Abundance at the Marsh station matched direction of BBS trends from Michigan (four species only, all increasing), but not those from Ontario. Trends in HY Abundance at the River station did not agree with BBS trend directions from either region. White-throated Sparrow was notable in showing significant trends in HY Abundance at both banding stations, but in opposite directions.

To determine whether productivity indices fluctuated in parallel, we examined correlation of detrended indices. (Detrending prevents correlation resulting solely from trends in the two sets of indices.) HY Abundance indices were positively correlated between stations, sometimes significantly so, as were HY Proportion indices (Table 4). HY Abundance and HY Proportion tended to fluctuate in parallel with each other within stations.

DISCUSSION

Date, weather, and moon phase had significant effects on HY Proportion in most species (as also found by Hussell *this volume*). Raw HY Proportion is therefore a more biased index than Adjusted HY Proportion, although all analyses gave similar results regardless of which HY Proportion index was used. This suggests that Raw HY Proportion may be a minimally acceptable index of productivity, despite the added variance caused by date and weather effects. More importantly, the similarity of results using both HY proportion indices strengthens our confidence that migration season productivity indices actually reflect proportion of young birds present in the population, and are not artifacts of weather effects.

Results indicated that young birds of all species were relatively more prevalent than adults at the River station, regardless of which station hosted the higher abundance (Tables 1 and 2). Not only were there differences between stations in absolute values of productivity indices, but occasionally in long-term trends as well (Table 3). HY proportions in migrants are also known to differ markedly between coastal and inland banding stations, and between samples of birds banded and those killed at lighted structures during nocturnal migration (Dunn and Nol 1980, Ralph 1981). These results show that productivity indices derived from migration banding are not reliable indicators of the absolute number of young produced per adult. Similar conclusions have been drawn for productivity indices derived from summer banding, in which there can be higher proportions of HY birds in particular habitats, and in samples of birds captured with particular trapping devices (Peach et al. 1996, Bart et al. 1999, Green 1999, Senar et al. 1999).

Nonetheless, even when summer productivity indices differ in absolute magnitude, they may fluctuate in parallel (Peach et al. 1996, Green 1999), showing that annual changes in the relative proportion of age groups can still be a good indicator of annual shifts in productivity. The same appears to be true of migration season productivity indices (Table 4). In this study, HY Abundance and HY Proportion fluctuated in parallel within and between stations in most species, although many of the correlations fell short of statistical significance. Parallel fluctuation occurred even when trends in these indices did not agree. For example, long-term trends in HY Abundance for White-throated Sparrow were significant at both stations but opposite in sign (Table 3), yet detrended annual indices fluctuated in parallel (Table 4). These results indicate that

TABLE 2. MEAN HY ABUNDANCE FOR TWO STATIONS, 1979–1991

Species	River		Marsh
Gray-cheeked Thrush	0.30 ± 0.11		0.29 ± 0.10
Hermit Thrush	0.72 ± 0.27	***	1.35 ± 0.49
Swainson's Thrush	1.02 ± 0.24	**	0.75 ± 0.29
Magnolia Warbler	0.65 ± 0.18	**	1.16 ± 0.42
Yellow-rumped Warbler	2.14 ± 0.57	***	0.55 ± 0.23
Dark-eyed Junco	0.11 ± 0.05	***	0.89 ± 0.48
White-throated Sparrow	0.64 ± 0.36	+	0.94 ± 0.33

Notes: Values shown are mean ± SD of values averaged across years. Symbols indicate significant difference (see text) between stations (paired t-tests between annual indices): *** = P < 0.001, ** = P < 0.01, * = P < 0.05, + = 0.5 < P < 0.1.

TABLE 3. TRENDS IN POPULATION SIZE AND PRODUCTIVITY INDICES, 1979–1991

	BBS		HY Abundance		HY Proportion	
Species	Ontario	Michigan	River	Marsh	River	Marsh
Hermit Thrush	2.6+	8.1**	2.3	8.5***	0.25	0.84
Swainson's Thrush	-1.2+	–	2.0	5.9	-0.24	-0.85
Magnolia Warbler	3.0+	9.2	-1.8	4.3+	-0.40	-0.63
Yellow-rumped Warbler	-2.8+	4.6*	1.2	3.8	-0.30	0.49
Dark-eyed Junco	-2.8	–	0.1	-4.9	-0.64	-0.18
White-throated Sparrow	-1.3*	1.2	-9.3**	7.4**	0.22	-0.52

Notes: BBS and HY Abundance trends are rates of change (%/yr). Trend in HY Proportion is average annual change (see Methods). Symbols indicate significance of trend (see text): *** = P < 0.001, ** = P < 0.01, * = P < 0.05, + = 0.5 < P < 0.1.

annual fluctuation in HY Abundance is quite strongly affected by reproductive success. Because it is also affected by annual change in population size, however, it is not as useful an indicator of reproductive success as is HY Proportion.

Several factors may have introduced bias into the productivity indices in this study, which could have reduced the strength of evidence for parallel fluctuation. Vegetation increased in height throughout the study period, and while nets at the Marsh station were moved to keep them in shrub habitat, at the River station they were not. Also, in some years there was a large berry crop at one station but not the other, and thrushes were noted to concentrate where berry crops were high, perhaps reducing correlation of HY Abundance between the stations.

In addition, there were methodological differences between the stations that may have affected results. Net numbers were not wholly standardized, with some nets added and others discontinued during the study period, and not all nets were opened on every day that netting took place. Such factors could alter the abundance, proportion, or both of HY birds at one station relative to the other, particularly if certain nets were more likely to capture birds of a particular age class, or if nets were opened at only one station when there was an influx of birds with unusual age distribution.

The MAPS and CES programs pool productivity data from many stations to calculate regional values, such that anomalies at individual stations are evened out. The same approach with fall migration indices may strengthen results. One difficulty with this approach, however, is defining the region within which all monitoring stations are capturing individuals from the same breeding population. There is evidence, for example, that migrants moving through southern Michigan come from both Michigan and Ontario (Dunn et al. 1997). When BBS trends differ in different parts of the breeding range from which migrants are drawn (as in Yellow-rumped Warbler; Table 3), we do not know which trend is most important for comparison to fall migration productivity indices from southern Michigan. Similarly, we do not know to what extent a more distant station—for example, in central or northern Michigan—would be sampling

TABLE 4. CORRELATIONS OF ANNUAL PRODUCTIVITY INDICES BETWEEN STATIONS, AND WITH EACH OTHER WITHIN STATIONS

	Correlation between River and Marsh		Correlation between HY Abundance and HY Proportion	
Species	HY Abundance	HY Proportion	River	Marsh
Gray-cheeked Thrush	0.33	0.32	0.45	0.61*
Hermit Thrush	0.60*	0.49+	0.08	0.75**
Swainson's Thrush	0.14	0.27	0.44	0.73**
Magnolia Warbler	0.50+	0.93***	-0.19	0.33
Yellow-rumped Warbler	0.46	0.42	0.68*	0.54+
Dark-eyed Junco	0.38	–	0.72*	0.43
White-throated Sparrow	0.51+	0.70**	0.72**	0.04

Notes: Values shown are correlation coefficients between detrended indices (residuals from regression of appropriately-transformed indices on year) and significance levels (see text): *** = P < 0.001, ** = P < 0.01, * = P < 0.05, + = 0.5 < P < 0.1.

the same population as the stations in Kalamazoo. Fall migration productivity data from very nearby stations can certainly be pooled for analysis (assuming stations all follow the same protocol), but it may not be justifiable to pool data from very distant stations.

It will be hard to associate fall migration productivity indices with specific breeding populations because of uncertainty as to breeding origin, so migration season productivity indices will have limited value in assessing impact on productivity of locally varying factors such as predation levels. Nonetheless, accurate information on annual shifts in productivity of migrants should be useful for other purposes. For example, there are known cases of reproductive success varying with weather, either routinely or in response to unusual conditions (e.g., DeSante and Geupel 1987, Bradley et al. 1997). Because weather often affects large geographic areas, data from migrating birds might be especially well suited to the study of such weather effects.

This paper is one of the first to critically examine fall migration productivity indices (see also Hussell *this volume*). Although we found evidence that different stations detected similar annual changes in productivity, our primary conclusion is that a good deal more basic research is in order. A recent study of Pink-footed Geese (*Anser brachyrynchos*) showed the importance of cross-validation and study of biases in data sources, including productivity indices, even for well-studied populations with excellent data (Gantner and Madsen 2001). Similar kinds of work are needed on fall migration productivity indices, including effects of habitat and net location on ages of birds captured, and degree of parallel fluctuation in productivity indices among nearby stations. For example, Harrison et al. (2000) found that habitat change at his late summer banding station altered the relative proportions of age groups in some species but not in others. Similar kinds of research are needed to determine the circumstances and species for which fall productivity indices are meaningful. Even more important is the need to validate migration season productivity indices through comparison with independently collected data on reproductive success. The most suitable comparison would be with MAPS results from probable breeding areas.

In the meantime, we offer several recommendations for the study of productivity through capture of fall migrants. Banders should routinely record the technique they use for ageing each bird handled, and keep careful records of daily effort, net number, and location, so that users of age data can analyze and interpret them correctly. Recording the net number where each bird is captured should permit analysis of net-site effects on age proportion. Capture effort should be as standardized as much as possible (Ralph et al. *this volume a*), to avoid bias in the numbers of each age group captured. Finally, many species have differential timing of fall migration, so it is especially important for avoiding bias to collect evenly spaced (preferably daily) samples throughout the entire migration period of the species.

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