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LONG-TERM POPULATION TRENDS OF FOREST-DWELLING NEARCTIC-NEOTROPICAL MIGRANT BIRDS: A QUESTION OF TEMPORAL SCALE[1]

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Abstract. Analyses of trends in the populations of nearctic-neotropical migrant birds using 1930s-1960s data have indicated declines in many cases. More recent reports, however, suggest that populations of most forest-dwelling migrants are stable or increasing. Our analyses of Breeding Bird Census data, 1940-1995, for 46 sites in the eastern and central United States indicate that 6 of 10 mature forest-dwelling nearctic-neotropical migrants exhibited significant declines over this period, and none increased. However, when only the recent (>1966) portion of data-sets were used, no significant declines were evident and one species increased. Standard errors did not differ between the two sample periods, so lack of significant trends during the latter period was not the result of increased variability in trend estimates due to reduced sample size. Rather, trend analyses appear to be affected by survey period, and our results indicate that population declines in the eastern and central United States are not evident in recent data (>1960s) because the bulk of declines had already occurred. Our conclusion emphasizes that an awareness of the limitations imposed by temporal scale is critical to the valid interpretation of avian population trends.

Key words: Bird declines, Forest birds, nearctic-neotropical migrant, North America, Bird surveys

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TENDENCIAS POBLACIONALES A LARGO PLAZO DE AVES DE BOSQUE MIGRATORIAS NEARTICAS-NEOTROPICALES: IMPORTANCIA DE LA ESCALA TEMPORAL

Resumen. Los análisis de tendencias poblacionales de aves migratorias neárticas-neotropicales utilizando datos de las décadas de 1930 a la de 1960 han identificado declives en muchos casos. Sin embargo, informes más recientes sugieren que las poblaciones de la mayoría de las especies de bosque se mantienen estables o van en aumento. Nuestros análisis de los datos del Breeding Bird Census entre 1940 y 1995 de 46 sitios en estados del este y centro de EE.UU., indican que 6 de 10 especies migratorias de bosque maduro mostraron declives significativos durante este periodo, y ninguna aumentó. Sin embargo, cuando utilizamos únicamente los datos recientes (>1966), no detectamos declive alguno y una de las especies aumentó. Los errores estándard fueron similares en ambos periodos de muestreo y por tanto la falta de resultados significativos durante el periodo reciente no se debe al aumento de variabilidad en la estimación de tendencias a raiz de la reducción en el tamaño de muestra. Por el contrario, los anáisis de las tendencias parecen estar influidos por el periodo de muestreo, y nuestros resultados indican que los declives poblacionales en el este y centro de EE.UU. no son aparentes en los datos recientes (>1960) porque gran parte de los declives ocurrieron antes. Concluimos que es necesario ser consciente de las limitaciones impuestas por la escala temporal a fin de interpretar tendencias poblacionales correctamente.

Palabras clave: Declives en aves, aves de bosque, migratorias neárticas-neotropicales, América del Norte, conteos de aves.

INTRODUCTION

The conservation of nearctic-neotropical migrants (hereafter neotropical migrants) has become a significant issue in conservation biology over the past several decades. The origin of this interest can be traced to early reports in which researchers noted the decline or disappearance of mature forest dwelling migrant birds from parks and preserves in the eastern United States (Briggs and Criswell 1979; Robbins 1979). Various factors have been implicated in these declines, including loss and fragmentation of temperate breeding habitat (Robinson et al. 1995, Trzcinski et al. 1999), destruction of tropical wintering habitat (Briggs and Criswell 1979; Hall 1984, Rappole et al. 2003), the combined effects of breeding and non-breeding habitat destruction (Sherry and Holmes 1995), or mortality during migration (Sillett and Holmes 2002).

Population trends of neotropical migrants exemplify the situation in which long-term studies are required to provide the context for interpreting local or shorter-term trends (Hill and Hagan 1991). Studies of forest migrant populations in eastern North America report evidence of population declines during the early 20th century (Rappole 1995), and in part this prompted the initiation of the Breeding Bird Survey (BBS) throughout the United States and Canada in 1966 (Droege 1990). Many of the earlier studies of migrant bird populations were limited by inadequate experimental design (James et al. 1996), and thus, the veracity of the declines reported is subject to debate (Hutto 1988, James et al. 1992). In contrast, the design of the more recently instituted BBS is statistically rigorous (Droege 1990), but it encompasses a relatively short time period (36 y) compared to the time-scale at which the destruction of temperate and tropical habitats has been progressing (Smith 1954, Sader and Joyce 1988, Dirzo and Garcia 1992, DeGraaf and Miller 1996, Askins 2001). Data from the BBS for this period indicate that overall population trends of neotropical migrants are stable (Sauer and Droege 1992)

In order to evaluate long-term trends in forest bird populations, we analyzed data from the Breeding Bird Census (BBC) for the years 1940-1995 using non-linear route regression. In addition, we compared our results with the results of the BBS for the years available (1966-1995) in order to evaluate the potential that results were affected by the time scale of analysis.

METHODS

We analyzed data from 46 sites in 19 U.S. states and one Canadian province (Appendix 1) following a standardized protocol. A BBC is conducted using the spot-mapping method, in which observers compile a record of locations of singing male birds during 8-10 visits to a single study plot each breeding season (Robbins 1970). Clusters of locations on composite maps of the study plot created at the end of each season designate breeding territories defended by individual birds (Robbins 1970). Although Verner and Milne (1990) reported substantial variation in survey results among observers, they concluded that for surveys such as ours in which the observers did not change among years, spot mapping is a valid and effective procedure (Verner and Milne 1990). BBC data were obtained from published summaries in Audubon Field Notes, American Birds, and the Journal of Field Ornithology, as well as from the U.S. Geological Survey (USGS) web site (http://www.mp1-wrc.usgs.gov/birds/bbc.html). We checked a subset of the data obtained from the USGS against the original published accounts and found no errors. There is a 4-y gap in the data between 1984 and 1989, and there were no data available after 1995. Most (70%) of the sites we used were in deciduous forest, fewer (22%) were in coniferous forest, and the remainder (8%) were in mixed deciduous coniferous forest. Site descriptions were reviewed, and any site that had undergone any substantial natural or anthropogenic disturbance, such as catastrophic wind-throw or clearcut timber harvest, was eliminated from consideration. All but 2 sites had been surveyed for ≥10 y between the first and last census, and all sites had been visited for ≥3 breeding seasons.

We restricted our analyses to the 10 most frequently encountered, mature forest-dwelling migrant species. Although we assumed that analysis of the 10 selected species would be sufficient for heuristic purposes, there remains the potential that population change patterns for species having patchy distributions or narrow geographic ranges may be fundamentally different from more widely distributed species (Wilcove and Terborg 1984). The bird species included were Eastern Wood-Pewee, Blue-gray Gnatcatcher, Wood Thrush, Yellow-throated Vireo, Blue-headed Vireo, Red-eyed Vireo, Black-and-white Warbler, Ovenbird, Hooded Warbler, and Scarlet Tanager (scientific names in Table 1).

The BBC data were analyzed using the standard non-linear route-regression used in the BBS analyses, where the number of territories on each BBC study plot C in year y is estimated with the model $C = ab^y$, where a is the intercept and b is the slope term, or trend estimate. Values of $b > 1$ indicate that the population is increasing, whereas values of $b < 1$ indicate decline. For each site for each species, this nonlinear model was fit using weighted non-linear least squares (PROC NLIN; SAS Institute 1989), where the weight was based on assuming that the variance in the errors was proportional to the mean. This turns out to be equivalent to the estimating equation approach used in the current BBS analyses (Geissler and Sauer 1990, Link and Sauer 1994). For each site, this analysis also produced an estimated standard error for the trend that was used to create an approximate test that the trend equals 1 (i.e., no trend) and/or to find an approximate confidence interval for the trend.

We did not add a term to the regression to account for the variability among observers in survey ability as is customary in this type of analyses (Geissler and Sauer 1990). Most of the surveys were done by single individuals, or groups of individuals of relatively stable membership, such that the inclusion of a term for observer added little relative to the loss of precision attributable to the inclusion of this term (James et al. 1996). Sites for which data did not conform to the assumptions of linearity [by examining log (C) versus time], or to the non-linear model $C = ab^y$ (as determined by examination of residuals) were eliminated from the analyses.

As in analyses of BBS data, the overall population trend b_p is estimated as a weighted average of trends on individual routes (or in our case, sites). That is:

$$b_p = \Sigma\,(w_i b_i),$$

where weights are proportional to the inverse of the variance of the trend estimate and to the abundance of each species at the median year (Geissler and Sauer 1990). So,

$$w_i = c_i / (\,\Sigma\, c_i),$$

where $c_i = a_i b_i y_0 / v_i$, with $a_i b_i y_0$ being the estimated abundance at y_0 = the midyear of the survey and v_i = variance associated with the estimated trend b_i. Bootstrapping was used to estimate variances of overall trends (Geissler and Sauer 1990), where the resampling involves resampling of sites. Statistical significance was

TABLE 1. Trend estimates (SE) and 95% confidence intervals from route-regression analyses of Breeding Bird Census (BBC) data from 46 sites in North America, as well as trend estimates (SE) from the Breeding Bird Survey (BBS). Trend values >1 indicate the population is increasing, whereas values of <1 indicate the population is declining (see text). Significant trends (α= 0.05) are indicated by an asterisk (*).

	Survey		
Species	BBC (1940-1995)	BBC (1966-1995)	BBS (1966-1995)
Eastern Wood-Pewee	0.99(0.01)*	1.00(0.01)	0.983(0.0003)*
Contopus virens	(0.98-0.99)	(0.98-1.03)	
Blue-gray Gnatcatcher	0.93(0.05)	1.00(0.01)	1.013(0.0001)*
Polioptila caerulea	(0.87-1.01)	(0.98-1.04)	
Wood Thrush	0.77(0.11)*	0.97(0.02)	0.982(0.0001)*
Hylocichla mustelina	(0.73-0.99)	(0.94-1.00)	
Yellow-throated Vireo	0.94(0.02)*	0.99(0.03)	1.007(0.0001)
Vireo flavifrons	(0.92-0.97)	(0.94-1.06)	
Blue-headed Vireo	0.77(0.11)	0.96(0.08)	1.052(0.0001)*
Vireo solitarius	(0.75-1.02)	(0.75-1.05)	
Red-eyed Vireo	0.99(0.01)*	0.98(0.03)	1.012(0.0001)*
Vireo olivaceus	0.97-0.99)	(0.99-1.01)	
Black-and-white Warbler	1.01(0.01)	1.01(0.00)*	1.005(0.0002)
Mniotilta varia	(0.99-1.02)	(1.01-1.02)	
Ovenbird	0.96(0.02)*	0.99(0.02)	1.008(0.0006)*
Seiurus aurocapillus	(0.93-0.99)	(0.96-1.03)	
Hooded Warbler	0.96(0.04)*	0.98(0.01)	1.004(0.0000)
Wilsonia citrina	(0.88-0.99)	(0.93-1.03)	
Scarlet Tanager	0.98(0.02)	1.00(0.01)	1.000(0.0000)
Piranga olivacea	(0.95-1.01)	(0.98-1.02)	

determined by calculating 95% confidence intervals on the population trend and declaring significance if that interval does not include 1 (which represents no trend.) This procedure was used to calculate trends for two time periods, the entire period for which we were able to obtain data (1940-1995) and a shorter period corresponding to that for which BBS data were available (1966-1995).

The results of the BBS analyses were obtained from the USGS website (Sauer et al. 2005). In contrast to BBCs, which are conducted away from roads, the BBS is conducted on ~ 4100 39.5-km stratified-randomly located survey routes along roads. Furthermore, BBCs yield counts of territories on each study plot derived from 10 or so visits repeated each season, whereas observers on BBS routes record numbers of birds detected during a 3-min interval within 386 m of the roadside sampling points on a single annual visit (Droege 1990). Both surveys are conducted annually during the temperate breeding season (typically June and July). We compared our results with BBS data from the combined Eastern and Central regions designated by the BBS despite the fact that more BBC studies were located in the eastern U.S. The results of our comparisons, however, were unchanged if we used only BBS data from the Eastern region.

Trends for all species were compared between surveys (BBC vs BBS) or time periods (1940-1995 vs 1966-1995) using two-sample t-tests. Trends of individual species were compared between surveys or time periods using Z-tests (where Z = the difference between the two trend estimates divided by the square root of the sum of the squared standard errors of the two trends). Statistical tests were considered significant at $\alpha < 0.05$.

RESULTS

We found that six of the 10 most frequently encountered mature forest migrant species

(Eastern Wood-Pewee, Wood Thrush, Yellow-throated Vireo, Red-eyed Vireo, Ovenbird, and Hooded Warbler) exhibited declines from 1940-1995 (Table 1). No species exhibited a significant increase for this period. In contrast, from 1966-1995 no migrants declined significantly in our analyses, and one (Black-and-white Warbler) increased (Table 1). Furthermore, declines of the Red-eyed Vireo were significantly greater (the trend estimate was smaller) from 1940-1966 than from 1966-1995 (Z = 1.92, P = 0.05). Combined analyses indicated that declines of all species together were greater from 1940-1995 than from 1966-1995 ($t_{(9)} = 2.63$, $P < 0.05$). The variance of the trend estimates was greater for the longer (1940-1995) than for the shorter study period (1966-1995; $F_{(9,9)}$ = 6.18, P = 0.01). This suggests that the lack of significant trends evident during the shorter period was not due to lower power because the trend estimate for the shorter period was actually more precise than that for the entire study period.

Bird population declines were more evident in the entire BBC data set (1940-1995) than they were from results of the BBS analyses 1966-1995. Whereas six species exhibited declines in the BBC analyses from 1940-1995 and none increased, only two species (Eastern Wood-Pewee and Wood Thrush) declined significantly in the BBS analyses, and four increased significantly (Blue-gray Gnatcatcher, Blue-headed Vireo, Red-eyed Vireo and Ovenbird; Table 1). Similarly, declines of five species (Wood Thrush, Yellow-throated Vireo, Blue-headed Vireo, Red-eyed Vireo and Ovenbird) were greater (the trend estimate was smaller) in our analyses than in the BBS analyses (Z-tests, P <0.05). Combined analyses indicated that declines of all species together were greater in the BBC data from 1940-1995 than in the BBS analyses for 1966-1995 ($t_{(9)}$ = 2.74, P <0.05).

The results of our analyses of the BBC data for 1966-1995 were more similar to the results of the BBS analyses for 1966-1995 than were the results of the BBC analyses for the entire study period (1940-1995). Trends for only one species differed significantly between the two analyses for the shorter time-period (increases of Black-and-white Warbler was greater in our analyses; Z = 2.07, P <0.04). Overall, declines in our data did not differ significantly from the BBS analyses for the shorter time period ($t_{(9)}$ = 1.98, P >0.05).

DISCUSSION

Evidence of declines in migrant populations at the 46 forest study sites is consistent with reports of forest migrant declines from sites all over eastern North America (Rappole 1995). Neotropical migrant birds comprise as much as 70% of individuals in forest bird communities (Rappole 1995), and potentially dampen outbreaks of defoliating insects (Crawford and Jennings 1989). Thus, reports of catastrophic declines and even local extirpation of these species from many temperate breeding sites have potentially far-reaching ecological implications.

Long-term studies have an essential role in ecology in cases where changes are slow, exhibit large annual variability, or are prone to episodic events (Likens 1983, Strayer et al. 1986). Our observation that population declines were pronounced during the entire 56-y study period, but were not evident in the analyses of the most recent 30 y of BBC data, demonstrate that the length of the study period can critically affect the outcome of trend analyses. This result is consistent with results of other analyses of long-term bird population data. Hill and Hagan (1991) found that restricting their analyses to the most recent 10 years of data from a 53-y data set revealed only 38% of the trends that were apparent over the entire period, and that the inclusion of the next 10 years only increased that proportion to 69%. Similarly, Ballard et al. (2003) reported that capture rates of neotropical migrants were stable for the first decade of their study; however the addition of an addition 10 years of data revealed significant population declines. Extensive anthropogenic changes in the availability of migrant breeding and wintering habitats have occurred over a long time-scale relative to our awareness of conservation issues concerning these species. For example, the forest cover in Cuba had been reduced to 15% of its original extent by the 1950s (Smith 1954), and over half of the forest cover had been cleared by the 1960s in Costa Rica (Sader and Joyce 1988) and the Tuxtlas region of Veracruz (Andrle 1964, Dirzo and Garcia 1992). Similarly, the extent of temperate breeding habitat in eastern North America was reduced by 50% during the period between the arrival of European colonists and the early 19th century (Pimm and Askins 1995). The possibility that the important habitat changes responsible for migrant declines occurred before widespread population monitoring was instituted in the mid 1960s is consistent with reports of the local extirpation of migrant populations during the early 20th century (e.g., Robbins 1979, Serrao 1985, Johnston and Winings 1987).

Migrant populations vary among years in relation to a variety of biotic and abiotic factors, such as food (Holmes et al. 1986, Crawford and Jennings 1989) as well as short-term (Holmes et al. 1986, Blake et al. 1992) and long-term (Sillet 2000) weather patterns. These sources of variability can confound efforts to discern longer-term patterns. For example, Sauer and Droege (1992) reported that overall population trends of neotropical migrants were stable from 1966-1988; however, within this period migrant populations increased from 1966-1978, but declined thereafter (Robbins et al. 1989). A variety of explanations have been offered to account for these trends including recovery from pesticide use (Robbins et al. 1989) or response to spruce budworm (*Choristoneura fumiferana*) outbreaks during the earlier years of the survey. Evidence for short-term responses to these factors, however, does not preclude the possibility that migrant populations might be exhibiting directional population changes over a longer time-scale (Blake et al. 1992), and the results of our analyses suggest that this is, in fact, the case.

We tried to minimize differences between the BBC and BBS analyses by employing the same type of route-regression analyses. Differences in the spatial and temporal scales at which the data were collected, however, limit the degree to which the results can be compared between these two data sources. Nevertheless, several statistically significant increases were apparent in the BBS data that were not indicated by the BBC analyses (Eastern Wood-Pewees, Blue-headed and Red-eyed vireos, and Ovenbirds). BBS routes are located along roads, which are typically subject to higher levels of habitat disturbance than non-roadside areas where the BBC surveys are conducted (Bart et al. 1995; Trombulak and Frissell 2000). Thus increasing trends of mature forest birds on BBS routes may reflect the local response of these species to the maturation of roadside habitats over the sampling period rather than actual regional trends (Askins et al. 1990, Bradstreet and Dunn 1997).

Reliable information on population trends is critical to efforts to prioritize species for conservation and identify agents of population change (Sauer and Droege 1990). Long-term, geographically extensive databases, currently available in the form of the BBC and BBS, are an important contribution in this regard, and we recommend that the ornithological community encourage the continuation of the BBC program. The utility of these data sources, however, is dependent on an understanding of their biases and limitations (Sauer and Droege 1990). Our conclusions that the results of bird-trend analyses are affected by the length of the survey period, and that the absence of declines in more recent studies might be due to the fact that declines occurred before widespread monitoring efforts were instituted, indicate that even the most extensive long-term data sets can be limited by temporal scale and, thus, that an awareness of these limitations is critical to their valid interpretation.

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APPENDIX 1. Survey information for 46 Breeding Bird Censuses included in our analyses.

Site Number[a]	State/Province	Citation[b]	Duration	No. Visits	Latitude	Longitude
CO0000001	CO	AFN 22:673	1968-1984	16	39.2	104.4
CO0000003	CO	JFO 62:56	1980-1995	8	38.57	104.5
CO0000020	CO	AB 36:90	1981-1992	7	39.58	105.2
CT1253099	CT	OEC 49:32	1953-1990	20	41.22	72.07
CT1261011	CT	AFN 15:8	1961-1973	4	41.06	73.43
CT2765006	CT	AFN 19:5	1965-1995	30	41.42	73.12
CT2765008	CT	AFN 19:11	1965-1995	29	41.43	73.12
CT2778262	CT	AB 33:62	1978-1990	13	41.42	73.1
DC0461014	DC	AFN 15:5	1961-1990	21	38.57	77.02
DC1060009	DC	AFN 14:31	1960-1983	24	38.55	77.05
GA0000001	GA	AFN 23:771	1969-1979	22	not available	
GA0000010	GA	AFN 18:555	1963-1973	11	31.58	81.04
IL3141003	IL	AM 43:30	1941-1983	37	40.08	88.08
KS0000001	KS	AB 33:66	1978-1991	7	38.48	95.12
KS0000002	KS	AB 33:66	1978-1991	7	38.48	95.12
MD0447015	MD	AFN 1:22	1947-1989	6	38.53	76.45
MD1047016	MD	AFN 1:23	1947-1990	38	38.58	77.08
MD1071036	MD	AB 25:10	1971-1990	10	39.13	76.55
MI1666034	MI	AFN 20:10	1966-1975	10	42.13	83.44
MN2048026	MN	AFN 9:1	1948-1960	7	45.25	93.12
NC0000001	NC	AB 31:41	1976-1995	15	35.21	79.01
NC0000002	NC	AB 32:63	1977-1995	14	35.53	79
NJ1064032	NJ	AFN 7:340	1964-1995	32	41.04	74.11
NM0000001	NM	AB 32:93	1959-1979	3	35.19	108.12
NY0000001	NY	AB 29:994	1975-1991	4	41.46	74.09
NY1674105	NY	AB 32:3	1974-1987	4	43.25	76.3
NY2471049	NY	AB 26:1	1971-1985	5	42.28	74.56
OH2237200	OH	AM 43:32	1940-1994	51	40.11	82.18
PA1377204	PA	AB 33:70	1982-1993	15	41.04	76.07
PA1377205	PA	AB 33:70	1982-1993	14	41.05	76.08
PA1382312	PA	AB:37:55	1982-1995	10	40.44	75.5
PA1382313	PA	AB 37:55	1982-1995	10	not available	
PA2274131	PA	AB 28:8	1974-1983	7	40.44	79.42
PA2474133	PA	AB 28:10	1974-1984	6	40.07	79.1
PA2474135	PA	AB 28:55	1974-1984	6	40.07	79.1
QU0000001	QU	not available	1964-1972	9	47.16	73.37
TN0000001	TN	AFN 19:593	1965-1974	10	35.55	83.56
UT0000001	UT	AB 38:137	1983-1995	7	38.48	109.35
VA1083031	VA	AB 38:76	1988-1995	8	38.24	78.29
VA1087013	VA	AB 38:76	1983-1995	9	38.24	78.29
VA1379356	VA	JFO 62:57	1979-1992	7	38.33	79.04
VA1391037	VA	AB 36:68	1981-1991	4	38.27	79.15
WV1366086	WV	AFN 20:13	1966-1981	3	37.55	80.17
WV1366087	WV	AFN 20:14	1966-1981	3	37.54	80.15
WV2464044	WV	AFN 18:20	1964-1988	4	38.37	79.5
WV2468079	WV	AFN 22:18	1968-1988	4	38.36	79.51

[a] Designation in USGS database.
[b] Journal, volume and page number of original site description. AB = *American Birds*; AF = *Audubon Field Notes*; AM = *Audubon Magazine*; JFO = *Journal of Field Ornithology*; OEC = *Oecologia*.