



DETECTING POPULATION TRENDS IN MIGRATORY BIRDS OF PREY

CHRISTOPHER J. FARMER,^{1,4} DAVID J. T. HUSSELL,² AND DAVID MIZRAHI³

¹*Hawk Mountain Sanctuary, Acopian Center for Conservation Learning, 410 Summer Valley Road, Orwigsburg, Pennsylvania 17961, USA;*

²*Ontario Ministry of Natural Resources, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada; and*

³*New Jersey Audubon Society, Cape May Bird Observatory Center for Research and Education, Cape May Court House, New Jersey 08210, USA*

ABSTRACT.—Counts of visible migrants at traditional watchsites throughout North America provide an opportunity to augment population-monitoring efforts for birds of prey. We analyzed hourly counts of migrating raptors at one inland (Hawk Mountain Sanctuary, Pennsylvania) and one coastal (Cape May Point, New Jersey) watchsite in northeastern North America. Hourly counts of migrants have been collected for 38 years at Hawk Mountain Sanctuary and for 28 years at Cape May Point. We compared effort-adjusted, arithmetic-mean passage rates to five geometric-mean indexes for 12 species. We used reparameterized polynomial regression to estimate trends in the indexes and to test the significance of trends from 1976–1978 (average index over three-year period) to 2001–2003. Effort-adjusted, arithmetic-mean indexes corresponded to more sophisticated indexes on the complete data sets but did not perform well on simulated data with missing observation days. We recommend the use of a regression-based, date-adjusted index for the analysis of hawk-count data. This index produced trends similar to other geometric-mean indexes, performed well on data sets simulating reduced sampling frequency, and outperformed other indexes on data sets with large blocks of missing observation days. Correspondence between trends at the watchsites and trends from Breeding Bird Surveys (BBSs) suggests that migration counts provide robust estimates of population trends for raptors. Furthermore, migration counts allow the monitoring of species not detected by BBS and produce trends with greater precision for species sampled by both methods. Analysis of migration counts with appropriate methods holds considerable promise for contributing to the development of integrated strategies to monitor raptor populations. *Received 7 March 2006, accepted 19 September 2006.*

Key words: Falconiformes, migration monitoring, population index, population trends, raptors.

DetECCIÓN DE TENDENCIAS POBLACIONALES EN AVES DE PRESA MIGRATORIAS

RESUMEN.—Los conteos realizados en sitios tradicionales de avistamiento en Norte América son un buen recurso para aumentar los esfuerzos de monitoreo de las poblaciones de aves rapaces. Analizamos datos de conteos de aves rapaces migratorias realizados cada hora en una isla (Hawk Mountain Sanctuary, Pensilvania) y en un sitio de observación en la costa (Cape May Point, Nueva Jersey) ubicados en el noreste de Norte América. Estos conteos han sido colectados por 38 años en Hawk Mountain Sanctuary y por 28 años en Cape May Point. Comparamos las medias aritméticas de las tasas de paso, ajustadas por esfuerzo, con cinco índices de medias geométricas para 12 especies. Utilizamos regresiones polinomiales reparametrizadas para estimar las tendencias de los índices y para probar si las tendencias entre 1976 – 1978 (índice

⁴E-mail: farmer@hawkmtn.org

promediado por un periodo de tres años) y 2001 – 2003 son significativas. Los índices de media aritmética ajustados por esfuerzo fueron índices más sofisticados para la base de datos completa, pero éstos no se desempeñaron bien con los datos simulados en que faltan algunos días de observación. Para el análisis de los datos de conteo de halcones recomendamos el uso de un índice basado en un análisis de regresión ajustado por fecha. Este índice produjo tendencias similares a las de otros índices de media geométrica, se desempeñó bien con datos que simularon una frecuencia de muestreo reducida y se desempeñó mejor que otros índices calculados con base en datos con grandes bloques de ausencias de días de observación. La correspondencia entre las tendencias en los sitios de observación y las tendencias registradas con los conteos de aves reproductivas (Breeding Bird Surveys), sugiere que los conteos de aves migratorias representan una estimación robusta de las tendencias poblacionales de las aves rapaces. Además, los conteos de aves migratorias permiten el monitoreo de especies que no son detectadas con los conteos de aves reproductivas y generan tendencias más precisas para las especies que son detectadas por los dos métodos. El análisis de los conteos de aves migratorias mediante métodos adecuados constituye una buena oportunidad para contribuir al desarrollo de estrategias integradas para monitorear las poblaciones de aves rapaces.

LONG-TERM MONITORING OF North American bird populations is crucial for efforts to identify species at risk, suggest potential limiting factors, and provide feedback for management actions (Hussell et al. 1992, Rich et al. 2004, Bart 2005). No single monitoring method provides adequate data for most species, so it is desirable to use various programs, including migration monitoring, to supplement one another (Downes et al. 2000). Monitoring predatory species such as raptors, which serve as biological indicators, can integrate signals from numerous processes and geographic scales within ecosystems (Bildstein 2001). Unlike many passerines, raptors typically occur at low densities, are secretive, and are often difficult to detect on their breeding and wintering grounds. These characteristics reduce the effectiveness of traditional monitoring techniques, such as Breeding Bird Surveys (BBSs) and Christmas Bird Counts (CBCs), for monitoring raptors (Fuller and Mosher 1981, 1987; Kirk and Hyslop 1998; Dunn et al. 2005). Consequently, most North American raptor populations are not well monitored, and prospects for improved breeding-ground monitoring are not promising for many species (Rich et al. 2004).

In a recent assessment, Dunn et al. (2005) concluded that 11 raptor species in northeastern North America are insufficiently monitored, either because the precision of existing trends is unknown or low or because more than one-third of the Canadian and U.S. breeding range

is not covered by a breeding-season survey. To address these deficiencies, they recommended an integrated approach to monitoring, including expanded BBS coverage, additional breeding-season surveys, improved CBC analyses, and migration monitoring. Such integration will prove valuable, for example, if migration monitoring and CBCs are used to provide early detection of population declines and breeding-season surveys are used to trace the declines to specific regions of the breeding range (Dunn et al. 2005).

Most North American raptor species are partial or complete migrants, and migration monitoring can be an effective component of integrated population monitoring, provided there is a robust method of deriving population indexes from counts of migrants. Migrating raptors are relatively easy to sample at geographic features that concentrate them (Titus and Fuller 1990, Dunn and Hussell 1995, Bildstein 1998, Smith and Hoffman 2000, Zalles and Bildstein 2000), and counts of visible migration of raptors have long been used to index populations (Spofford 1969, Nagy 1977, Hussell 1985, Dunne and Sutton 1986, Mueller et al. 1988, Bednarz et al. 1990, Titus and Fuller 1990, Kjellén and Roos 2000, Hoffman and Smith 2003). The validity of using migration counts to monitor bird populations has been questioned (Fuller and Mosher 1981, Kerlinger and Gauthreaux 1985, Smith 1985, Kerlinger 1989), but numerous studies have found sufficient correspondence between

migration counts and other indicators of population change to conclude that they provide reasonable estimates of population trends (Mueller et al. 1988, Bednarz et al. 1990, Hussell and Brown 1992, Dunn and Hussell 1995, Francis and Hussell 1998, Ballard et al. 2003, Hoffman and Smith 2003).

Migration monitoring derives indexes from daily counts at a fixed location based on the assumption that they sample a bird population as it passes the location (Dunn and Hussell 1995). Daily counts within a season have skewed frequency distributions (Hussell 1981), making the median (or geometric mean) a better estimate of central tendency than the arithmetic mean. Several authors have attempted to address the issue of skew by applying log-transformation to annual count totals (e.g., Hoffman and Smith 2003, Lloyd-Evans and Atwood 2004), but this does not remove biases resulting from skewed distribution of daily counts. Correction of this bias can be achieved by log-transforming daily counts before calculation of an annual index (Hussell 1981, 1985). The effects of date and weather on the behavior and numbers of active migrants are also not accounted for in an arithmetic-mean passage rate, but those variables can be included in a regression-based index (Hussell 1981, 1985; Hussell et al. 1992; Dunn et al. 1997; Francis and Hussell 1998).

We used counts of visible migrants from two long-term raptor-migration watchsites in North America—Hawk Mountain Sanctuary, Pennsylvania (40°38'N, 75°59'W), and Cape May Point, New Jersey (39°54'N, 74°49'W)—to develop annual population indexes and trends for 12 species of migratory raptors that are non-irruptive in their migrations. Arithmetic-mean passage rates are common in the scientific and popular literature, and we compared them with geometric-mean passage rates and four indexes derived from analysis of covariance (ANCOVA) at each watchsite. Our objective was to identify the best index for estimating population trends from migration counts. We examined index performance using one complete and three simulated data sets comprising subsets of the complete counts from each watchsite. Given the functional difference between leading lines and diversion lines (Geyer von Schweppenburg 1963), we expected that the two watchsites would differ in the way wind patterns affected migration counts and in the composition of

the count population (*sensu* Dunn and Hussell 1995). An effective migration index should allow accurate estimation of trends at both types of watchsite.

METHODS

Hawk counts.—We used hourly counts of visible migrating raptors during autumn migration (August–December) at Hawk Mountain Sanctuary and Cape May Point to develop population indexes. Migration counts have been conducted from the North Lookout at Hawk Mountain Sanctuary since 1934, and data have been recorded in hourly format since 1966. Hourly counts have been conducted from Cape May Point State Park since 1976. At Hawk Mountain Sanctuary, counts were conducted by trained volunteers and staff, with primary responsibility given to one or two people each day and with considerable interannual overlap in personnel. At Cape May Point, counts were conducted primarily by one or two trained staff but not the same personnel throughout the study period.

Observations at the two watchsites were typically recorded from 0600 to 1700 hours EST. At both sites, observations sometimes extended beyond these times or terminated earlier. At Hawk Mountain Sanctuary, the mean number of hours of observation ($\bar{x} \pm SD$) each day from 1966 to 2003 ranged from 7.3 ± 2.5 in 1967 ($n = 76$ days) to 8.7 ± 2.6 in 2001 ($n = 139$ days), with an overall average daily coverage of 8.0 ± 2.7 ($n = 105$ days). At Cape May Point, the mean number of hours of observation ranged from 7.3 ± 1.8 in 1977 ($n = 70$ days) to 10.8 ± 2.5 in 1985 ($n = 85$ days), with an overall average daily coverage of 8.9 ± 2.20 ($n = 86$ days). Annual counts of raptors averaged ~20,000 at Hawk Mountain Sanctuary and ~51,000 at Cape May Point.

Total hours of observation varied from day to day and among years, so we standardized the count day at each watchsite. For each species, we identified a daily passage window during which the middle 95% of individuals were counted. No important differences were found among species' daily windows, so we combined them into a standard period for each site: 0700 to 1600 hours at Hawk Mountain Sanctuary and 0600 to 1500 hours at Cape May Point. We excluded raptors counted outside of the daily standard period from analysis. For days

with incomplete coverage during the standard period, we estimated the daily count as $N = C \times H/h$, where C was the count during the standard hours, h was the number of hours of observation, and H was the number of hours in the standard period.

We chose a seasonal passage window for each species that included days when the middle 95% of the individuals of that species were counted across all years. Increases in number of count days across years can increase the frequency of low counts, producing spurious trends in passage rates (Titus et al. 1989). Using a 95% seasonal passage window reduces the effect of changes in coverage.

Weather.—Wind speed and direction are believed to be the weather variables that most directly affect the concentration of raptors near migration watchsites (Mueller and Berger 1961, Haugh 1972, Richardson 1978, Newton 1979, Kerlinger 1989). We obtained hourly surface data from the National Weather Service (see Acknowledgments) for the station nearest each watchsite. At Hawk Mountain Sanctuary, the nearest station (Lehigh Valley International Airport, 40°39'N, 72°27'W) is ~47 km east-southeast of the watchsite. At Cape May Point, the nearest station (Atlantic City International Airport, 39°27'N, 74°34'W) is ~67 km north-northeast of the watchsite. We derived wind variables, E (east), SE (southeast), S (south), and SW (southwest), from vector addition of wind speeds and directions at 0700, 1000, and 1300 hours. We calculated vectors so that positive and negative values of E represented east and west winds, respectively, positive and negative values of SE represented southeast and north-west winds, etc. We also used second-order wind variables, which enabled us to model curvilinear effects of wind speed and direction (Francis and Hussell 1998).

Migration count index.—We compared arithmetic-mean indexes (Bednarz et al. 1990, Titus and Fuller 1990, Hoffman and Smith 2003) to those allowing compensation for missing days and additional covariates (e.g., weather). The latter have been described previously (Hussell 1981, 1997; Hussell et al. 1992; Dunn et al. 1997; Francis and Hussell 1998). We also examined two models that included date * year interactions, allowing for the possibility that seasonal patterns of migration may differ among years. In our description of the six

methods (brief descriptions below, details in Appendix 1), “count” always means the daily number of hawks counted or estimated within the daily and seasonal windows. Adding wind variables in some analyses led to smaller sample sizes, because we excluded days for which wind data were missing. In addition, the four methods with date covariates included a regression to eliminate days at the start and end of the seasons that would result in poor distribution of residuals. To keep indexes comparable, we limited the sample size (days) for calculating each index to the smallest set available for any method.

For each watchsite, the annual arithmetic-mean passage rate index (AM) was the mean count of migrants in a standard count day in year j , weighted by daily hours of effort. The remaining five indexes were geometric-mean passage rate (GM), date-adjusted estimated geometric-mean ($GM[\text{date}]$), date-adjusted estimated geometric-mean with wind covariates ($GM[\text{date}, \text{wind}]$), date-adjusted estimated geometric-mean with date * year interactions ($GM[\text{date}, \text{date} * \text{year}]$), and date-adjusted estimated geometric-mean with date * year interactions and wind covariates ($GM[\text{date}, \text{wind}, \text{date} * \text{year}]$). These indexes were all estimates of the annual mean daily counts, derived from regression estimates of the “geometric mean” daily count, adjusted for covariates. The full regression model with all covariates was:

$$\ln(N_{ij} + 1) = a_0 + \sum_{j=1}^J a_j Y_j + \sum_{k=1}^4 b_k i^k + \sum_{j=0}^J \sum_{k=1}^4 c_{jk} (Y_j i^k) + \sum_{l=1}^L d_l W_{lij} + e_{ij} \quad (1)$$

where N_{ij} was the number of one species counted (or estimated) during the standard hours on day i in year j ; Y_j was a series of dummy variables that were set equal to one when year = j and were zero in all other years; i^k values were first-through fourth-order terms in date; values of $(Y_j i^k)$ were date * year interaction terms created by multiplying each Y_j by each i^k ; W_{lij} was the value of weather variable l on day i in year j ; a_0 was the intercept estimated by the regression; a_j , b_k , c_{jk} , and d_l were coefficients estimated by the regression representing the effects of each independent variable on $\ln(N_{ij} + 1)$; and e_{ij} represented unexplained variation. This regression

model was a one-way ANCOVA with year terms as factors and all other independent variables as covariates. Regression analyses were weighted in proportion to the number of hours of observation on each day, h_{ij} . The method of deriving geometric-mean indexes was similar to methods used previously (Hussell 1981, 1985; Hussell et al. 1992; Dunn et al. 1997; Francis and Hussell 1998), except that each index was expressed as the estimated mean count per day.

Significance tests for effects of independent variables in the regression require each day's count to be an independent sample of the monitored population (*sensu* Dunn and Hussell 1995). This assumption is violated if migrants stop at a watchsite for more than one day or if individual migrants are counted multiple times on the same day. Count protocols are designed to minimize these violations, but the assumption is probably violated to varying degrees, depending on the characteristics of the site and species involved. For example, multiple counting is likely to be more frequent at bottlenecks, such as Cape May Point, than at leading lines, such as Hawk Mountain Sanctuary. Moreover, at Cape May Point, there are likely to be fewer multiple counts of *Falco* spp. and Northern Harriers, which readily cross water barriers, than of *Buteo* spp. and *Accipiter* spp., which do not. However, provided that the rate of multiple counting does not change over time, the assumption of independence of daily counts is not critical to the goal of our index regression, which is to create a reliable annual index of abundance. Therefore, our assumption is not that daily counts are completely independent samples, but that, for each species at each site, the rate of multiple counting does not change consistently over time.

Trend analysis.—Trends in annual indexes were estimated as the geometric-mean rate of change over a specified time interval for each site (Link and Sauer 1997). Preliminary examination of index * year plots suggested that most species did not follow log-linear trajectories. We analyzed trajectories by fitting a polynomial regression to the time series of $\log(\text{index})_i$ values. To reduce correlations among the polynomial terms, each regression was centered at the midpoint year in the series.

A best-fitting polynomial model was identified for each species using a three-step process. To avoid overfit, the number of possible models

was limited to the set for which the number of regression coefficients was $\leq n/5$, where n was the number of years in the regression (Tabachnick and Fidell 1989). Positive and negative autocorrelation indicate poor fit and overfit, respectively, so we identified a subset of candidate models for which autocorrelation of residuals was minimized ($-0.20 \leq a \leq 0.20$). A best-fit model was then chosen from this subset by selecting the single model that minimized Akaike's Information Criterion corrected for sample size (AIC_c; Burnham and Anderson 2002), retaining all lower-order terms in the model.

Trend estimates and their significance were derived by reparameterizing the year terms (Francis and Hussell 1998). This method takes into account the trend within the set of years being compared and uses the variance around the entire trajectory. It provides greater statistical power for the detection of trends than linear regressions, which often do not fit the trajectory of the index. We chose the proportional rate of change from 1976 to 2003 to compare index models and the trend estimates they produced. The reparameterization transformed year terms so that the first-order term estimated the rate of change between the two sets of years and was, therefore, equivalent to the slope of a log-linear regression. To reduce the potential effect of extreme trajectories at the ends of the polynomial model, we compared mean indexes for the three-year periods 1976–1978 and 2001–2003. These estimates of the mean were influenced by the observed index in all years, thereby accounting for any trend within the averaged years (Francis and Hussell 1998). Similarly, tests of trend significance were based on the mean squared deviation from the regression curve of all index values, not just those in the averaged years.

Index performance.—We evaluated indexes by measuring the correspondence among migration indexes at the two watchsites and between migration indexes and an independent population survey (BBS). Indexes were compared using the root-mean-squared error of the best-fit trajectory regression of $\log(\text{index})_i$ on year for each method. The root-mean-squared error served as an estimate of the interannual variability that was not assigned to the trajectory described by the regression equation. Annual indexes of biological populations are expected to be autocorrelated, so we view minimal

dispersion of indexes around a fitted trajectory as an indication of minimal error in the indexes. Moreover, higher dispersion of the indexes reduces the power to detect trends.

Both data sets had fewer missing days of observation than those from many active migration watchsites. Therefore, we examined root-mean-squared error values of trend regressions for each index on several reduced data sets to simulate the use of data from watchsites with lower sampling frequencies. The reduced data sets used in the analysis simulated (1) five-day-per-week, (2) two-day-per-week, and (3) intermittent sampling (50% of the years were missing ≤ 55 contiguous days). Missing blocks in simulation (3) were distributed among years so that approximately one-third were early-, one-third were mid-, and one-third were late-season. We used two-way analysis of variance (ANOVA) and multiple contrasts (Tukey's test, $\alpha = 0.05$) to test for significant differences in root-mean-squared error.

Trend estimates for the six indexes were compared with one another and with estimates from BBS using Pearson's correlation coefficients and reduced major-axis regression, which is more appropriate than ordinary least-squares regression when both the independent and dependent variables are measured with error (Sokal and Rohlf 1981). Despite its limitations for monitoring many migratory raptors (see below), the BBS provides the only available large-scale, long-term estimates of population trends for our study species that are completely independent of our migration-monitoring methodology. Detection rates are low for most raptors in BBS, and the corresponding trend estimates consequently have low precision (Fig. 1). Moreover, BBS does not survey all areas where migrants passing the two watchsites may breed. Therefore, only approximate correspondence should be expected between migration monitoring and BBS. We evaluated this correspondence for a region containing the most likely breeding areas of migrants detected at the watchsites on the basis of telemetry and banding studies (Clark 1985, Struve 1992, Brodeur et al. 1996, Fuller et al. 1998, Martell et al. 2001, Laing et al. 2005, Dunn et al. 2007, N. Bolgiano pers. comm.). This "northeastern region" consisted of Connecticut, Massachusetts, Maine, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, and Vermont in the United States, and of New Brunswick, Nova

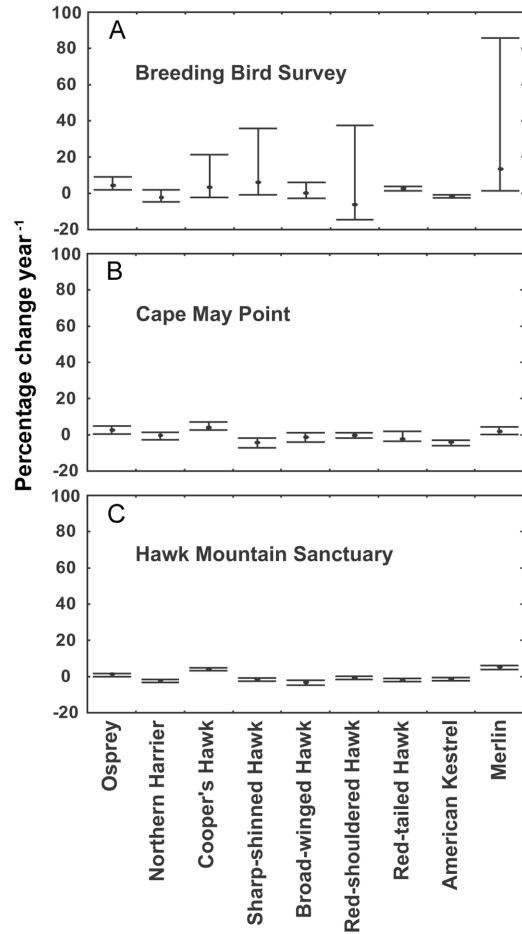


FIG. 1. Population trend estimates and 95% confidence intervals for raptors monitored by (A) Breeding Bird Surveys and at migration watchsites at (B) Cape May Point, New Jersey, and (C) Hawk Mountain Sanctuary, Pennsylvania. Breeding Bird Survey trends are for a northeastern region comprising Connecticut, Massachusetts, Maine, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, and Vermont in the United States and New Brunswick, Nova Scotia, Ontario, and Quebec (east of 79°W) in Canada. Migration-monitoring trends are for date-adjusted geometric-mean indexes.

Scotia, Ontario, and Quebec (east of 79°W) in Canada. Although BBS provides trend estimates for 11 raptor species in this region, we compared only the nine nonirruptive migrants for which BBS trends were estimated from ≥ 20 routes (Francis and Hussell 1998).

It is unlikely that BBS trends for most raptor species would be identical to migration trends, but some correspondence between the two data sets is expected if BBS and migration monitoring both measure changes in bird populations. Therefore, the degree of correspondence between migration indexes and the BBS offers one means of evaluating different index methods. For any two estimation methods to produce corresponding trends, (1) slope of the reduced major-axis regression should equal one, (2) intercept of the reduced major-axis regression should equal zero, and (3) there should be a high positive correlation between the trends. Satisfaction of criteria (1) and (2) indicates a 1:1 correspondence between the sets of trend estimates.

RESULTS

Migration count index.—Annual indexes derived from the six estimation methods were highly correlated for each species at each watchsite, with correlation coefficients averaging 0.91 (SD = 0.07, $n = 12$ species) at Hawk Mountain Sanctuary and 0.94 (SD = 0.04, $n = 12$ species) at Cape May Point (Appendix 2). The lowest correlations were between *AM* and the *GM*(date, wind) and *GM*(date, wind, date * year) indexes. All within-site correlations among indexes were highly significant ($P \leq 0.01$). For the five regression-based indexes, the addition of wind variables and interaction terms generally increased the variation incorporated by the regression (Appendix 2).

Trend analysis.—For most species at both sites, the indexes differed in their estimate of the magnitude of population trend, but not its significance or direction (Table 1). Migration counts for 5 of 12 species increased or remained stable at both watchsites. Decreasing trends were found for 6 of 12 species at both watchsites. Trends at the two watchsites were in opposite directions for Golden Eagles (scientific names in Table 1). Trends at the two watchsites were significantly correlated ($r = 0.85\text{--}0.94$, $P \leq 0.01$) and showed 1:1 correspondence (reduced major-axis regression, $b = 1.08\text{--}1.14$, $P > 0.05$) for all indexes.

Index performance.—For both watchsites, average root-mean-squared error of the trend regression for the complete data set was lower for all geometric-mean indexes than for *AM* (Table 2), indicating that the latter provided

a poorer fit to trend regressions. The *GM* and *GM*(date) indexes had the lowest root-mean-squared error, which suggests that fit of the trend regression was not improved by the addition of wind variables or date * year interactions. Two-way ANOVA on root-mean-squared errors indicated significant main effects of watchsite ($F = 117.08$, $df = 1$ and 132 , $P \leq 0.001$) and index method ($F = 3.30$, $df = 5$ and 132 , $P = 0.008$) on the fit of the trend regressions, but no site * method interaction ($F = 0.17$, $df = 5$ and 132 , $P = 0.97$). Tukey's HSD test ($\alpha = 0.05$) indicated that all geometric-mean indexes had significantly lower root-mean-squared error than *AM*.

In five-day-per-week simulations, average root-mean-squared error was lowest for *GM* and *GM*(date) indexes (Table 3). Two-way ANOVA indicated significant main effects of watchsite ($F = 134.12$, $df = 1$ and 132 , $P \leq 0.001$) and index method ($F = 4.40$, $df = 5$ and 132 , $P = 0.001$), but no site * method interaction ($F = 0.56$, $df = 5$ and 132 , $P = 0.73$). Tukey's HSD test for multiple comparisons ($\alpha = 0.05$) indicated that *GM* and *GM*(date) indexes had significantly lower root-mean-squared error than *AM*, and that *GM* was significantly lower than *GM*(date, wind, date * year).

In two-day-per-week simulations, average root-mean-squared error was lowest for *GM* and *GM*(date, wind) indexes (Table 3). Two-way ANOVA indicated significant main effects of watchsite ($F = 51.90$, $df = 1$ and 132 , $P \leq 0.001$) and index method ($F = 4.56$, $df = 5$ and 132 , $P \leq 0.001$), but no site * method interaction ($F = 0.49$, $df = 5$ and 132 , $P = 0.78$). Tukey's HSD test ($\alpha = 0.05$) indicated that *GM* and *GM*(date, wind) indexes had significantly lower root-mean-squared error than *GM*(date, date * year) and that *GM*(date, wind) was significantly lower than *AM*.

In simulations of intermittent sampling (missing blocks of days), average root-mean-squared error was lowest for *GM*(date) and *GM*(date, wind) indexes (Table 3). Two-way ANOVA indicated significant main effects of watchsite ($F = 55.10$, $df = 1$ and 132 , $P \leq 0.001$) and index method ($F = 4.28$, $df = 5$ and 132 , $P = 0.001$), but no site * method interaction ($F = 0.09$, $df = 5$ and 132 , $P = 0.99$). Tukey's HSD test ($\alpha = 0.05$) indicated that *GM*, *GM*(date), and *GM*(date, wind) indexes had significantly lower root-mean-squared error than *AM*.

Hawk Mountain Sanctuary trend estimates averaged 1.4–2.5% per year lower, and Cape

TABLE 1. Trends in six indexes of migration counts (1976–1978 to 2001–2003) at Hawk Mountain Sanctuary (HMS), Pennsylvania, and Cape May Point (CMP), New Jersey, and in Breeding Bird Surveys (BBS; 1976 to 2003) for northeastern North America. Trends for BBS are derived from estimating equations for route regression for regions with ≥ 20 routes reporting the species. Significance of trend is shown by: + $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.01$.

Species	Site	AM ^a	GM ^b	DA ^c	DAW ^d	DY ^e	DYW ^f	BBS ^g
Osprey (<i>Pandion haliaetus</i>)	HMS	0.4	1.2**	1.6**	2.1**	1.4**	1.6**	4.6**
	CMP	2.5*	2.7*	2.8*	2.6*	3.0*	2.6*	
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	HMS	7.1**	5.1**	5.2**	6.4**	5.2**	6.4**	5.9
	CMP	11.5**	7.6**	8.5**	8.3**	8.8**	8.8**	
Northern Harrier (<i>Circus cyaneus</i>)	HMS	-2.5**	-2.2**	-2.1**	-2.0**	-2.0**	-2.0**	-2.1
	CMP	0.0	-0.2	-0.2	-0.2	-0.1	-0.2	
Cooper's Hawk (<i>Accipiter cooperii</i>)	HMS	3.8**	3.7*	4.2**	4.9**	4.5**	5.2**	3.6
	CMP	4.2**	4.2**	4.2**	3.5**	4.6**	3.8**	
Sharp-shinned Hawk (<i>A. striatus</i>)	HMS	-2.8**	-1.3**	-1.4**	-1.2*	-2.1**	-1.5**	6.2
	CMP	-3.6**	-4.1**	-4.1**	-4.4**	-4.5**	-5.2**	
Broad-winged Hawk (<i>Buteo platypterus</i>)	HMS	-3.2**	-4.0**	-3.0**	-3.1**	-3.2**	-3.3**	0.4
	CMP	-2.2	-1.1	-1.1	-1.6	-0.6	-1.7	
Red-shouldered Hawk (<i>B. lineatus</i>)	HMS	-0.3	-0.5	-0.6	-0.3	-0.5	-0.3	-6.0
	CMP	-1.1	-0.1	-0.2	-0.9	-0.1	-1.6	
Red-tailed Hawk (<i>B. jamaicensis</i>)	HMS	-1.7**	-1.8**	-1.8**	-0.5	-1.8**	-0.6	2.8**
	CMP	-0.2	-1.9	-2.2 +	-2.8*	-1.9	-2.5	
Golden Eagle (<i>Aquila chrysaetos</i>)	HMS	2.8**	2.0**	2.2**	3.7**	2.4**	3.9**	na ^h
	CMP	-1.5	-1.1	-1.2	-0.5	-1.5	-0.9	
American Kestrel (<i>Falco sparverius</i>)	HMS	-1.7**	-1.3**	-1.1*	0.5	-1.2*	0.0	-1.4**
	CMP	-3.2**	-4.0**	-3.9**	-3.5**	-4.0**	-3.5**	
Merlin (<i>F. columbarius</i>)	HMS	5.6**	4.1**	5.6**	6.4**	5.9**	6.8**	13.6*
	CMP	2.3*	2.0 +	2.0 +	2.7*	2.0 +	2.2*	
Peregrine Falcon (<i>F. peregrinus</i>)	HMS	4.9**	3.5**	5.1**	5.4**	5.7**	5.9**	na
	CMP	7.7**	5.6**	6.0**	6.0**	7.0**	7.0**	

^aAM = effort-weighted mean passage rate.

^bGM = effort-weighted geometric-mean passage rate.

^cDA = estimated birds day⁻¹ index, date and year terms (GM[date]).

^dDAW = estimated birds day⁻¹ index, date and year terms, wind terms (GM[date, wind]).

^eDY = estimated birds day⁻¹ index, date and year terms, date * year interactions (GM[date, date * year]).

^fDYW = estimated birds day⁻¹ index, date and year terms, date * year interactions, wind terms (GM[date, wind, date * year]).

^gBBS northeastern region = Connecticut, Massachusetts, Maine, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont, New Brunswick, Nova Scotia, Ontario, and Quebec (east of 79°W).

^hna = BBS trend not available.

May Point estimates averaged 1.7–2.5% per year lower than BBS trends (Table 3). Correlations between Hawk Mountain Sanctuary and BBS trends were positive for all indexes (range: 0.59–0.66) but were significant ($\alpha = 0.05$) only for date-adjusted indexes. Correlations between Cape May Point and BBS trends were lower than those for Hawk Mountain Sanctuary (range: 0.32–0.39) and were not significant (Table 3). Reduced major-axis regression of BBS trends on migration trends indicated an approximate 1:1 correspondence (Table 3). Precision of migration-monitoring

trend estimates was greater than that of BBS for most species (Fig. 1).

DISCUSSION

Index performance.—The high correlations among indexes suggest that trends in migration counts are robust and can be detected with even relatively crude (i.e., AM) analytical methods. Even so, the analysis of root-mean-squared error of trend regressions shows that geometric-mean indexes perform better than arithmetic-mean indexes. Our analysis further shows that the

TABLE 2. Average root-mean-squared error (means \pm SD) among trend regressions for six migration indexes calculated from counts of visible, nonirruptive migrants at Hawk Mountain Sanctuary (HMS), Pennsylvania, and Cape May Point (CMP), New Jersey. Results are shown for (1) the full data set, and for three reduced data sets that simulate sampling (2) five days per week, (3) two days per week, and (4) intermittently, in which blocks of 55 contiguous days were removed from early-, mid-, or late-season observations in 50% of the years.

		AM ^a	GM ^b	DA ^c	DAW ^d	DY ^e	DYW ^f
(1)	HMS	2.12 \pm 0.44	1.70 \pm 0.33	1.71 \pm 0.31	1.74 \pm 0.36	1.88 \pm 0.39	1.96 \pm 0.41
	CMP	3.23 \pm 0.87	2.64 \pm 0.60	2.65 \pm 0.60	2.72 \pm 0.58	2.73 \pm 0.62	3.01 \pm 0.69
(2)	HMS	1.81 \pm 0.40	1.46 \pm 0.27	1.46 \pm 0.26	1.54 \pm 0.30	1.60 \pm 0.26	1.78 \pm 0.42
	CMP	3.00 \pm 0.90	2.32 \pm 0.43	2.36 \pm 0.39	2.41 \pm 0.38	2.78 \pm 0.91	2.92 \pm 0.79
(3)	HMS	1.71 \pm 0.37	1.39 \pm 0.24	1.38 \pm 0.32	1.38 \pm 0.38	1.74 \pm 0.43	1.75 \pm 0.70
	CMP	2.30 \pm 0.43	1.90 \pm 0.31	2.08 \pm 0.60	1.83 \pm 0.36	2.43 \pm 0.62	2.13 \pm 0.51
(4)	HMS	2.39 \pm 0.70	1.90 \pm 0.36	1.69 \pm 0.28	1.73 \pm 0.32	1.91 \pm 0.38	1.93 \pm 0.37
	CMP	3.18 \pm 0.93	2.59 \pm 0.79	2.43 \pm 0.65	2.44 \pm 0.57	2.73 \pm 0.85	2.83 \pm 0.82

^aAM = effort-weighted mean passage rate.

^bGM = effort-weighted geometric-mean passage rate.

^cDA = estimated birds day⁻¹ index, date and year terms (GM[date]).

^dDAW = estimated birds day⁻¹ index, date and year terms, wind terms (GM[date, wind]).

^eDY = estimated birds day⁻¹ index, date and year terms, date * year interactions (GM[date, date * year]).

^fDYW = estimated birds day⁻¹ index, date and year terms, date * year interactions, wind terms (GM[date, wind, date * year]).

TABLE 3. Pearson's correlation coefficients ($n = 9$ species) between trends for Breeding Bird Surveys (BBS) and those for six migration indexes at Hawk Mountain Sanctuary (HMS), Pennsylvania, and Cape May Point (CMP), New Jersey, mean differences between trends, and intercepts (95% confidence intervals [CI] in parentheses) and slopes (b ; 95% CI in parentheses) of reduced major-axis regression between migration indexes and BBS^g (Sokal and Rohlf 1981). Significance of correlation is indicated by: + $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.01$.

Index	r	Difference	Intercept	b^h
HMS				
AM ^a	0.59+	-2.27	-1.39 (-4.45 to 0.69)	0.68 (-0.28 to 1.38)
GM ^b	0.61+	-2.47	-1.27 (-3.60 to 0.40)	0.56 (0.33 to 1.15)
DA ^c	0.66*	-2.08	-0.97 (-3.36 to 0.66)	0.59 (0.38 to 1.15)
DAW ^d	0.65*	-1.43	-0.44 (-3.08 to 1.42)	0.64 (0.40 to 1.26)
DY ^e	0.63*	-2.14	-1.10 (-3.68 to 0.72)	0.62 (0.37 to 1.17)
DYW ^f	0.65*	-1.51	-0.60 (-3.33 to 1.32)	0.67 (-4.99 to 1.02)
CMP				
AM ^c	0.39	-1.73	-1.23 (-4.79 to 1.55)	0.82 (-0.46 to 1.86)
GM ^d	0.34	-2.23	-1.33 (-4.67 to 1.50)	0.67 (-0.68 to 1.48)
DA ^e	0.34	-2.16	-1.38 (-4.94 to 1.53)	0.72 (-0.72 to 1.53)
DAW ^f	0.39	-2.37	-1.60 (-5.05 to 0.99)	0.72 (-0.65 to 1.55)
DY ^g	0.32	-2.04	-1.33 (-4.99 to 1.75)	0.74 (-0.80 to 1.62)
DYW ^h	0.37	-2.47	-1.81 (-5.66 to 1.00)	0.76 (-0.73 to 1.67)

^aAM = effort-weighted mean passage rate.

^bGM = effort-weighted geometric-mean passage rate.

^cDA = estimated birds day⁻¹ index, date and year terms (GM[date]).

^dDAW = estimated birds day⁻¹ index, date and year terms, wind terms (GM[date, wind]).

^eDY = estimated birds day⁻¹ index, date and year terms, date * year interactions (GM[date, date * year]).

^fDYW = estimated birds day⁻¹ index, date and year terms, date * year interactions, wind terms (GM[date, wind, date * year]).

^gBBS northeastern region = Connecticut, Massachusetts, Maine, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, Vermont, New Brunswick, Nova Scotia, Ontario, and Quebec (east of 79°W).

^h b = slope of major axis (model II regression; Sokal and Rohlf 1981).

ANCOVA method with date adjustment is superior to a simple geometric-mean passage rate for data sets missing substantial days of observations. This is an important finding, because many migration watchsites rely on volunteer labor, and days of active migration are sometimes missed when observers are not available. Additionally, some days are missed because of inclement weather, and it is not known whether migratory flights cease on those days. The date-adjusted index assigns expected numbers of hawks to these missing days on the basis of the seasonal pattern, which can reduce interannual variation stemming from missed days. We recommend that precision of trend estimates should be evaluated for migration watchsites sampling <5 days per week before they are used as a monitoring tool.

Birds of prey are difficult to monitor with BBS methods (Kirk and Hyslop 1998), resulting in high CVs (28–468% for northeastern region) for BBS raptor indexes. With the exception of the American Kestrel and Red-tailed Hawk species monitored at migration watchsites are difficult to detect during the breeding season and unlikely to nest in proximity to roads, giving them a low probability of detection on a road-based survey. Furthermore, BBS monitors primarily breeding and nonbreeding adults, whereas autumn migration counts additionally monitor young of the year. This could weaken correlations between BBS and migration watchsites that count primarily young of the year (e.g., Cape May Point; Clark 1985). Still, BBS is the best independent source of trend estimates for most raptors, and the correspondence of migration-monitoring trends with BBS trends indicates that both measure real changes in monitored populations. The weight of evidence concerning correspondence with BBS trends suggests that the date-adjusted index (GM[date]) is the most suitable for migration monitoring. The lack of perfect correspondence between migration monitoring and BBS trends suggests that both programs can make important and complementary contributions to long-term monitoring of raptor populations in North America (see Dunn et al. 2005). The greater precision of migration monitoring trends for many species (Fig. 1) further suggests that their use will improve monitoring efforts.

Importance of weather adjustment.—Weather, particularly wind speed and direction, is often

cited as a factor that may potentially confound migration counts as a means of estimating population trends (Mueller and Berger 1961, Broun 1963, Alerstam 1978, Titus and Mosher 1982, Kerlinger 1989). We found that adjusting for the effects of wind increases the amount of variation that is explained by the index regression (Appendix 2) but does not generally improve the fit of trend regressions over that achieved with date adjustment (Table 3). Accounting for date appears to be more important than adjusting for the effects of wind in the derivation of annual indexes for raptors, a finding in agreement with previous research in the Appalachians (Titus and Mosher 1982). We suggest that weather variables such as wind direction and speed affect daily raptor passage within a year but not interannual variation in counts (see Allen et al. 1996). This conclusion is based on the assumption that no trend occurs in weather patterns over the study period, however, and should be treated with caution if such a trend is detected. Weather variables are generally correlated, and the failure of wind variables to explain interannual variation in hawk counts leads us to believe that additional weather covariates are unlikely to prove important for the accurate estimation of trends. Even so, we recommend that they be examined during future index development (see Hussell and Brown 1992).

Our analysis of simulated two-day-per-week sampling suggests that adjustment for weather can become important when there are very few observation days in a season. However, this level of sampling falls far below the minimum coverage of 75% of a species' seasonal migration window recommended by Hussell and Ralph (2005) for effective migration monitoring. It also greatly reduces statistical power to detect trends (Thomas et al. 2004). We therefore do not believe that a two-day-per-week sampling frequency is adequate for population monitoring using migration counts.

Migration counts as indicators of population trends.—Titus and Fuller (1990) noted that migration counts were an efficient means of monitoring some raptor populations, and Bednarz et al. (1990) established that migration count trends agree qualitatively with independent predictions for species undergoing strong, sustained population changes. Several authors have demonstrated correspondence of migration trends with independent trend

estimates for passerines (Hussell et al. 1992, Dunn and Hussell 1995, Dunn et al. 1997, Francis and Hussell 1998) and raptors (Hussell and Brown 1992).

Hawk Mountain Sanctuary is an inland site that concentrates migrants taking advantage of favorable conditions (leading line, *sensu* Geyer von Schweppenburg 1963), whereas Cape May Point concentrates migrants avoiding conditions on one side of a diversion line (Atlantic coast), often after having drifted there on prevailing winds. For some species, juveniles are more prone to wind drift (Thorup et al. 2003) and constitute a larger proportion of the count at coastal watchsites like Cape May Point (Clark 1985) than adults. We believe the greater variability of indexes and larger confidence intervals of trends at Cape May Point compared with Hawk Mountain Sanctuary (Fig. 1) reflect fluctuations in annual productivity for some species as well as the possibility of greater variation in the rate of multiple counting at Cape May. These two factors are likely the causes of lower correlations with BBS at Cape May Point. Our analysis of trend root-mean-squared error suggests that indexes from coastal diversion-line watchsites are more variable, but the high intersite correlations, 1:1 correspondence between trends, and lack of site * index interactions at these watchsites show that migration indexes are robust to variations in migration geography and suitable for estimation of population trends. Correspondence with BBS trends for the breeding areas of our source populations further supports this interpretation.

The potential for relatively high rates of multiple counting is sometimes raised as a fatal flaw in migration monitoring. However, unless there is a trend across years in the rate of multiple counting, it will not adversely affect estimates of trend. The lack of site * index interactions in our analysis suggests that a trend in the rate of multiple counting is not present at these watchsites. Future studies of the level and year-to-year variability of multiple counting at a variety of watchsites would be helpful in addressing this potential concern.

The Partners in Flight North American Landbird Conservation Plan recommends "improvement of migration monitoring to meet information needs of many raptors" (Rich et al. 2004:29). A recent Partners in Flight update of

monitoring needs indicates that only 6 of 19 species of diurnal raptors that breed in Canada and Alaska are adequately monitored at a range-wide scale and recommends migration monitoring to improve knowledge of population trends of 18 of these species (Dunn et al. 2005). The analysis method we recommend makes it possible to use counts of visible migrants to help fill this gap. The benefits of large-scale citizen science as a source of monitoring data are clear in programs such as BBS and CBC. More than 50 active raptor watchsites in North America have collected migration count data for at least 10 years (Zalles and Bildstein 2000), often using volunteer citizen scientists to collect the data (Bildstein 1998). With recent efforts at networking (MacLeod 2004) and the development of powerful methods of trend estimation (Hussell 1981, 1985; Hussell and Brown 1992; Francis and Hussell 1998), the ingredients are now available to incorporate migration monitoring into an integrated system for monitoring raptor populations.

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APPENDIX 1

MIGRATION COUNT INDEX REGRESSION

Annual arithmetic-mean passage rate in year j , $(AM)_j$, was calculated by summing counts for each species across its seasonal passage window in year j , dividing these sums by the total number of count hours, and multiplying by the number of hours in the standard count day (H). The result was an arithmetic-mean daily passage rate for each species corrected for hours of effort at each site (i.e., for one site):

$$(AM)_j = \left(\frac{\sum_{i=1}^I C_{ij}}{\sum_{i=1}^I h_{ij}} \right) \times H \quad (1)$$

where C_{ij} and h_{ij} are the count and the number of hours of observation on day i in year j , respectively, and i varies from 1 to I (the number of days in the species' seasonal migration window).

The geometric-mean passage rate in year j , $(GM)_j$, was determined from the weighted regression (equation 1 in text), including only the year terms, Y_j (which is equivalent to a

one-way ANOVA with year as the factor). The estimate of the “transformed” geometric mean (i.e., of $\ln(N_{ij} + 1)$) for year j was

$$(TGM)_j = a_0 + a_j \tag{2A}$$

which was identical to the weighted mean of the transformed counts calculated directly as

$$\left(\frac{\sum_{i=1}^I h_{ij} \{ \ln(N_{ij} + 1) \}}{\sum_{i=1}^I h_{ij}} \right) \times H \tag{2B}$$

This estimate was then back-transformed to the original scale to obtain

$$(GM)_j = \exp[(TGM)_j + V/2] - 1 \tag{2C}$$

where V is the error variance of the regression (equal to the weighted variance of the raw transformed counts pooled over all years). On the assumption that $(N_{ij} + 1)$ conforms to a log normal distribution, adding $V/2$ to $(TGM)_j$ prior to back-transformation provides an estimate of the average number of hawks per day for the selected migration window for the species. Although this index is calculated from the geometric mean of $\ln(N_{ij} + 1)$, it is reported as an estimate of the arithmetic mean. This makes no difference to the relationships of the annual indexes to each other or to estimates of trends or their significance, but seasonal sums of the counts will conform more closely to the numbers recorded in the raw data than if we reported geometric-mean rates of passage. This applies also to the remaining four indexes.

To improve the distribution of residuals in the subsequent analysis, we performed an identical preliminary regression in all of the four remaining analyses (Hussell 1981, Hussell et al. 1992). Independent variables in the preliminary analysis were first- and second-order date terms and first- to fourth-order year terms (i.e., year was treated as a continuous variable, not as a categorical dummy variable). Cases (days) with predicted values less than zero in the preliminary regression were deleted from the data for the main analysis. This could have the effect of deleting days at the start or end of the migration window of some species in some or all years.

The midpoint of the passage window was set as the zero date, so that deviations were both positive and negative, limiting the correlation

among higher-order terms. Likewise, in the preliminary regression, the midpoint year in the series of years analyzed was set as the zero year.

Date-adjusted estimated geometric-mean daily count $(GM[date])_j$ was estimated from the regression model including year and date terms only, that is

$$\ln(N_{ij} + 1) = a_0 + \sum_{j=1}^J a_j Y_j + \sum_{k=1}^4 b_k t^k + e_{ij} \tag{3A}$$

This index was designed to eliminate bias introduced by days when no data were collected. The estimated geometric-mean count (back-transformed) for each day in each year was then calculated, summed each year over the migration period, and divided by the number of days in the season and retransformed to obtain $(TDA)_j$. Then:

$$(GM[date])_j = \exp[(TDA)_j + V/2] - 1 \tag{3B}$$

Date-adjusted, estimated geometric-mean daily count with wind covariates index $(GM[date, wind])_j$ was derived in the same manner as the $(GM [date])_j$ index, with the addition of 12 variables incorporating wind speed and direction ($E, SE, S, SW, E^2, \dots, SW^3$, represented by

$$\sum_{l=1}^L d_l W_{lij}$$

in the regression model). For this index, however, the estimated geometric-mean count (back-transformed) for each day in each year was calculated assuming that the value of each wind variable on all days in all years was equal to the mean value of that variable in the data.

Date-adjusted, estimated geometric-mean daily count with date * year interactions $(GM[date, date * year])_j$ index was derived in the same manner as the $(GM[date])_j$ index, with the addition of first- to fourth-order interaction terms between date and year (represented by

$$\sum_{j=0}^J \sum_{k=1}^4 c_{jk} (Y_j)^k$$

in the model). These terms were included to allow for interannual variations in the timing and pattern of migration. We used stepwise regression analysis (P to enter = 0.01, P to exit = 0.01001) to select interaction terms only

for years in which they strongly affected the regression model. Interaction terms were evaluated in blocks (first- to fourth-order) for each year, and could only enter the model if they were significant as a block for any given year.

Date-adjusted, estimated geometric-mean daily count with date * year interactions and wind covariates ($GM[date, wind, date * year]$); index was derived in the same manner as ($GM[date, date * year]$), with the addition of 12

variables representing wind speed and direction ($E, SE, S, SW, E^2...SW^3$). This method used all terms in the full regression model described above, except that the date * year interactions were included only if they met the criteria for entry in the stepwise procedure. The effect of wind variables on the estimated geometric-mean count was treated in the same way as for the ($GM[date, wind]$);index (see above).

APPENDIX 2. Annual count totals (count), sample sizes (days), average inter-index correlation (r), and adjusted R^2 values for annual hawk migration indexes derived from five regression models ($n = 12$ species) at Hawk Mountain Sanctuary (HMS), Pennsylvania, and Cape May Point (CMP), New Jersey.

Species	Site	Count	Days	r	Adjusted R^2				
					GM ^a	DA ^b	DAW ^c	DY ^d	DYW ^e
Osprey	HMS	500	1,916	0.88	0.02	0.30	0.36	0.36	0.42
	CMP	2,346	1,448	0.97	0.12	0.29	0.41	0.41	0.53
Bald Eagle	HMS	77	3,645	0.96	0.09	0.15	0.22	0.18	0.24
	CMP	87	1,681	0.99	0.23	0.25	0.33	0.30	0.37
Northern Harrier	HMS	268	2,257	0.99	0.07	0.20	0.20	0.22	0.22
	CMP	1,657	2,155	0.98	0.10	0.17	0.36	0.25	0.43
Cooper's Hawk	HMS	520	2,231	0.97	0.09	0.41	0.52	0.48	0.55
	CMP	2,497	1,762	0.95	0.12	0.38	0.50	0.43	0.56
Sharp-shinned Hawk	HMS	6,079	1,623	0.87	0.04	0.39	0.51	0.48	0.59
	CMP	27,224	1,712	0.96	0.10	0.25	0.40	0.34	0.49
Broad-winged Hawk	HMS	8,653	1,075	0.90	0.07	0.45	0.46	0.52	0.54
	CMP	2,344	1,044	0.87	0.05	0.11	0.27	0.20	0.35
Red-shouldered Hawk	HMS	268	1,871	0.94	0.01	0.20	0.27	0.24	0.33
	CMP	444	1,412	0.90	0.02	0.11	0.26	0.11	0.29
Red-tailed Hawk	HMS	3,730	2,176	0.79	0.03	0.38	0.50	0.44	0.55
	CMP	1,943	1,726	0.90	0.06	0.27	0.42	0.29	0.45
Golden Eagle	HMS	72	1,897	0.93	0.04	0.11	0.22	0.16	0.27
	CMP	12	1,306	0.97	0.01	0.05	0.11	0.08	0.15
American Kestrel	HMS	533	2,102	0.79	0.03	0.12	0.32	0.15	0.36
	CMP	9,106	1,531	0.90	0.05	0.11	0.42	0.14	0.45
Merlin	HMS	75	1,875	0.97	0.11	0.30	0.35	0.34	0.38
	CMP	1,463	1,393	0.96	0.08	0.28	0.44	0.30	0.48
Peregrine Falcon	HMS	28	1,623	0.98	0.04	0.25	0.26	0.29	0.30
	CMP	632	1,180	0.98	0.19	0.50	0.52	0.58	0.58

^aGM = effort-weighted geometric-mean passage rate.

^bDA = estimated birds day⁻¹ index, date and year terms (GM[date]).

^cDAW = estimated birds day⁻¹ index, date and year terms, wind terms (GM[date, wind]).

^dDY = estimated birds day⁻¹ index, date and year terms, date * year interactions (GM[date, date * year]).

^eDYW = estimated birds day⁻¹ index, date and year terms, date * year interactions, wind term (GM[date, wind, date * year]).