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Source: Journal of Raptor Research, 44(2) : 101-112

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/JRR-09-31.1

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J. Raptor Res. 44(2):101–112
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SEASONAL DIFFERENCES IN MIGRATION COUNTS OF RAPTORS: UTILITY OF SPRING COUNTS FOR POPULATION MONITORING

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ABSTRACT.—Long-term monitoring is important for ensuring effective conservation of raptor populations. Raptors also can serve as indicators of biodiversity and ecosystem condition. Therefore, effective monitoring of raptor populations yields the added benefit of helping to evaluate the status of ecosystems. Spring counts of migrating raptors at concentration points may contribute to these goals, particularly by providing insight into the vital demographic rates underlying population trends. Although much is known about the monitoring value of autumn migration counts in North America, little research has addressed the value of spring counts. We compared counts at seven spring watchsites to those at seven autumn watchsites matched by region (Southwest, Great Lakes, and Northeast) to assess the value of spring counts for population monitoring. Our analyses suggested that population indexes derived from spring migration counts provided estimates of population change that differed overall from autumn migration counts in the same region. The concordance of spring and autumn trends was higher in the Southwest and Northeast than in the Great Lakes region, suggesting greater variation in the seasonal representation of populations in the latter region. The average precision of spring trend estimates was better than for autumn estimates in the same region in two of three regions, and the estimated rates of change often were lower in spring. Spring counts enhanced the ability to estimate population trends for species that are less common in autumn counts, including the Rough-legged Hawk (*Buteo lagopus*) and Red-shouldered Hawk (*B. lineatus*). To realize fully the value of spring counts, we recommend the establishment of additional spring watchsites in areas that concentrate migrants in autumn, but do so to a lesser extent in spring, as well as additional research to define the populations sampled by autumn and spring counts.

KEY WORDS: *migration counts*; *monitoring techniques*; *North America*; *population*; *raptors*; *seasonal dynamics*; *trend.*

DIFERENCIAS ESTACIONALES EN LOS CONTEOS DE AVES RAPACES DURANTE LA MIGRACIÓN: LA UTILIDAD DE LOS CONTEOS DE PRIMAVERA PARA EL MONITOREO DE LAS POBLACIONES

RESUMEN.—El monitoreo de largo plazo es importante para asegurar la conservación efectiva de las poblaciones de aves rapaces. Además, las rapaces pueden servir como indicadoras de la biodiversidad y la condición de los ecosistemas. Por esto, los monitoreos efectivos de las poblaciones de aves rapaces también proporcionan el beneficio de ayudar a evaluar el estado de los ecosistemas. Los conteos de primavera en puntos de concentración de aves rapaces que se encuentran migrando pueden contribuir a estos objetivos, particularmente al proveer una idea sobre las tasas demográficas vitales que subyacen a las tendencias poblacionales. A pesar de que se sabe bastante sobre el valor de los conteos migratorios de otoño en Norteamérica, pocas investigaciones han abordado el valor de los conteos de primavera. Comparamos los conteos en siete puntos de observación de primavera con los de siete puntos de observación de otoño pareados en cada región (Sudoeste, Grandes Lagos y Noroeste) para determinar el valor de los conteos de primavera para el monitoreo de las poblaciones. Nuestro análisis sugirió que los índices poblacionales que derivaron de los conteos migratorios de primavera brindaron estimados de cambios poblacionales que fueron en general diferentes de los derivados a partir de conteos migratorios de otoño realizados en una misma región. La concordancia entre las tendencias de primavera y de otoño fue mayor en el Sudoeste y en el Noreste que en la región de los Grandes Lagos, lo que sugiere que existe una mayor variación en la

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representación estacional de las poblaciones en esta última región. La precisión promedio de los estimados de las tendencias de primavera fue mayor que la de los estimados de otoño en dos de las tres regiones y las tasas de cambio estimadas fueron generalmente menores en primavera. Los conteos de primavera aumentaron la capacidad de estimar tendencias poblacionales para las especies que son menos comunes en los conteos de otoño, como *Buteo lagopus* y *B. lineatus*. Para entender completamente el valor de los conteos de primavera, recomendamos que se establezcan sitios de observación de primavera adicionales en áreas que concentren un gran número de rapaces migratorias durante el otoño pero en menor grado durante la primavera. También recomendamos realizar investigaciones adicionales para definir cuáles son las poblaciones muestreadas durante los conteos de primavera y de otoño.

[Traducción del equipo editorial]

Raptors possess many of the characteristics of ideal biological indicator species (Woodward et al. 1999, Bildstein 2001). They integrate biological information across large spatial, temporal, and habitat scales, and provide early indications of major change within ecosystems (Bildstein 2001). These characteristics may be particularly useful in efforts to preserve habitat conditions supporting a wide array of migratory bird and other wildlife species. A substantial literature in population and community ecology suggests that apex predators can exert strong influences on the structure of biological communities (e.g., Wootton 1993, Schmitz et al. 2000, Borer et al. 2006, Trussell et al. 2006, Myers et al. 2007). The loss of apex predators affects community structure because, generally, there is little redundancy at this trophic level and interactions with prey species tend to be strong (Duffy 2003). Accordingly, raptors can also serve as indicators of local biodiversity, such that monitoring and conservation focused on them can efficiently provide broad biodiversity benefits (Sergio et al. 2005). Given their strong associations with biodiversity (Sergio et al. 2005) and strong influences on community structure (Duffy 2003), the development and refinement of methods to monitor these apex predators should pay broad conservation dividends.

Raptors have been designated species of concern in many state wildlife action plans within the United States (e.g., eight species in Pennsylvania and six species in New York). In some cases, the species themselves are of conservation concern; in other cases, they are considered indicative of habitat conditions supporting numerous other species (Anonymous 2005, 2008).

For these reasons, monitoring raptor populations is an important component of biodiversity surveillance. Conventional breeding season surveys have proven difficult and often unreliable, however, due to the low breeding densities and secretive behavior of many species (Fuller and Mosher 1981, 1987, Kirk and Hyslop 1998, Dunn et al. 2005). Previous work has established that autumn counts of visible migrating raptors at traditional watchsites can fulfill an important population monitoring function that produces accurate, cost-effective trend estimates corresponding to other independent indicators (Bednarz et al. 1990, Bildstein 2001, Hoffman and Smith 2003, Farmer et al. 2007, 2008b).

Most raptor migration counts in North America occur at autumn watchsites primarily because migrants are both more abundant and tend to concentrate along topographic features to a greater extent in autumn than in spring (Bildstein 2006, Goodrich and Smith 2008). Comparing autumn counts to spring counts may facilitate greater understanding of migration and population dynamics, yet heretofore few spring counts have undergone rigorous analysis (but see Hoffman and Smith 2003), whereas a broad range of autumn counts from across the continent have (Bildstein et al. 2008). No previous efforts have specifically assessed the value of spring migration counts as a monitoring tool for raptors.

We compare annual counts of 18 raptor species at seven spring and seven autumn migration watchsites located in the United States and Canada. Our objectives were to compare the species composition of, and population trend estimates derived from, spring and autumn counts in three regions, and to draw inferences regarding the relative utility of spring and autumn counts in monitoring populations of migratory raptors for conservation purposes.

METHODS

We compared annual counts of migrating raptors from seven spring and seven autumn watchsites in the United States and Canada (Fig. 1). Spring sites were located in New Jersey, New York, Maryland, Michigan, and New Mexico in the United States, and in Ontario, Canada. Site-specific coverage varied from 14–30 yr of consecutive annual counts (Table 1). Autumn watchsites were located in New

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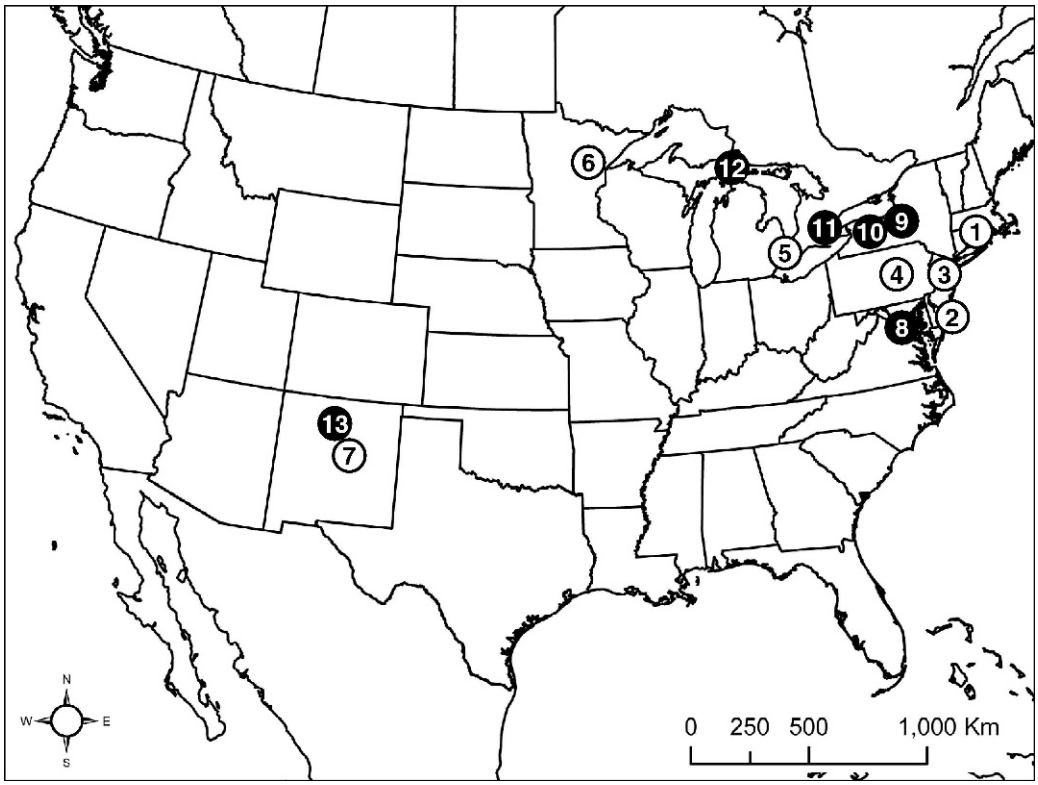


Figure 1. Locations of autumn (open circles) and spring (closed circles) watchsites used to compare raptor migration counts: (1) Lighthouse Point, Connecticut, U.S.A.; (2) Cape May Point, New Jersey, U.S.A.; (3) Montclair Hawk Lookout, New Jersey; (4) Hawk Mountain Sanctuary, Pennsylvania, U.S.A.; (5) Holiday Beach Migration Observatory, Ontario, Canada; (6) Hawk Ridge Bird Observatory, Minnesota, U.S.A.; (7) Manzano Mountains, New Mexico, U.S.A.; (8) Fort Smallwood Park, Maryland, U.S.A.; (9) Derby Hill Bird Observatory, New York, U.S.A.; (10) Braddock Bay, New York; (11) Beamer Conservation Area, Ontario; (12) Whitefish Point, Michigan, U.S.A.; and (13) Sandia Mountains, New Mexico.

Jersey, Pennsylvania, Minnesota, New Mexico, and Ontario. Coverage extended beyond 20 yr for all autumn watchsites (Table 1). We divided the watchsites into three regional groups: northeast coast/eastern Great Lakes, hereafter ''Northeast''; central and western Great Lakes, hereafter ''Great Lakes''; and southwestern U.S., hereafter ''Southwest'' (Table 1).

At all watchsites, observers used 7–10× binoculars to detect and identify migrating raptors, and sometimes telescopes to identify, but not to detect, raptors. Depending on weather and the volume of migration, observations sometimes extended beyond or terminated before the end of standardized daily sampling periods described below.

For each species at each site, we calculated mean annual counts and coefficients of variation for the periods of record described above. We used hourly counts to calculate annual population indexes (geometric mean birds per day) following Hussell (1981) for all species at all sites where the average annual count of a given species was ≥20 migrants (Farmer and Hussell 2008). This method uses a regression-based ANCOVA to estimate population indexes as birds per standard day while controlling for seasonal patterns in passage rates (Francis and Hussell 1998, Farmer et al. 2007, Farmer and Hussell 2008). The full regression model with all covariates was:

$$\ln(N_{ij}+1) = a_0 + \sum_{j=1}^{J} a_j Y_j + \sum_{k=1}^{4} b_k i^k + e_{ij} \qquad (1)$$

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 which

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Table 1. Locations and data collection periods for raptor migration watchsites in three regions of the United States and Canada.

REGION	LOCATION	LATITUDE	LONGITUDE	DATES OF OPERATION	YEAR BEGUN[a]
Northeast	Lighthouse Point, CT, U.S.A.	41°15′N	72°54′W	1 Sep–30 Nov	1974
	Cape May Point, NJ, U.S.A.	39°56′N	74°57′W	1 Sep–30 Nov	1976
	Hawk Mountain Sanctuary, PA, U.S.A.	40°38′N	75°59′W	15 Aug–15 Dec	1934 (1974)
	Montclair Hawk Lookout, NJ, U.S.A.	40°50′N	74°13′W	15 Mar–15 May	1978
				1 Sep–30 Nov	1974
	Fort Smallwood Park, MD, U.S.A.	39°10′N	76°33′W	mid-Feb–mid-Jun	1994
	Derby Hill Bird Observatory, NY, U.S.A.	43°32′N	76°14′W	1 Mar–31 May	1979
	Braddock Bay, NY, U.S.A.	43°19′N	77°43′W	1 Mar–31 May	1977
Great Lakes	Hawk Ridge Bird Observatory, MN, U.S.A.	46°45′N	92°02′W	15 Aug–30 Nov	1952 (1974)
	Holiday Beach Migration Observatory, ON, Canada	42°02′N	83°03′W	1 Sep–30 Nov	1974
	Beamer Conservation Area, ON, Canada	43°11′N	79°34′W	1 Mar–15 May	1977
	Whitefish Point, MI, U.S.A.	46°46′N	84°57′W	15 Mar–31 May	1979
Southwest	Manzano Mountains, NM, U.S.A.	34°42′N	106°24′W	27 Aug–5 Nov	1985
	Sandia Mountains, NM, U.S.A.	35°05′N	106°25′W	24 Feb–5 May	1985

[a] Years in parentheses indicate first year of data included in analyses. Analyzed datasets extended from these start years through 2004 (Northeast, Great Lakes) or 2005 (Southwest) for autumn counts (Farmer et al. 2008a, Smith et al. 2008) and through 2007 for spring counts.

were set equal to one when year = j and were zero in all other years, i^k were 1st through 4th order terms in date, a_j and b_k 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, all other independent variables as covariates, and daily count estimates 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 previous applications (Hussell 1981, Francis and Hussell 1998), except that we expressed each index as the estimated mean count per day.

We estimated species- and site-specific trends in annual indexes as the geometric-mean rate of change over a specified time interval (Link and Sauer 1997). We derived trend estimates and their significance by re-parameterizing the year terms following Francis and Hussell (1998; also see Farmer et al. 2007). The re-parameterization 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 at each end of the time series under consideration. The indexes for all years influenced these estimates of the mean, thereby accounting for any trend within the averaged years (Francis and Hussell 1998). Similarly, we based tests of trend significance and calculation of confidence intervals on the mean squared deviation from the regression curve of all index values, not just those in the averaged years. For each spring watchsite, we estimated trends and their significance over the periods of record for each species (Table 1).

We compared the spring trends to previously published trends for the seven autumn watchsites (Farmer et al. 2008a,b, Smith et al. 2008). In the Great Lakes and Southwest regions, the periods analyzed in spring and autumn were comparable across all sites (i.e., mid-1970s to mid-2000s in the Great Lakes and mid-1980s to mid-2000s in the Southwest; Table 1). This was also true in the Northeast (mid-1970s to mid-2000s), except that the Fort Smallwood Park (MD) count did not begin until 1994. Because of this substantial difference in data periods, we excluded the Fort Smallwood data from most analyses; however, we also calculated trends for all sites in the Northeast region for the common period 1994–2004 to evaluate whether inferences about concordance of seasonal trends differed depending on the length of period analyzed.

We were unable to combine data from multiple watchsites numerically to derive valid, composite re-

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gional trend estimates for each species-season combination (see Dunn and Hussell 1995), but we assessed the strength of concordance between spring and autumn trends in several ways. We used a binomial test (Zar 1996) on matches between qualitative patterns in seasonal trends to assess concordance on conclusions reached at regional scales. For this test, we classified regional trends for each species into four general categories: increasing, decreasing, stable, or variable. A significant test result indicated more matches than would be expected to occur at random.

Although regional averages were not valid as estimates of a composite regional trend, they were useful to compare the typical estimate provided by autumn and spring migration counts. Therefore, within the three regions, we assessed the numerical concordance between spring and autumn trends using paired *t*-tests to investigate differences in the magnitude and precision of spring and autumn trend estimates within regions. The data points for these analyses were species-specific seasonal averages calculated across sites within regions, with the precision analyses based on one-sided widths of 95% confidence intervals (CIs). We used binomial tests to examine relationships between the degree of agreement of qualitative spring and autumn trend estimates (agree vs. disagree) and migrant type (partial-short, partial-medium, partial-long, irruptive, complete-medium, or complete-long; see Bildstein 2006) and primary flight mode on migration (soaring, powered, or combination). We tested for relationships between degree of agreement and trend magnitude using ANOVA on a dependent variable constructed by averaging the absolute values of trend magnitudes across seasons within species.

We considered trend estimates significant with $P \leq 0.10$ and all other test statistics significant with $P \leq 0.05$. We conducted all trend analyses using SAS 9.1.3 (SAS Institute, Inc., Cary, North Carolina, U.S.A.) and other statistical analyses using Statistica 7.1 (Statsoft, Inc., Tulsa, Oklahoma, U.S.A.).

RESULTS

The total combined count at the seven spring watchsites averaged 131 119 raptors of 18 species per season (Table 2), which was approximately half the average at the seven autumn watchsites (251 817; Farmer et al. 2008a, Smith et al. 2008). Broad-winged Hawks (*Buteo platypterus*, 40%), Sharp-shinned Hawks (*Accipiter striatus*, 33%), and Turkey Vultures (*Cathartes aura*, 14%) together made up more than 80% of all spring counts, but species composition varied among regions. In the Northeast, Sharp-shinned Hawks, Broad-winged Hawks, American Kestrels, and Turkey Vultures composed >80% of all counts, in descending order of abundance. At Great Lakes watchsites, Sharp-shinned Hawks, Broad-winged Hawks, Turkey Vultures, and Red-tailed Hawks comprised >80% of the counts. At the Sandia Mountains Southwest watchsite, Sharp-shinned Hawks, Cooper's Hawks (*A. cooperii*), Red-tailed Hawks, American Kestrels, and Turkey Vultures predominated.

Spring Population Trends. *Northeast.* Significant declines occurred in spring counts of American Kestrels along the Atlantic Coast, whereas trend estimates for eastern Great Lakes (New York) watchsites were nonsignificantly negative (Table 3). Northern Harriers, Broad-winged Hawks, and Red-tailed Hawks each declined at one watchsite and showed no significant trends elsewhere (Table 3). Bald Eagles (*Haliaeetus leucocephalus*) increased substantially at all three sites where they were counted in sufficient numbers for analysis. Cooper's Hawks, Merlins (*Falco columbarius*), and Peregrine Falcons (*F. peregrinus*) each increased at two sites and showed no other significant trends. Ospreys, Sharp-shinned Hawks, Red-shouldered Hawks (*Buteo lineatus*), and Golden Eagles (*Aquila chrysaetos*) each increased at one site and showed no other significant trends. Northern Goshawks (*Accipiter gentilis*), Rough-legged Hawks (*B. lagopus*), Black Vultures (*Coragyps atratus*), and Turkey Vultures showed no significant trends in this region.

Great Lakes. Bald Eagles, Northern Harriers, and Turkey Vultures increased at both spring watchsites in this region (Table 4). Trend estimates also were positive at both sites for Ospreys and Cooper's Hawks, but significantly so only at one site. Golden Eagles, Merlins, and Peregrine Falcons increased at Whitefish Point, but were not recorded at Beamer Conservation Area in sufficient numbers for analysis. The Sharp-shinned Hawk was the only species that declined significantly at both sites. Northern Goshawks, Red-tailed Hawks, and American Kestrels showed significant declines at one site and no significant trends at the other site. Red-shouldered Hawks increased significantly at Whitefish Point, but declined significantly at Beamer Conservation Area. Broad-winged and Rough-legged hawks showed no significant trends in this region.

Southwest. Ospreys, Swainson's Hawks, and Peregrine Falcons increased in the Sandia Mountains at

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Table 2. Average (CV) annual counts of 18 raptor species and all raptors combined at seven spring migration watchsites in three regions of the United States and Canada (see Table 1 for periods of record).

	SOUTHWEST	GREAT LAKES		NORTHEAST			
SPECIES	SANDIA MOUNTAINS NM	WHITEFISH POINT MI	BEAMER CONSERVATION AREA ON	BRADDOCK BAY NY	DERBY HILL NY	MONTCLAIR NJ	FORT SMALLWOOD PARK MD
Black Vulture	na[a]	na	na	na	na	7 (141)	193 (36)
Turkey Vulture	1361 (45)	173 (76)	2094 (78)	6658 (69)	4440 (62)	319 (50)	4024 (19)
Osprey	63 (40)	117 (41)	38 (43)	216 (68)	404 (40)	168 (37)	423 (42)
Bald Eagle	14 (60)	148 (95)	24 (90)	102 (89)	86 (101)	5 (67)	48 (46)
Northern Harrier	58 (24)	307 (51)	128 (37)	804 (75)	650 (37)	42 (46)	128 (30)
Sharp-shinned Hawk	494 (50)	8438 (43)	3190 (35)	5983 (78)	4666 (47)	503 (51)	2405 (25)
Cooper's Hawk	756 (37)	65 (59)	188 (32)	536 (83)	476 (37)	36 (92)	512 (17)
Northern Goshawk	11 (64)	72 (60)	20 (90)	40 (70)	60 (80)	1 (241)	1 (111)
Red-shouldered Hawk	na	na	875 (64)	782 (96)	818 (37)	42 (66)	196 (42)
Broad-winged Hawk	6 (103)	5269 (63)	2904 (49)	25 875 (74)	17 327 (46)	1652 (66)	1197 (94)
Swainson's Hawk	54 (40)	na	na	na	na	na	na
Red-tailed Hawk	340 (37)	2108 (68)	2629 (19)	4281 (69)	6568 (44)	170 (44)	328 (38)
Rough-legged Hawk	<1	792 (76)	73 (54)	379 (79)	326 (34)	na	na
Golden Eagle	353 (46)	25 (78)	7 (49)	24 (58)	33 (61)	na	na
American Kestrel	197 (46)	461 (46)	92 (40)	546 (71)	394 (48)	296 (60)	515 (47)
Merlin	10 (77)	65 (67)	10 (70)	18 (85)	22 (53)	15 (79)	56 (41)
Peregrine Falcon	45 (67)	24 (61)	3 (81)	10 (91)	5 (82)	3 (110)	4 (76)
Prairie Falcon	24 (43)	na	na	na	na	na	na
All raptors	3900	18 159	12 919	46 473	36 291	3295	10 084

[a] Not applicable: species abundance at site insufficient to support robust trend analyses.

rates varying from 2.0–14.6%/yr (Table 4). No other significant trends occurred at this site.

Trend Comparisons. The overall regional patterns in spring trends agreed qualitatively with those from corresponding autumn watchsites for 8 of 14 species monitored during both seasons in the Northeast, 8 of 15 species in the Great Lakes, and 7 of 11 species in the Southwest (Table 5). Binomial tests indicated this degree of concordance could be expected at random in all three regions (Northeast $P = 0.183$; Great Lakes $P = 0.196$; Southwest $P = 0.161$; Table 5). Species for which spring and autumn trend estimates agreed were characterized by larger average trend magnitudes (3.0 ± 0.65 [SE] % change/yr) than those for which there was seasonal disagreement (1.2 ± 0.92% change/yr; $F_{1,34} = 7.901$, $P = 0.008$), and this relationship was not significantly influenced by region ($F_{2,34} = 0.184$, $P = 0.833$), or the region × agreement interaction ($F_{2,34} = 0.333$, $P = 0.719$).

Species for which there were no qualitative differences between the long-term seasonal trend indicators within regions included Osprey, Bald Eagle (Great Lakes and Northeast only), Swainson's Hawk (Southwest only), Golden Eagle, Merlin, and Peregrine Falcon. Within the Southwest and Northeast regions, no species showed diametrically opposed seasonal trend indicators, whereas in the Great Lakes region, counts of Northern Harriers increased in spring but decreased in autumn, and counts of Northern Goshawks and American Kestrels decreased in spring but increased in autumn (Table 5). Binomial tests indicated no significant differences in concordance of seasonal trend estimates for species in different migrant-type or flight-behavior categories.

At Montclair, New Jersey, the only watchsite at which migrants were counted in both seasons, spring and autumn trend estimates for nine species common to both seasons were strongly and positively correlated (Pearson $r = 0.87$, $P = 0.003$; Table 3). Overall, the magnitude of spring trend estimates (0.1 ± 1.56% change/yr) averaged significantly lower than for the autumn estimates (2.2 ± 1.66% change/yr; paired t-test: $t = -2.42$, df = 8, $P = 0.042$).

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Table 3. Population trends (average % change/yr [±95% confidence interval]) for 18 raptor species at four spring and four autumn migration watchsites in the northeastern United States (see Table 1 for periods of record). Source of autumn trends is Farmer et al. (2008a).

Species	Braddock Bay NY (Spring)	Derby Hill NY (Spring)	Hawk Mountain PA (Autumn)	Montclair Hawk Lookout NJ (Spring)	Montclair Hawk Lookout NJ (Autumn)	Fort Smallwood Park MD (Spring)	Cape May Point NJ (Autumn)	Lighthouse Point CT (Autumn)
Black Vulture	na[a]	na	na	na	na	1.5 (2.7)	6.9 (2.1)**[b]	na
Turkey Vulture	1.4 (3.8)	−0.7 (3.6)	12.5 (1.8)**	2.5 (4.3)	10.5 (2.7)**	3.7 (14.2)	1.5 (3.8)	8.8 (1.3)**
Osprey	0.2 (3.6)	3.2 (1.2)**	1.5 (0.9)**	−1.0 (1.4)	2.4 (1.7)**	−3.5 (14.0)	2.4 (2.1)*	5.1 (2.2)**
Bald Eagle	6.8 (1.4)**	9.6 (1.0)**	4.7 (0.6)**	na	7.7 (2.4)**	5.8 (3.4)**	8.4 (1.7)**	15.7 (7.0)**
Northern Harrier	0.8 (3.4)	−0.8 (1.4)	−2.0 (0.9)**	0.3 (2.3)	0.6 (1.9)	−5.2 (5.0)*	−0.7 (2.6)	0.7 (1.5)
Sharp-shinned Hawk	3.5 (5.3)	−0.7 (4.0)	−1.1 (0.9)**	−0.4 (5.9)	1.4 (1.7)	9.4 (8.0)*	−4.5 (2.6)**	1.8 (1.3)*
Cooper's Hawk	6.0 (4.1)**	0.5 (1.5)	4.1 (0.8)**	10.3 (2.4)**	10.2 (1.4)**	−3.0 (3.3)	4.6 (2.3)**	7.5 (2.2)**
Northern Goshawk	1.2 (2.7)	−0.4 (3.0)	−2.7 (1.7)**	na	na	na	−0.6 (1.9)	na
Red-shouldered Hawk	−0.1 (3.9)	1.6 (2.2)	−0.6 (0.8)	1.6 (1.9)+	1.3 (1.1)	−1.9 (4.8)	−0.3 (1.4)	3.3 (1.5)**
Broad-winged Hawk	−1.5 (4.2)	−0.3 (4.6)	−3.1 (1.0)**	−3.7 (5.4)	−1.8 (3.0)	−9.7 (7.4)*	−1.4 (2.5)	−0.4 (1.8)
Swainson's Hawk	na	na	na	na	na	na	na	na
Red-tailed Hawk	0.2 (1.9)	0.1 (5.6)	−1.9 (0.9)**	−2.4 (2.3)*	−1.7 (2.3)	−3.4 (5.0)	−1.8 (2.8)	3.1 (1.3)**
Rough-legged Hawk	−0.2 (4.0)	1.5 (1.8)	na	na	na	na	na	na
Golden Eagle	1.4 (1.9)	4.7 (1.3)**	2.1 (1.3)**	na	na	na	na	na
American Kestrel	−0.2 (2.9)	−0.2 (1.7)	−1.6 (0.9)*	−6.3 (2.5)**	−3.3 (1.3)**	−11.3 (4.4)**	−4.5 (1.5)**	−3.1 (1.5)**
Merlin	8.3 (3.6)**	3.5 (1.7)**	5.1 (0.7)*	na	7.2 (2.6)**	−0.6 (4.5)+	1.8 (2.0)+	7.8 (2.7)**
Peregrine Falcon	7.6 (2.4)**	5.2 (3.5)**	4.3 (1.1)*	na	na	−2.4 (14.9)	6.0 (2.0)**	7.8 (2.0)**
Prairie Falcon	na	na	na	na	na	na	na	na

[a] Not applicable: species abundance at site insufficient to support robust trend analyses.
[b] Significance of trend estimate: + $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.01$.

Table 4. Long-term population trends (average % change/yr [±95% confidence interval]) for 18 raptor species at two spring and two autumn migration watchsites in the Great Lakes region and one spring and one autumn migration watchsite in the southwestern United States (see Table 1 for periods of record). Sources of autumn trends are Farmer et al. (2008a) and Smith et al. (2008).

	SOUTHWEST		GREAT LAKES			
SPECIES	SANDIA MOUNTAINS NM (SPRING)	MANZANO MOUNTAINS NM (AUTUMN)	WHITEFISH POINT MI (SPRING)	HAWK RIDGE MN (AUTUMN)	BEAMER CONSERVATION AREA ON (SPRING)	HOLIDAY BEACH ON (AUTUMN)
Turkey Vulture	0.3 (2.7)	10.4 (5.9)**[a]	8.4 (1.4)**	4.0 (1.9)**	8.9 (1.1)**	10.3 (2.1)**
Osprey	3.4 (1.5)**	6.8 (3.8)**	0.5 (1.4)	4.3 (1.3)**	3.3 (0.9)**	0.8 (1.6)
Bald Eagle	na[b]	na	5.8 (0.9)**	10.4 (1.2)**	7.0 (1.1)**	7.8 (2.5)**
Northern Harrier	−0.1 (1.3)	3.0 (3.8)	2.4 (2.4)*	0.6 (1.8)	1.4 (1.6)+	−2.6 (2.5)+
Sharp-shinned Hawk	−0.9 (2.5)	2.2 (2.0)*	−3.0 (2.1)+	0.7 (1.2)	−1.7 (1.0)**	−0.5 (1.1)
Cooper's Hawk	1.3 (2.1)	4.5 (1.9)**	0.3 (2.3)	4.0 (1.9)**	1.8 (0.7)**	2.6 (1.2)**
Northern Goshawk	na	na	−1.9 (2.1)+	1.7 (2.7)	0.1 (3.6)	4.4 (3.2)**
Red-shouldered Hawk	na	na	4.5 (2.9)**	na	−1.8 (1.1)**	−1.3 (2.2)
Broad-winged Hawk	na	na	0.8 (4.7)	1.1 (2.9)	−0.3 (1.6)	−5.2 (3.8)**
Swainson's Hawk	2.0 (1.6)*	13.7 (10.2)**	na	na	na	na
Red-tailed Hawk	0.5 (2.0)	2.1 (1.6)*	−3.0 (3.3)+	0.9 (1.2)	−0.4 (0.1)	−2.4 (2.7)+
Rough-legged Hawk	na	na	−1.7 (3.4)	−1.2 (1.7)	0.4 (1.7)	−6.6 (3.6)**
Golden Eagle	−0.4 (2.4)	1.2 (2.6)	2.4 (1.7)**	5.7 (1.3)**	na	1.5 (2.8)
American Kestrel	−0.1 (1.6)	0.1 (1.6)	0.9 (2.0)	3.2 (1.3)**	−1.3 (1.0)*	−0.4 (1.6)
Merlin	na	10.1 (5.0)**	6.0 (2.1)**	12.0 (1.8)**	na	11.9 (2.4)**
Peregrine Falcon	14.6 (2.9)**	14.4 (4.8)**	8.2 (2.1)**	7.8 (2.0)**	na	4.7 (1.9)**
Prairie Falcon	0.4 (1.9)	6.1 (4.0)*	na	na	na	na

[a] Significance of trend estimate: + $P \leq 0.10$, * $P \leq 0.05$, ** $P \leq 0.01$.

[b] Not applicable: species abundance at site insufficient to support robust trend analyses.

Average, long-term (1970s to 2000s, excluding Fort Smallwood Park) trend estimates in the Northeast did not differ significantly between spring (2.0 ± 0.87% change/yr) and autumn (2.4 ± 1.08% change/yr; $t = -0.58$, df = 13, $P = 0.571$). Species-specific average 95% CIs for the two seasons (Table 3; n = 3–4 sites per season, 14 species commonly analyzed) were uncorrelated ($r = -0.01$) and the CIs for spring estimates (2.9 ± 0.29% change/yr) averaged significantly wider (lower precision) than for the autumn CIs (1.8 ± 0.12% change/yr; $t = 3.43$, df = 13, $P = 0.004$). With the data period restricted to 1994–2004 so that the Fort Smallwood data could be considered, the qualitative concordance of regional trends was poorer (7 of 15 species). The average trend estimates for 1994–2004 did not differ between spring (0.0 ± 0.91% change/yr) and autumn (−0.6 ± 0.85% change/yr; $t = 0.92$, df = 14, $P = 0.372$), and the 95% CIs averaged roughly twice as wide in both seasons (see Smith et al. [2008] for discussion of the effects of project duration on trend precision). Average CIs for this period were positively correlated between seasons ($r = 0.51$), and the difference in the average precision of the seasonal estimates was less pronounced (spring CIs: 4.7 ± 0.46% change/yr; autumn CIs: 3.9 ± 0.43% change/yr; $t = 1.84$, df = 14, $P = 0.088$).

In the Great Lakes region, average trend estimates did not differ significantly between spring (2.2 ± 0.91% change/yr) and autumn (2.6 ± 1.14% change/yr; $t = -0.66$, df = 14, $P = 0.518$). Average 95% CIs (Table 4; n = 2 sites per season, 15 species commonly analyzed) were positively correlated ($r = 0.86$) and the CIs for spring estimates (1.9 ± 0.15% change/yr) averaged significantly narrower than the autumn CIs (2.1 ± 0.16% change/yr; $t = -2.21$, df = 14, $P = 0.043$)

In the Southwest, the two watchsites are located 34 km apart along a common north-south, montane axis and probably monitor similar populations of many species (Hoffman et al. 2002, Goodrich and Smith 2008). Trend estimates averaged significantly lower in spring (1.9 ± 1.32% change/yr) than in autumn (5.9 ± 1.50% change/yr; $t = -3.44$, df = 10, $P = 0.006$). Average 95% CIs (Table 4; n = 2

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Table 5. Regional patterns in long-term raptor migration count trends across six spring and seven autumn watchsites in three regions of North America.

	SOUTHWEST		GREAT LAKES		NORTHEAST	
SPECIES	SPRING (1 SITE)	AUTUMN (1 SITE)	SPRING (2 SITES)	AUTUMN (2 SITES)	SPRING (3 SITES)	AUTUMN (4 SITES)
Black Vulture	na[a]	na	na	na	na	Increase[b]
Turkey Vulture	Stable	Stable	Increase	Increase	Stable	Increase
Osprey	Increase	Increase	Increase	Increase	Increase	Increase
Bald Eagle	na	na	Increase	Increase	Increase	Increase
Northern Harrier	Stable	Stable	Increase	Decrease	Stable	Decrease
Sharp-shinned Hawk	Stable	Increase	Decrease	Stable	Stable	Variable
Cooper's Hawk	Stable	Increase	Increase	Increase	Increase	Increase
Northern Goshawk	na	na	Decrease	Increase	Stable	Decrease
Red-shouldered Hawk	na	na	Variable	Stable	Increase	Increase
Broad-winged Hawk	na	na	Stable	Decrease	Stable	Decrease
Swainson's Hawk	Increase	Increase	na	na	na	na
Red-tailed Hawk	Stable	Increase	Decrease	Decrease	Decrease	Variable
Rough-legged Hawk	na	na	Stable	Decrease	Stable	na
Golden Eagle	Stable	Stable	Increase	Increase	Increase	Increase
American Kestrel	Stable	Stable	Decrease	Increase	Decrease	Decrease
Merlin	na	Increase	Increase	Increase	Increase	Increase
Peregrine Falcon	Increase	Increase	Increase	Increase	Increase	Increase
Prairie Falcon	Stable	Increase	na	na	na	na

[a] Too uncommon in region to support trend analysis.

[b] Decrease = majority of estimates negative, some estimates significant; Increase = majority of estimates positive, some estimates significant; Stable = no significant trends and typically a mix of positive and negative estimates when more than one site involved; Variable = at least one significant increase and one significant decrease.

sites per season, 15 species commonly analyzed) were uncorrelated ($r = -0.07$) and the spring CIs ($1.9 \pm 0.15\%$ change/yr) averaged narrower than the autumn CIs ($2.1 \pm 0.16\%$ change/yr; $t = -2.21$, df = 10, $P = 0.043$).

DISCUSSION

Our analyses indicated that the overall concordance in regional patterns of trends between seasons was at best marginal and, in the Northeast, declined when the analysis period was reduced from three decades to only one. At the same time, the average magnitude of species' trend estimates within regions did not differ significantly between seasons except in the Southwest, and the precision of spring estimates was higher than for autumn estimates except in the Northeast. What is known of migration geography in North America suggests that spring and autumn counts within regions should sample the same populations on a regional scale. With one exception, only single-season counts, either autumn or spring, were collected at the watchsites available for our analyses. Therefore, in comparing our spring results to previous autumn results, we must assume that changes in individual migration counts reflect population changes occurring on a regional basis. This assumption appears to be borne out by previous research showing that migration counts agree with other indicators of regional trends (e.g., Bednarz et al. 1990, Hoffman and Smith 2003, Farmer et al. 2007), as well as a large degree of overlap in recoveries of birds banded near various watchsites within a region (Goodrich and Smith 2008).

Assuming spring and autumn counts within regions do indeed sample the same migrating populations, the equivocal evidence concerning trend agreement either arises from differences in the two analyses we employed, or suggests that demographic processes prevailing between seasons (e.g., winter mortality) are reflected in seasonal trend estimates. Our analysis of qualitative regional patterns in trends assigned some species to categories based on, for example, single significant trend estimates. This technique avoided the pitfalls of averaging trend estimates from multiple sites without knowl-

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edge of appropriate weighting factors (Dunn and Hussell 1995), but sometimes obscured greater numerical similarities between seasons. Conversely, our analyses of average trend estimates allowed these numerical similarities to dominate the analysis, but did not discriminate significant from nonsignificant estimates.

According to the criteria set forth by Farmer et al. (2008a), long-term spring trend estimates averaged moderate precision in the Great Lakes and Southwest, but low precision in the Northeast. Taken together, the equivocal evidence of trend concordance between seasons and the often better precision of spring trend estimates suggest that spring migration counts may be as effective as autumn counts for monitoring migratory raptors. Further insight about regional migration geography and population representation at different sites will be necessary to clarify the relative merits of spring and autumn migration counts. Efforts also are needed to improve the precision of spring estimates in the Northeast through greater standardization or improved modeling.

Perhaps our most interesting finding is that the degree of agreement between spring and autumn trend estimates appeared to depend on the strength of the population trend, rather than on aspects of migration biology such as migrant types and primary flight modes. This suggests that migration monitoring is very good at detecting strong population trends, but may need to be augmented with other monitoring strategies to accurately estimate weaker trends (see Dunn et al. 2005).

Northeast. Counts in this region demonstrated overall qualitative agreement between spring and autumn monitoring, and the long-term spring trend estimates typically averaged at least slightly lower and less precise than in autumn for most species. Bildstein et al. (2008) suggested that spring migration counts may allow us to assess the relative influence of overwinter mortality and productivity as primary causes of population trends when they are compared to autumn trends derived from the same regional population. Eight species exhibited less-positive long-term trends in spring than in autumn in the Northeast, most notably American Kestrels and Broad-winged Hawks (Tables 3 and 5). These species declined at least slightly at all autumn sites, but showed much higher magnitude declines at some spring sites (Table 3). Following Bildstein et al.'s (2008) reasoning, a potential explanation for this pattern is that winter or post-fledging survival is more limiting than productivity in these populations. Focused demographic research on breeding and wintering ranges is needed to test this hypothesis.

Great Lakes. Trends for all three *Accipiters*, Bald Eagles, and Merlins were lower in spring than in autumn, a pattern similar to that seen in the Northeast. In contrast, trends for Northern Harriers were increasing in spring but stable to declining in autumn. This pattern may indicate that the migration geography of harriers in this region is shifting either away from traditional autumn watchsites or more toward the locations of existing spring watchsites.

Declines in counts of American Kestrels and Broad-winged Hawks in the eastern portion of this region, but increases in the western portion (Table 4), suggest that the central Great Lakes watchsites draw migrants of these species from areas overlapping those sampled by watchsites in the Northeast (also showing decreases for these species), whereas western Great Lakes watchsites draw migrants from distinct populations. For Broad-winged Hawks, evidence of increases in the western Great Lakes also is consistent with evidence of recent increases in western North America (Smith et al. 2001, Hoffman and Smith 2003). Overall results suggest that for many species the eastern and western portions of the Great Lakes region sample distinct regional populations.

Southwest. In the Southwest, the close proximity of the Manzano and Sandia sites and more than four dozen exchanges of banded birds between the two sites since 1990 (Hoffman et al. 2002, HawkWatch International unpubl. data), suggest that these projects monitor similar migrating populations of several species. As was true for several species in the Northeast and Great Lakes regions, the almost universally lower spring trend estimates in this region may reflect the disproportionate influence of migration-season and/or overwinter mortality on the population demographics of most species. If this interpretation is correct, these results generally support focusing conservation efforts on migrating and wintering birds and associated geographic ranges rather than on breeding birds and habitats; however, focused research on breeding and wintering ranges is needed to test this hypothesis.

Relative Seasonal Coverage. Spring counts clearly enhance population monitoring for several species that are not as well represented numerically at autumn watchsites. In particular, Rough-legged Hawks averaged 3.5 times more numerous in spring (average annual combined total for seven sites of 1570 migrants; Table 2) than in autumn (average annual

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combined total for seven sites of 453 migrants; Farmer et al. 2008a, Smith et al. 2008), and only spring trend analyses were possible for this species in the Northeast due to low autumn numbers (Table 3). The difference in apparent abundance may reflect relatively poor sampling coverage in autumn when the species' southward flow occurs along a particularly broad front and may extend well into winter after all counts have ceased. Spring monitoring may be better timed to cover the species' return migrations and therefore sample considerably more migrants. A similar pattern may be responsible for the Golden Eagle count averaging roughly three times higher during spring in the Sandia Mountains (354) than during autumn in the Manzano Mountains (116). Red-shouldered Hawks averaged 1.6 times more numerous in spring (2713) than in autumn (1681), largely due to high counts in the central and eastern Great Lakes. The abundance of Turkey Vultures differed less between spring and autumn (19 069 vs. 15 050); however, spring counts were more evenly distributed across the available watchsites, whereas 61% of the autumn count occurred at one Great Lakes watchsite.

CONCLUSIONS

At regional scales, qualitative agreement of spring and autumn count trends for many species and roughly comparable trend precision suggest that both can be effective tools for monitoring populations of migratory raptors. The equivocal, overall qualitative and quantitative agreement between the two seasons indicates, however, that caution is needed when combining inferences from monitoring in different seasons. For several species, variation in trend indicators within seasons in both the Great Lakes and Northeast regions further suggested that different watchsites may sample relatively discrete segments of these species' regional populations. Understanding the conservation significance of these trends will therefore be aided by an increased understanding of raptor migration geography (Bildstein et al. 2008).

It appears that two additional steps are needed to fully realize the value of spring counts: (1) additional spring watchsites are needed, particularly in areas that concentrate migrants in autumn, but may do so to a lesser extent in spring; and (2) research is needed to more thoroughly define the breeding areas sampled by autumn watchsites, the wintering areas sampled by spring sites, and the degree of connectivity between the sampled regions.

ACKNOWLEDGMENTS

We thank the numerous migration observers and count compilers who contributed data to this analysis. We thank K. Bildstein and L. Goodrich for commenting on early drafts of the manuscript. The manuscript also benefited from the thoughtful comments of three anonymous reviewers. This is Hawk Mountain Sanctuary Contribution to Conservation Science No. 186.

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Received 5 May 2009; accepted 16 January 2010
Associate Editor: Fabrizio Sergio

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