Original Article



Monitoring Landscape-Level Distribution and Migration Phenology of Raptors Using a Volunteer Camera-Trap Network

DAVID S. JACHOWSKI, 1,2 Department of Forestry and Environmental Conservation, Clemson University, 258 Lehotsky Hall, Clemson, SC 29631-0310, USA

TODD KATZNER, U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 970 Lusk Street, Boise, ID 83706, USA JANE L. RODRIGUE, U.S. Forest Service, Northern Research Station, Princeton, WV 24740, USA

W. MARK FORD, U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit and Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA

ABSTRACT Conservation of animal migratory movements is among the most important issues in wildlife management. To address this need for landscape-scale monitoring of raptor populations, we developed a novel, baited photographic observation network termed the "Appalachian Eagle Monitoring Program" (AEMP). During winter months of 2008–2012, we partnered with professional and citizen scientists in 11 states in the United States to collect approximately 2.5 million images. To our knowledge, this represents the largest such camera-trap effort to date. Analyses of data collected in 2011 and 2012 revealed complex, often species-specific, spatial and temporal patterns in winter raptor movement behavior as well as spatial and temporal resource partitioning between raptor species. Although programmatic advances in data analysis and involvement are needed, the continued growth of the program has the potential to provide a long-term, cost-effective, range-wide monitoring tool for avian and terrestrial scavengers during the winter season. Perhaps most importantly, by relying heavily on citizen scientists, AEMP has the potential to improve long-term interest and support for raptor conservation and serve as a model for raptor conservation programs in other portions of the world. © This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS Aquila chrysaetos, camera trap, citizen science, golden eagle, landscape, migration, monitoring, raptor.

Understanding the distribution and phenology of large-scale migratory movements is a central question in wildlife management and is of great importance to conservation of biodiversity. Migratory movements result in seasonal changes in distribution of many species of vertebrates and invertebrates (Milner-Gulland et al. 2011). These changes have concomitant consequences for processes at scales from the molecular to ecosystem level (Altizer et al. 2011, Cooke et al. 2012). Additionally, the large spatial extent of seasonal distributional changes makes motile species particularly vulnerable to human perturbation and global change (Schuter et al. 2011). Therefore, the study of migration is an area of pressing research need, to document current patterns and to predict responses to ongoing global change (Jaffré et al. 2013) that can guide current and future conservation actions (Milner-Gulland et al. 2011).

Received: 12 September 2014; Accepted: 21 March 2015

Many birds of prey undertake relatively long-distance migrations to exploit seasonally abundant resources (Newton 2008). Although raptors can take advantage of thermal features and updrafts to conserve energy during long-distance movements, such movements are still physiologically taxing (Smith et al. 1986). Additionally, migration exposes birds to a suite of natural and anthropogenic threats (Janss 2000, De Lucas et al. 2008). Mortality rates of raptors during migratory periods are sixfold higher than during stationary periods (Newton 2008, Klaassen et al. 2014). Therefore, there is a critical need to understand patterns of raptor movements across both space and time to account for potential impacts on those species' populations (Miller et al. 2014).

Recent advances in satellite-based tracking have greatly advanced our understanding of movement ecology of individual raptors. Clearly, the tendency for most northern hemisphere raptors to migrate during autumn and spring is well-known (Bildstein 2006); however, only recent Global Positioning System (GPS)-based tracking technology has revealed the extent, timing, and flight characteristics of these movements for a small group of marked individuals (Miller et al. 2014). Such detailed information on avian movement

¹E-mail: djachowski@gmail.com

 $^{^2}$ School of Life Science, $ar{University}$ of KwaZulu–Natal, Durban, South Africa

can be used to assess the potential impact of disturbances such as wind-energy development and provide valuable information that can be utilized in mitigation, conservation, and regulatory actions (Miller et al. 2014). Unfortunately, migratory behavior from tracking studies is based on small sample sizes of limited temporal duration, making it difficult to draw broad-scale conclusions about long-term use of winter range at the population level.

To account for such large, landscape-scale monitoring needs, avian ecologists have long made use of citizen scientists. Popular raptor "watches" have been conducted from fixed points along frequently used migratory routes for many years. For example, Hawk Mountain Sanctuary in eastern Pennsylvania, USA, has tallied daily or hourly counts of migratory raptors during autumn migration (15 Aug-15 Dec) for 8 decades (Therrien et al. 2012). These counts provide valuable data for monitoring temporal patterns of migratory behavior and long-term demographic trends (Bednarz et al. 1990), but they cannot provide spatially explicit details on winter range use or migratory behavior. Other citizen science approaches, such as the Christmas Bird Count (Butcher et al. 1990) have provided spatially explicit but coarse indices of abundance across years. For example, Christmas Bird Count numbers for raptor species are often biased low, suggesting that Christmas Bird Count has limited utility for monitoring raptor populations because of inconsistent survey effort among sites and the suburban or urban location of most sites (Kochert and Steenhof 2002). Accordingly, there is a need for a spatially explicit, largescale, long-term monitoring program specific for raptors.

Herein, we report a novel, long-term, spatially explicit approach to monitoring raptors during the winter period using a network of carrion-baited camera traps. Over the past several decades, use of automatic, motion-sensing camera traps has emerged as an increasingly common tool for studying carnivore ecology and broader monitoring of mammalian populations (Kucera and Barrett 2011). Most recently, the strategic placement of camera traps has been used to monitor migration phenology of terrestrial species (Tape and Gustine 2014). However, similar monitoring efforts for avian species are logistically problematic, requiring sampling across a large geographic area because of the long-distance migratory patterns of birds. We developed the Appalachian Eagle Monitoring Program (AEMP; www.appachianeagles.org), which is a network of baited camera-trap sites across the Appalachian region and adjacent portions of the eastern United States operated by hundreds of professional and citizen scientists. The primary objective of the present study was to evaluate the utility of AEMP to monitor patterns of raptor spatial and temporal distribution over the course of the winter season when probability of coming to a baited camera trap (i.e., scavenging) was likely highest. Specifically, we tested competing hypotheses that the prevalence of site use (i.e., daily presence or absence) by each of our study species was related to the presence of another raptor species at carrion bait sites (i.e., presence or absence of a potential competitor at some point during the same day), as well as an interaction between latitude and day of the year. Understanding such spatio-temporal patterns of raptor distributions is important in setting management objectives and providing insight into general species ecology. In addition, we discuss the potential strengths and limitations of such a network as a tool for monitoring raptor communities.

METHODS

Study Area

The Appalachian Mountains (hereafter referred to as "Appalachians") constitute an important migratory corridor for raptors in eastern North America (Bildstein 2006, Newton 2008). Extending 2,400 km from Quebec, Canada, through the eastern United States south to Alabama, the Appalachians form a network of northeast- to southwestoriented ridges and valleys separating the Piedmont and Atlantic Coastal Plain in the East from the Midwest interior of North America. The region is heavily forested (approx. 80%), though large areas of the landscape are devoted to suburban-urban development, agriculture, and mineralforest resource extraction (Thompson et al. 2013). Additionally, updrafts generated by the Appalachians facilitate latitudinal migratory movement by raptors (Kerlinger 1989, Bildstein 2006), but these same updrafts are increasingly being utilized to supply wind energy (Kunz et al. 2007). This has led to growing concern about the impact of regional wind-energy development on migratory raptor populations (Miller et al. 2014).

Site Selection and Deployment

We created a network of >180 motion-sensitive trail camera sites extending from Maine to Alabama, USA (Fig. 1). We attempted to standardize monitoring programs by providing a uniform protocol to be followed at each site. We asked site operators to place camera traps on open hilltops or ridges or the highest local topographic feature. In forested areas, we advised establishing sites in small forest gaps or clearings (>10-20 m in diam). To encourage eagles to visit, we baited each site with a road-killed white-tailed deer (Odocoileus virginianus) carcass secured to the ground or a nearby tree using a stake or cable. We asked all volunteers to check and comply with local and state regulations regarding the collection or movement of deer carcasses. We instructed volunteers to revisit sites at least weekly to evaluate camera operation and replace carcasses if they had been largely consumed by visiting wildlife, particularly where coyote (Canis latrans) and vulture (Cathartes aura and Coragyps atratus) activity was high. Because of the logistics of checking a camera periodically and delivering a carcass during the winter months, most sites were in relatively close proximity to secondary or tertiary roads that typically received only infrequent vehicle traffic (i.e., typically <10 vehicles/day).

Volunteers used motion-sensing digital cameras to record images on removable solid-state memory cards. Although volunteers used multiple camera brands, we instructed that cameras were to be placed 1 m from the ground and 2–3 m from the carcass, pointed at the carcass. Protocol required that motion-triggered cameras were programmed to record an image, and then pause for ≥ 1 min prior to taking an additional motion-triggered image. A camera was to be

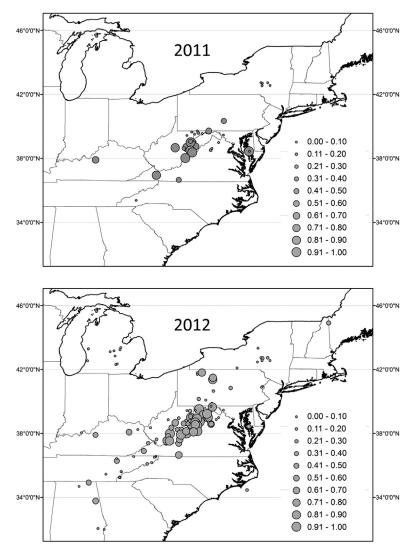


Figure 1. Distributional map of citizen-science camera-trap sites in 2011 (upper panel, n = 37) and 2012 (lower panel, n = 121) as part of winter Appalachian Eagle Monitoring Project (USA). Size of point represents the percentage of days that a golden eagle (*Aquila chrysaetos*) was detected at a deployed camera-trap site.

active at each site for ≥2 weeks, targeted for operation between 15 January and 15 February, after the cessation of most white-tailed deer hunting seasons when high rates of human activity could disturb or impact raptor behavior. However, many volunteers extended trapping throughout the winter from 1 December through 15 April. Sites were typically visited every 2–7 days to check on camera function and to download image files.

Image Analyses

All images collected by AEMP volunteers were collated by state coordinators and forwarded on to a single individual (JLR) who identified raptors to species and created binary records (0 and 1) of each species' daily presence at each site. Since the AEMP was first initiated in West Virginia, in 2008, the number of participating volunteers and geographic scope have increased rapidly from 7 camera-trap sites in West Virginia in 2009 to 121 sites from Maine, west to Michigan and south to Alabama in 2012 (Fig. 1). In winter 2013, >180 sites were monitored.

More than 2.5 million images were collected and analyzed between 2008 and 2012, making AEMP the largest cameratrap network reported to date. We observed 12 raptor species: turkey vulture (*Cathartes aura*), black vulture (*Coragyps atratus*), bald eagle (*Haliaeetus leucocephalus*), golden eagle (*Aquila chrysaetos*), northern goshawk (*Accipiter gentilis*), Cooper's hawk (*Accipiter cooperii*), sharp-shinned hawk (*Accipiter striatus*), rough-legged hawk (*Buteo lagopus*), redshouldered hawk (*Buteo lineatus*), red-tailed hawk (*Buteo jamaicensis*), barred owl (*Strix varia*), and great horned owl (*Bubo virginianus*). For this study, we specifically focused on 7 larger diurnal raptors encountered most frequently: black vulture, turkey vulture, bald eagle, golden eagle, rough-legged hawk, red-shouldered hawk, and red-tailed hawk (Fig. 2).

Evaluating Spatial and Temporal Patterns in Raptor Prevalence

To test the effectiveness of the AEMP's ability to detect movement phenology of raptors, we evaluated how the prevalence of each of our study species varied over both space



Figure 2. Example photographs of golden eagle (*Aquila chrysaetos*) and bald eagle (*Haliaeetus leucocephalus*; Plate A), 2 red-tailed hawks (*Buteo jamaicensis*; Plate B), turkey vulture (*Cathartes aura*) and black vultures (*Coragyps atratus*; Plate C), and red-shouldered hawk (*Buteo lineatus*; Plate D) taken between 2009 and 2013 by motion-activated camera traps placed on white-tailed deer carcasses in this study of raptor migration ecology in eastern North America.

and time. For this study, we specifically focused on data collected in winter of 2011–2012 when the number of sites was largest (n = 121) and distribution of sites was widest (11 states; Fig. 1; data 2013 to present remain to be analyzed). The opportunistic nature of site placement by volunteers and the large movement capacities of raptors (thereby violating the closure assumption that no change in occupancy occurs during the survey period) restricted our use of occupancy models (e.g., O'Connell and Bailey 2011). However, the automated nature of camera traps likely removed much of the potential for observer bias among sites, and the standardized placement of cameras along ridge tops and forest clearings during set periods of time (i.e., only during winter season) limited some potentially confounding environmental variables (e.g., some factors related to habitat and climate). Therefore, we constrained our analysis to evaluate the extent to which daily presence or absence of our focal species was explained by either presence of another species or an interaction between latitude and day of the year.

We used mixed-model logistic regression within an information theoretic model-selection approach to evaluate support for competing hypotheses about the effect of interspecific, spatial, and temporal factors on raptor prevalence (Table 1). Prevalence of raptors at carrion can be influenced by competitive interactions and exclusive use of carcasses (Halley and Gjershaug 1998, Blázquez et al. 2009). Previous studies show that interspecific dominance among avian scavengers at a carcass is correlated with body mass (Kruuk 1967, Anderson and Horwitz 1979, Wallace and Temple 1987). Therefore, we predicted that prevalence of an individual raptor species being investigated would be negatively influenced by the presence of a larger, potentially dominant, eagle, hawk, or vulture species. Although such interactions can occur at fine temporal scales (e.g., it was not unusual for red-tailed hawks to visit carcasses shortly after

eagle departure), for this initial study we focused on longer term patterns of daily prevalence.

Raptor species at our camera sites likely engaged in 1 of 2 types of migratory movement during our period of study. First, the species of eagles and hawks that we detected at our camera sites are known to migrate from northern breeding grounds to southern wintering grounds in the mid- and lower-Appalachian region (Katzner et al. 2012). By deploying cameras on 1 December and halting surveys by 15 April, we did not collect data during the entire autumn or spring migration. Rather, our cameras likely sampled the end of the autumn migration period, and the beginning and middle of the spring migratory period for raptors. Therefore, we predicted that hawk and eagle presence would be most frequent in mid-latitudes (i.e., a quadratic effect of latitude). Alternatively, some cold-tolerant raptor species might reside in northern latitudes or we might capture the early return of these species to northern breeding grounds (i.e., a positive pseudo-threshold effect of latitude). The second major category of migratory movement we predicted to occur was for species to move south of our study area completely and into tropical areas during the winter season. Vulture species are resident throughout our study area during most of the year, but are cold sensitive and known to migrate farther south into warm-temperate and subtropical areas during winter (Mandel et al. 2008). Therefore, we predicted that vulture presence would be highest at southern latitudes during our study, and we evaluated support for a linear and negative pseudo-threshold effect of latitude for both vulture species.

Food limitation and energetic demands were also likely to be important determinants of raptor scavenger use of carrion (Preston 1990). To evaluate these patterns, we hypothesized that raptor prevalence was influenced by the time period when the site was active. We predicted that in the middle of winter, food would be most limited and energetic demands

Table 1. Description of *a priori* hypothesized models used to predict prevalence of raptor species at citizen-science camera-trap sites across eastern North America over the course of the winter months between 1 December 2011 and 15 April 2012. Model variables included different distributions of latitude and day of the year (parentheses after variable indicate when a distribution of the variable was evaluated other than linearly). A hypothesized categorical effect of other raptor species present was also included in models under the description 'competition,' although we use this term loosely because we also hypothesized that in some instances conspecific attraction to the bait site could occur.

	Model description	Model structure
1	Competition & latitude	$\beta_0 + \beta_1 \text{ (eagle)} + \beta_2 \text{ (hawk)} + \beta_3 \text{ (vulture)} + \beta_4 \text{ (Lat)}$
2	Competition & latitude _(quadratic)	$\beta_0 + \beta_1$ (eagle) + β_2 (hawk) + β_3 (vulture) + β_4 (Lat) + β_5 (Lat _q)
3	Competition & latitude _(pseudothreshold)	$\beta_0 + \beta_1$ (eagle) + β_2 (hawk) + β_3 (vulture) β_4 (Lat _p)
4	Competition & day of the year	$\beta_0 + \beta_1$ (eagle) + β_2 (hawk) + β_3 (vulture) + β_4 (JD)
5	Competition & day of the year _(pseudothreshold)	$\beta_0 + \beta_1$ (eagle) + β_2 (hawk) + β_3 (vulture) + β_4 (JD _p)
6	Competition & day of the year _(quadratic)	$\beta_0 + \beta_1$ (eagle) + β_2 (hawk) + β_3 (vulture) + β_4 (JD) + β_5 (JD _q)
7	Competition	$\beta_0 + \beta_1$ (eagle) + β_2 (hawk) + β_3 (vulture)
8	Interactive effect of latitude & day of the	$\beta_0 + \beta_1 \text{ (Lat)} + \beta_2 \text{ (JD}_p) + \beta_3 \text{ (Lat} \times \text{JD}_p)$
9	year _(pseudothreshold) Interactive effect of latitude & day of the	$eta_0 + eta_1 \; (Lat) + eta_2 \; (JD) + eta_3 \; (JD_q) + eta_4 \; (Lat imes JD) + eta_5 \; (Lat imes JD_q)$
	year _(quadratic)	
10	(quadratic)	$\beta_0 + \beta_1 \ (Lat) + \beta_2 \ (Lat_q) + \beta_3 \ (JD) + \beta_4 \ (Lat \times JD) + \beta_5 \ (Lat_q \times JD)$
11	year	0 + 0 (I +) + 0 (ID) + 0 (I + + ID)
11	Interactive effect of latitude _(pseudothreshold) & day of the year	$\beta_0 + \beta_1 \text{ (Lat_p)} + \beta_2 \text{ (JD)} + \beta_3 \text{ (Lat_p} \times \text{JD)}$
12	Competition, interaction latitude & day of the	$\beta_0+\beta_1$ (eagle) $+$ β_2 (hawk) $+$ β_3 (vulture) $\beta_4(Lat)+\beta_5$ (JD _p) $+$ β_6 (Lat \times JD _p)
	year _(pseudothreshold)	
13	Competition, interaction: latitude & day of the	$\beta_0 + \beta_1$ (eagle) $+ \beta_2$ (hawk) $+ \beta_3$ (vulture) β_4 (Lat) $+ \beta_5$ (JD) $+ \beta_6$ (JD _q) $+ \beta_7$ (Lat × JD)
	$year_{(quadratic)}$	$+ \beta_8 (\text{Lat} \times \text{JD}_{\text{q}})$
14	Competition, interaction: latitude _(quadratic) & day of	$\beta_0 + \beta_1$ (eagle) $+ \beta_2$ (hawk) $+ \beta_3$ (vulture) β_4 (Lat) $+ \beta_5$ (Lat _q) $+ \beta_6$ (JD) $+ \beta_7$ (Lat \times JD)
	the year	$+ \beta_8 (\text{Lat}_{\text{q}} \times \text{JD})$
15	Competition, interaction: latitude _(pseudothreshold) & day of the year	$\beta_0 + \beta_1$ (eagle) + β_2 (hawk) + β_3 (vulture) $\beta_4(Lat_p) + \beta_5$ (JD) + β_6 (Lat _p × JD)

would be highest, leading to increased prevalence of raptors at bait sites. We posited that this would be true for both obligate scavengers (that forage more when temperatures are coldest) and seasonal and facultative scavengers (such as many Buteo species that face energetic constraints and also have more difficulty finding live prey). Therefore, we evaluated support for a quadratic effect of day of the year in our models (Table 1). At the northern or southern extremes of their winter distribution, prevalence could be dependent on whether sites were active during early or late winter; therefore, we evaluated support for a linear and pseudo-threshold effect of day of the year on prevalence. Finally, we also evaluated support for 6 models containing hypothesized interactive effects of day of the year and latitude on raptor prevalence (Table 1). Within the mixed model, we defined site as a random effect. We conducted all analyses using PROC GLIMMIX syntax in a SAS software environment (SAS/STAT software version 9.3, Cary, NC).

RESULTS

Our camera-trapping data revealed the presence of complex spatial and temporal patterns in the distribution and movement behavior of raptors. Three species (bald eagle, red-shouldered hawk, and rough-legged hawk) were encountered so infrequently that data were insufficient to fit the relatively complex interactive effect of latitude with the quadratic distributions of day of the year; therefore, we omitted fitting that specific model for these species. For models evaluated, we observed a relatively high amount of interspecific variability in what model best explained prevalence of a given raptor species (Table 2). However, for each species individually, we observed a relatively low

amount of model uncertainty (Table 2). As such, to evaluate support for our competing hypotheses regarding presence of other raptors, latitude, and day of the year on the prevalence of each raptor species, we focused on interpreting parameter coefficients from top-ranking models for each species.

Eagles

Golden eagle prevalence was higher in the central Appalachian region of West Virginia, Virginia, and Pennsylvania (Figs. 1 and 3). Outlying areas, including lower elevation sites in Maryland, West Virginia, Pennsylvania, Virginia, and New York, had relatively fewer golden eagle visits than did the higher elevation central Appalachian sites (Fig. 1). We found support for an interactive effect of latitude and date, where use was predicted to increase later into the winter, particularly at mid-latitudes (Fig. 3). Bald eagles were comparatively less prevalent (Fig. 3), primarily occurring in northern latitudes during late-winter months of February and March.

In contrast to our original predictions about competitive exclusion, bald and golden eagles were positively associated with each other (Table 3). The average probability of detecting a bald eagle at a site increased by 82% (β = 1.821, SE = 0.175) if a golden eagle was detected at that site on the same day, and golden eagles were, on average, 55% (β = 1.773, SE = 0.177) more likely to be observed at a site if a bald eagle was similarly detected that day. Thus, although the 2 species differed in their prevalence across our study area in both space and time, when they occurred in a common area they were likely to be observed at the same carrion-baited camera site on a given day. We observed that bald eagle prevalence was similarly positively associated with presence of vultures (β = 0.530, SE = 0.237), but a similarly strong positive correlation did not exist for golden eagles (β = -0.146, SE = 0.208).

Table 2. Ranking of a priori hypothesized models used to predict prevalence of 7 raptor species in eastern North America over the course of the winter months between 1 December 2011 and 15 April 2012. Support for each model in explaining prevalence by raptor species was based on Akaike's Information Criterion for small sample sizes (AIC_ε). Only most supported models (i.e., those within 4 ΔAIC_ε units) are reported. Raptor species we monitored included golden eagle (Aquila chrysaetos), bald eagle (Haliaeetus leucocephalus), red-tailed hawk (Buteo jamaicensis), red-shouldered hawk (B. lineatus), rough-legged hawk (B. lagopus), turkey vulture (Cathartes aura), and black vulture (Coragyps atratus).

Species	Model	AIC_c	ΔAIC_c	AIC _c wt
Golden eagle	Competition + latitude _(quadratic) \times day of the year	2,712.89	0.00	0.875
<u> </u>	Competition + latitude \times day of the year _(quadratic)	2,862.19	3.91	0.124
Bald eagle	Competition + latitude \times day of the year _(pseudo-threshold)	2,221.66	0.00	0.982
Turkey vulture	Competition + latitude _(quadratic) \times day of the year	1,833.29	0.00	0.930
Black vulture	Competition + latitude _(quadratic) \times day of the year	749.38	0.00	0.355
	Competition + latitude × day of the year _(pseudo-threshold)	749.93	0.55	0.269
	Competition + latitude _(pseudo-threshold) × day of the year	750.09	0.71	0.249
Red-tailed hawk	Competition + day of the year _(quadratic)	4,204.64	0.00	1.000
Red-shouldered hawk	Competition + day of the year	471.55	0.00	0.774
	Competition + latitude _(pseudo-threshold) \times day of the year	475.38	3.83	0.114
Rough-legged hawk	Competition + latitude	340.10	0.00	0.743

Vultures

Both turkey and black vultures exhibited distinct seasonal and latitudinal trends in prevalence at carrion-baited sites. Turkey vultures were largely absent from carrion-baited sites during December and January (Fig. 3). By February, turkey vulture prevalence began to increase across our study area, particularly at northern latitudes where our models predicted them to be present at nearly all sites by late March (Fig. 3). Black vultures were less frequently encountered, and most prevalent only at the mid- and lower-latitude sites. At these sites, black vulture

predicted prevalence varied seasonally, with a distinct peak at the start of camera trapping in early December and again in late March. These patterns are likely indicative of our cameras capturing the phenology of movement away from and back toward summer use areas as vultures migrate at the start and end of camera-trapping seasons (Fig. 3).

Prevalence of both vulture species was positively correlated with all other raptor species (Table 3), suggesting limited competitive exclusion and possibly conspecific attraction at carcass sites. Comparatively uncommon, black vultures were

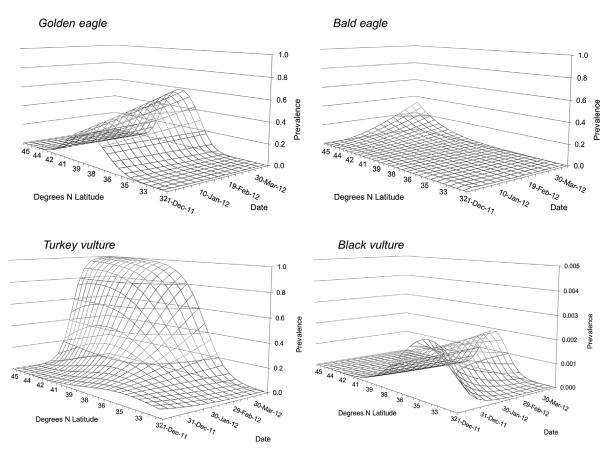


Figure 3. Predicted prevalence (as a function of the interaction between date and °N latitude) during winter of 2011–2012 for golden eagle (*Aquila chrysaetos*), bald eagle (*Haliaeetus leucocephalus*), turkey vulture (*Cathartes aura*), and black vulture (*Coragyps atratus*) at citizen science baited camera-trap sites in eastern North America. Parameter coefficients were determined based on best approximating model for each species (see Table 3). Note that black vulture prevalence is plotted on a different scale, indicative of its infrequent detection during our study.

12% (β = 2.005, SE = 0.251) more likely to occur at a site if turkey vultures were also detected at that site on a given day. However, spatio-temporal patterns in prevalence suggest that behavioral differences between species (see above) likely were occurring at larger spatial and temporal scales (Fig. 3).

Hawks

The 3 hawk species we encountered exhibited vastly different prevalence patterns that varied as a function of location or time of year surveyed. Red-tailed hawks, detected on 51% of days that sites were operating, were one of the most prevalent raptors encountered. Red-tailed hawk prevalence at camera sites reached a peak in the middle of our winter sampling period, before declining precipitously in the late winter months of March and April (Fig. 4). Conversely, roughlegged hawk prevalence varied primarily by location, where with the exception of northern latitudes, they remained at low prevalence levels throughout the season (Fig. 4). Red-shouldered hawks were only detected on 8% of days that sites were operating, with highest probability of detection during the early winter (Fig. 4).

Each hawk species was more likely to be detected at a site if another congener species was also present on that day (Table 3). At our daily scale of investigation, we observed limited support for our size-dominance hypothesis, because red-tailed hawks on average only exhibited a 1% decline

 $(\beta=-0.145, SE=0.117)$ in prevalence if an eagle was detected at a site on a day when either eagle species was also present (Table 3). Conversely, red-shouldered hawks were 77% ($\beta=1.489$, SE=0.438) more likely to be detected at a site if eagles also were detected at the site that day. Predicted prevalence of red-tailed hawks was expected to increase by 30% ($\beta=0.613$, SE=0.149) when either vulture species was detected at a site on the same day. We observed similar conflicting influences of eagle ($\beta=-0.068$, SE=0.545) and vulture ($\beta=-3.534$, SE=7.889) presence on rough-legged hawk prevalence (Table 3), but standard error values overlapping 0 limit our confidence in these estimates.

DISCUSSION

This analysis shows that the Appalachian Eagle Monitoring Program has the potential to provide a long-term, cost-effective, range-wide monitoring tool for raptor populations. The spatial and temporal patterns in raptor movement that we observed are consistent with historical accounts of winter range use and extent (Robbins et al. 2001, Katzner et al. 2012). However, those accounts are largely based on individual movements or single-point data; our camera-trapping data provide important regional insight into the intensity and distribution of raptor use of carrion. In this sense, AEMP builds on the long history of migratory count

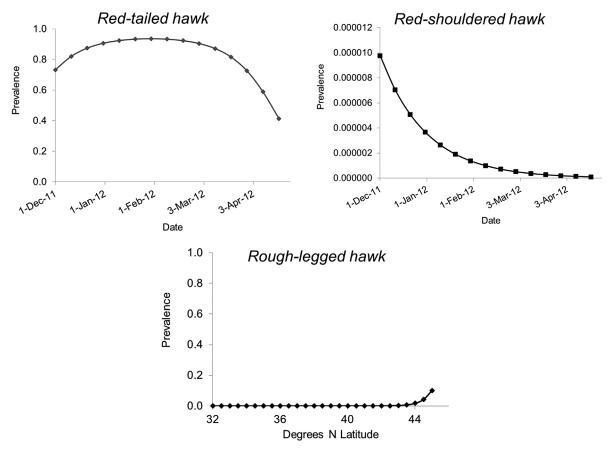


Figure 4. Predicted prevalence (as a function of date or °N latitude) during winter of 2011–2012 for red-tailed hawk (*Buteo jamaicensis*), rough-legged hawk (*Buteo lagopus*), and red-shouldered hawk (*Buteo lineatus*) at citizen-science baited camera-trap sites in eastern North America. Parameter coefficients were determined based on best approximating model for each species (see Table 3). Note that red-shouldered hawk prevalence is plotted on a different scale, indicative of its infrequent detection during our study.

Table 3. Parameter coefficient (with SE) from top approximating model for 7 species of raptor encountered at baited camera-trap sites in eastern North America between 1 December 2011 and 15 April 2012. Raptor species monitored included golden eagle (*Aquila chrysaetos*), bald eagle (*Haliaeetus leucocephalus*), red-tailed hawk (*Buteo jamaicensis*), red-shouldered hawk (*B. lineatus*), rough-legged hawk (*B. lagopus*), turkey vulture (*Cathartes aura*), and black vulture (*Coragyps atratus*).

	Golden	eagle	Bald e	eagle	Turl vulti	•	Black v	ulture	Red-t		Red-show		Rough-	00
Variable	Coeff.	SE	Coeff.	SE	Coeff.	SE	Coeff.	SE	Coeff.	SE	Coeff.	SE	Coeff.	SE
Intercept	-1.295	0.384	-7.902	1.020	-3.932	0.285	-8.790	1.239	1.009	0.359	-11.536	1.306	-12.406	2.905
Latitude	-0.598	0.133	-0.703	0.344	-0.616	0.111	-0.919	0.389					1.858	0.776
$Latitude_{(pseudo-threshold)}$														
Latitude _(quadratic)	-0.204	0.036			-0.057	0.021	-0.076	0.066						
Date	0.009	0.003			0.051	0.002	-0.013	0.009	0.056	0.009	-0.033	0.010		
Date _(pseudo-threshold)			0.926	0.234										
Date _(quadratic)									-0.001	0.000				
Latitude ´ Date	-0.001	0.001			0.010	0.003	-0.012	0.009						
Latitude(quadratic) \(^{\text{Date}}\)	-0.001	0.000			0.000	0.000	-0.002	0.001						
Latitude			0.239	0.081										
$Date_{(pseudo-threshold)}$														
Golden eagle			1.821	0.175										
Bald eagle	1.773	0.177												
Eagle					0.014	0.188	0.855	0.374	-0.145	0.117	1.489	0.438	-0.068	0.545
Turkey vulture							2.005	0.251						
Black vulture					2.169	0.243								
Vulture	-0.146	0.208	0.530	0.237					0.613	0.149	0.159	0.452	-3.534	7.889
Red-tailed hawk											0.353	0.390	0.737	0.382
Red-shouldered hawk									0.324	0.368			5.267	2.418
Rough-legged hawk									0.737	0.383	3.848	1.871		
Hawk	0.073	0.086	0.130	0.132	0.486	0.155	0.905	0.275						

data from observation points (e.g., Therrien et al. 2012) to monitor raptor migration phenology by using a spatially explicit, volunteer-driven and repeatable approach to quantifying raptor activity.

In addition to providing spatially explicit metrics of prevalence, AEMP provides time series data on movement and behavioral phenology of the various raptors, information that is potentially important for management across their winter range. For example, the 2 vulture species we monitored were rarely encountered during midwinter months of January and February, but prevalent in March and April. This was likely due to cold-sensitive vulture species moving from the central and northern Appalachian region to the southeastern United States and areas farther south toward the equator during these coldest winter months (Mandel et al. 2008). Thus, such spatio-temporal patterns in vulture prevalence and the prevalence of other raptor species could be directly related to climatic conditions. Accordingly, these camera-trap data can be used to evaluate long-term patterns in migration phenology and residence time that are likely to shift in response to global change (Jaffré et al. 2013).

Although not expressly developed to provide insight into behavioral interactions among raptors, AEMP has the clear potential to investigate the roles of competition and conspecific attraction to carrion sources. Considerable scientific evidence suggests that there is a size-based dominance hierarchy among avian scavengers at a carcass (Kruuk 1967, Anderson and Horwitz 1979, Wallace and Temple 1987), and particularly strong effects by eagle species on other raptors during winter have been documented in the northern hemisphere (Halley and Gjershaug 1998, Blázquez et al. 2009). Our failure to observe similar trends is likely to

be due to our tallying of presence or absence at a site on a daily scale in the current examination, thereby missing finer scale (within-day) temporal separation in carcass use by raptors. However, the 3 hawk species, which are sometimes prey for eagles (Fig. 2), were rarely detected at any particular site in the same image as bald or golden eagles. Additionally, because of the importance of wind and thermal features on raptor movement (Mandel et al. 2008, Bohrer et al. 2012), movement on a given day when thermal features were optimal could have facilitated carcass detection for all species simultaneously and thus increased interspecific interactions. Further research is warranted to examine the finer scale spatial and temporal relationships between wind patterns and interspecific interactions that could be occurring at these sites.

Further research also is needed to evaluate the effect that shifts in feeding ecology could have on prevalence of different raptor species across the region over time. Multiple raptor species we monitored were facultative scavengers, likely switching their diet opportunistically to take advantage of available food items, thus influencing their use of carrionbaited sites. For example, the quadratic effect of time observed in red-tail hawk visitation of carrion-baited camera traps could be indicative of migratory movements, or simply the switching of feeding behaviors by resident birds from being predators in autumn to primarily facultative scavengers midwinter and back to predators in spring as a result of shifts in small mammal availability (Preston 1990). Understanding the interacting effects of migration and shifting feeding ecology is critical to interpreting patterns of prevalence at camera sites and in linking those patterns to animal ecology and management opportunity.

Potential Future Applications

In addition to gaining insights into raptor spatial and community ecology, this type of long-term and spatially explicit monitoring can provide data to better assess the impact of forest succession, changing land use, and energy development on migratory raptors. Recent findings on the fine-scale movement behaviors and migratory corridors revealed through GPS tracking technology (Katzner et al. 2012, Miller et al. 2014) could be integrated with long-term AEMP monitoring of marked and unmarked raptors to gain spatially explicit estimates of increases or decreases in activity over time. Although potentially influenced by "luring" of raptors to carcasses, these types of data can then be used to guide future fine-scale research and management action to identify threats and aid in the conservation of raptor and other avian scavenger populations. For example, if camera traps had been deployed during the initial West Nile Virus outbreaks in eastern North America (Marra et al. 2004), AEMP could have been used to monitor population fluctuations in corvids and other strongly impacted species.

Many nonavian scavenger species are detected at cameratrap stations, making the AEMP data of value in monitoring landscape-level trends for species other than raptors and in investigating scavenger community ecology. Camera traps placed on carcasses provide time-referenced photographs, allowing for investigation of arrival, activity patterns and competitive interactions among carnivore species at the carcass (Pereira et al. 2014). Thus, it is possible to investigate interactions between primarily diurnal avian and primarily crepuscular and nocturnal mammalian scavengers. Further, such an extensive and wide-ranging network of baited stations can be used to detect the presence of carnivore species in areas where they were thought to be rare or absent. For example, AEMP has provided valuable new information on distribution of eastern spotted skunk (Spilogale putorius), a species that is generally believed to have undergone severe population reductions over the past decades (Gompper and Hackett 2005); this suggests that within certain habitat types in the Appalachians it remains relatively abundant (D S. Jachowski, unpublished data).

Finally, and perhaps most importantly, by virtue of primarily relying on citizen scientists, AEMP helps garner public interest in raptor conservation. A dramatic rise in voluntary participation over time illustrates willingness of the public to undertake an intensive project of collecting roadkilled white-tailed deer, placing cameras and bait in relatively remote areas, maintaining bait sites, and sending data to a central location. Such dedication not only solidifies interest in raptor and scavenger ecology in particular and conservation in general, but provides a network for the exchange of observations and findings among interested participants. This form of "middle-out conservation" (Shoreman-Ouimet 2011) disseminates information through interested citizen scientists who have social influence in local affairs at locations throughout the Appalachian region. Collectively, we believe AEMP represents a novel approach to both monitoring and garnering support for raptor conservation that could benefit conservation programs in other regions throughout the world.

Limitations and Practical Considerations for Wildlife Management

Although the existing AEMP provides a large and rich data set for managers and ecologists, the potential for AEMP could be maximized through future concerted, strategic planning (Hochachka et al. 2012). One of the key benefits of AEMP is that through the use of camera traps and a standardized protocol, observer bias associated with many voluntary and citizen science projects is minimized (Sauer et al. 1994, Dickinson et al. 2010). However, we encourage future evaluations of how closely volunteers follow protocol and potential biases (e.g., differences in sensitivity or reliability between camera brands). In addition, in large part because of the program's voluntary nature, a number of sampling issues arise that currently preclude more advanced, detailed statistical analyses. First, the timing and duration of site operation varies by individual volunteers, limiting our ability to analyze temporal patterns in raptor migration phenology based on a uniform distribution in the timing and location of active sites. The establishment of additional sites that are monitored for extended periods of time could enhance long-term monitoring of trends in raptor populations and migratory behavior.

Second, the spacing of camera sites for such highly mobile species is of critical importance. Ideally, sites would meet closure assumptions needed for occupancy analyses (e.g., O'Connell and Bailey 2011), but the spacing and extent of existing sites constrains our ability to use some advanced presence-absence based metrics. Future growth of the program across eastern North American combined with subsampling or novel analytical approaches could dramatically improve the inferences gained from such monitoring data. For example, the use of a more highly structured and spatially balanced sampling design (such as a Generalized Random-Tessellation Stratified Design [Stevens and Olsen 2004]) similar to that proposed for the North American Bat Monitoring Program could be used to inform optimal placement and operation of cameras (i.e., effort) across the study region. In addition, strategic site placement in portions of the Appalachians expected to be impacted by development, such as wind energy or mineral extraction, could allow for valuable before-after-control-impact study designs to address critical conservation issues.

Third, to date, most sites have been placed in forest clearings at higher elevations (>615 m), to optimize recording of our original target species, golden eagles. This approach also provides useful information on species with similar habitat preferences (e.g., ravens, *Corvus corax*). However, detection of other species could be optimized by sampling additional habitat types across a wider elevation gradient. For example, the overall lower rates of detection for bald eagles compared with golden eagles was likely due to our selection of small openings on high-elevation ridges where golden eagles were more likely to use bait stations. As such, modifying protocols to include bait stations in larger openings at lower elevations and along major watercourses might improve this as a tool to monitor bald eagles. Similarly, detection of several hawk species might have been

biased low based on location of camera sites. For example, certain species might be more prone to avoiding roads (a key aspect of current site placement). Finally, although a single individual (JLR) has to date stored, organized, and analyzed all 2.5 million images used for this study, these tasks are not sustainable if the network continues to expand. Once images are collected from volunteers, the most time-consuming component is the identification and tallying of species within images. Clearly, this process would benefit from the inclusion of automated pattern recognition software systems similar to those used to identify individual animals within photographs based on morphometric and marking patterns (Swinnen et al. 2014). An alternative approach is to place the photos on a central web portal and involve citizen scientists in the identification of species in individual photos (http:// www.snapshotserengeti.org/). Regardless of the techniques employed for photo data processing, an automated computer network database is needed, similar to what is being developed for the *eMammal* citizen-science camera-trap program (R. Kays, North Carolina State University, personal communication) to help organize and store the millions of images along with their associated meta-data.

MANAGEMENT IMPLICATIONS

Camera-trap networks offer a new opportunity to enhance monitoring of species that are difficult to monitor at local and landscape scales. The rapidly growing Appalachian Eagle Monitoring Program has already delivered new information on distribution and phenology of migratory raptors that are not well-sampled with other techniques. The program also has the potential to provide a long-term, cost-effective monitoring network for determining impacts of land-use change such as energy development. By using a standardized carcass-baited protocol, AEMP provides unprecedented insights into the community ecology of raptors and other avian and mammalian scavengers at a broad landscape scale. Further expansion of volunteer participation, particularly in the northern and southern portions of the region, will improve the utility of AEMP. In particular, prioritizing camera-site placement both spatially and temporally across the landscape could facilitate more robust statistical analyses based on presence-absence that will be vital to understanding long-term patterns in raptor migratory behavior. Finally, by virtue of involving citizen scientists, AEMP has the potential to improve long-term support for raptor conservation and serve as a model for raptor conservation programs in other portions of the world.

ACKNOWLEDGMENTS

We thank the hundreds of volunteers who helped carry out this project and continue to carry it forward into the future. A group of >250 volunteers and agency personnel contributed to data collection for this project. They are acknowledged in the Appalachian Eagles Annual Report, available from TEK. In addition, T. Miller, K. O'Malley, K. Heyden, S. Somershoe, C. Todd, C. Martin, T. Salo, C. Kelly, D. Cuthrell, D. Brinker, E. Soehren, and S. Allen assisted with coordination of the camera-trapping effort. Financial

support was provided by the West Virginia University Division of Forestry and the U.S. Department of Agriculture Forest Service Northern Research Station. Finally, we thank C. Jachowski for advice on quantitative analysis. The use of any trade, product, or firm names in this manuscript does not imply endorsement by the U.S. government. We thank R. Jachowski, the Associate Editor, and two anonymous reviewers for their constructive comments on earlier drafts of this manuscript.

LITERATURE CITED

- Altizer, S., R. Bartel, and B. A. Han. 2011. Animal migration and infectious disease risk. Science 331:296–302.
- Anderson, D. J., and R. T. Horwitz. 1979. Competitive interactions among vultures and other avian competitors. Ibis 121:505–509.
- Bednarz, J. C., D. Klem, L. J. Goodrich, and S. E. Senner. 1990. Migration counts of raptors at Hawk Mountain, Pennsylvania, as indicators of population trends, 1934–1986. The Auk 107:96–109.
- Bildstein, K. L. 2006. Migrating raptors of the world: their ecology and conservation. Cornell University Press, Ithaca, New York, USA.
- Blázquez, M., J. A. Sánchez-Zapata, F. Botella, M. Carrete, and S. Eguía. 2009. Spatio-temporal segregation of facultative avian scavengers at ungulate carcasses. Acta Oecologica 35:645–650.
- Bohrer, G., D. Brandes, J. T. Mandel, K. L. Bildstein, T. A. Miller, M. Lanzone, T. Katzner, C. Maisonneuve, and J. A. Tremblay. 2012. Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. Ecology Letters 15:96–103.
- Butcher, G. S., M. R. Fuller, L. S. McAllister, and P. H. Geissler. 1990. An evaluation of the Christmas Bird Count for monitoring population trends of selected species. Wildlife Society Bulletin 18:129–134.
- Cooke, S. J., S. G. Hinch, M. R. Donaldson, T. D. Clark, E. J. Eliason, G. T. Crossin, G. D. Raby, K. M. Jeffries, M. Lapointe, K. Miller, D. A. Patterson, and A. P. Farrell. 2012. Conservation physiology in practice: how physiological knowledge has improved our ability to sustainably manage Pacific salmon during up-river migration. Philosophical Transactions of the Royal Society B: Biological Sciences 367:1757–1769.
- De Lucas, M., G. F. Janss, D. P. Whitfield, and M. Ferrer. 2008. Collision fatality of raptors in wind farms does not depend on raptor abundance. Journal of Applied Ecology 45:1695–1703.
- Dickinson, J. L., B. Zuckerberg, and D. N. Bonter. 2010. Citizen science as an ecological research tool: challenges and benefits. Annual Review of Ecology, Evolution, and Systematics 41:149–172.
- Gompper, M. E., and H. M. Hackett. 2005. The long-term, range-wide decline of a once common carnivore: the eastern spotted skunk (*Spilogale putorius*). Animal Conservation 8:195–201.
- Halley, D. J., and J. O. Gjershaug. 1998. Inter-and intra-specific dominance relationships and feeding behaviour of golden eagles *Aquila chrysaetos* and sea eagles *Haliatetus albicilla* at carcasses. Ibis 140:295–301.
- Hochachka, W. M., D. Fink, R. A. Hutchinson, D. Sheldon, W. K. Wong, and S. Kelling. 2012. Data-intensive science applied to broad-scale citizen science. Trends in Ecology and Evolution 27:130–137.
- Jaffré, M., G. Beaugrand, E. Goberville, F. Jiguet, N. Kjellén, G. Troost, P. J. Dubois, A. Lepêtre, and C. Luczak. 2013. Long-term phenological shifts in raptor migration and climate. PloS ONE 8: e79112.
- Janss, G. F. E. 2000. Avian mortality from power lines: a morphologic approach of a species-specific mortality. Biological Conservation 95:353–359.
- Katzner, T., B. W. Smith, T. A. Miller, D. Brandes, J. Cooper, M. Lanzone,
 D. Brauning, C. Farmer, S. Harding, D. E. Kramar, C. Koppie, C.
 Maisonneuve, M. Martell, E. K. Mojica, C. Todd, J. A. Tremblay, M.
 Wheeler, D. F. Brinker, T. E. Chubbs, R. Gubler, K. O'Malley, S. Mehus,
 B. Porter, R. P. Brooks, B. D. Watts, and K. L. Bildstein. 2012. Status,
 biology, and conservation priorities for North America's eastern golden
 eagle (Aquila chrysaetos) population. The Auk 129:168–176.
- Kerlinger, P. 1989. Flight strategies of migrating hawks. University of Chicago Press, Chicago, Illinois, USA.
- Klaassen, R. H. G., M. Hake, R. Strandberg, B. J. Koks, C. Trierweiler, K-M. Exo, F. Bairlein, and T. Alerstam. 2014. When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. Journal of Animal Ecology 83:176–184.

- Kochert, M. N., and K. Steenhof. 2002. Golden eagles in the US and Canada: status, trends, and conservation challenges. Journal of Raptor Research 36:32–40.
- Kruuk, H. 1967. Competition for food between vultures in East Africa. Ardea 55:171–193.
- Kucera, T. E., and R. H. Barrett. 2011. A history of camera trapping. Pages 9–26 in A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. Camera traps in animal ecology. Springer, Tokyo, Japan.
- Kunz, T. H., E. B. Arnett, B. M. Cooper, W. P. Erickson, R. P. Larkin, T. Mabee, M. L. Morrison, M. Strickland, and J. M. Szewczak. 2007. Assessing impacts of wind-energy development on nocturnally active birds and bats: a guidance document. Journal of Wildlife Management 71:2449–2486.
- Mandel, J. T., K. L. Bildstein, G. Bohrer, and D. W. Winkler. 2008. Movement ecology of migration in turkey vultures. Proceedings of the National Academy of Sciences 105:19102–19107.
- Marra, P. P., S. Griffing, C. Caffrey, M. A. Kilpatrick, R. McLean, C. Brand, E. Saito, A. P. Dupuis, L. Kramer, and R. Novak. 2004. West Nile virus and wildlife. BioScience 54:393–402.
- Miller, T. A., R. P. Brooks, M. Lanzone, D. Brandes, J. Cooper, K. O'Malley, C. Maisonneuve, J. Tremblay, A. Duerr, and T. Katzner. 2014. Assessing risk to birds from industrial wind energy development via paired resource selection models. Conservation Biology 28:745–755.
- Milner-Gulland, E. J., J. M. Fryxell, and A. R. E. Sinclair. 2011. Animal migration: a synthesis. Oxford University Press, Oxford, England, United Kingdom.
- Newton, I. 2008. The migration ecology of birds. First edition. Academic Press, Burlington, Massachusetts, USA.
- O'Connell, A. F., and L. L. Bailey. 2011. Inference for occupancy and occupancy dynamics. Pages 191–204 in A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. Camera traps in animal ecology. Springer, Tokyo, Japan.
- Pereira, L. M., N. Owen-Smith, and M. Moleón. 2014. Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. Mammal Review 44:44–55.
- Preston, C. R. 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure. Condor 97:107–112.

- Robbins, C. S., B. Bruun, H. S. Zim, and A. Singer. 2001. Birds of North America: a guide to field identification. Golden Guides from Saint Martin's Press, New York, New York, USA.
- Sauer, J. R., B. G. Peterjohn, and W. A. Link. 1994. Observer differences in the North American breeding bird survey. The Auk 111:50–62.
- Schuter, J. L., A. C. Broderick, D. J. Agnew, N. Jonzén, B. J. Godley, E. J. Milner-Gulland, and S. Thirgood. 2011. Conservation and management of migratory species. Pages 172–206 in E. J. Milner-Gulland, J. M. Fryxell, and A. R. E. Sinclair, editors. Animal migration: a synthesis. Oxford University Press, Oxford, England, United Kingdom.
- Shoreman-Ouimet, E. 2011. Middle-out conservation. Pages 234–256 in H. Kopnina and E. Shoreman-Ouimet, editors. Environmental anthropology today. Routledge, New York, New York, USA.
- Smith, N. G., D. L. Goldstein, and G. A. Bartholomew. 1986. Is long-distance migration possible for soaring hawks using only stored fat? The Auk 103:607–611.
- Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association 99:262–278.
- Swinnen, K. R. R., J. Reijniers, M. Breno, and H. Leirs. 2014. A novel method to reduce time investment when processing videos from camera trap studies. PLoS ONE 9: e98881.
- Tape, K. D., and D. D. Gustine. 2014. Capturing migration phenology of terrestrial wildlife using camera traps. BioScience 64:117–124.
- Therrien, J. F., L. J. Goodrich, D. R. Barber, and K. L. Bildstein. 2012. A long-term database on raptor migration at Hawk Mountain Sanctuary, northeastern United States: ecological archives E093-174. Ecology 93:1979.
- Thompson, J. R., D. N. Carpenter, C. V. Cogbill, and D. R. Foster. 2013.

 Four centuries of change in Northeastern United States forests. PLoS ONE 8: e72540
- Wallace, M. P., and S. A. Temple. 1987. Competitive interactions within and between species in a guild of avian scavengers. The Auk 104:290–295.

Associate Editor: Boal.