



Integrating citizen-science data with movement models to estimate the size of a migratory golden eagle population



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ABSTRACT

Estimating population size is fundamental to conservation and management. Population size is typically estimated using survey data, computer models, or both. Some of the most extensive and often least expensive survey data are those collected by citizen-scientists. A challenge to citizen-scientists is that the vagility of many organisms can complicate data collection. As a result, animal-movement effects on data collection can adversely affect modeling of those data. Thus, it would be helpful to develop methods that integrate citizen-science datasets with models that account for animal movement. We used hawk-count data collected by citizen-scientists to estimate the number of golden eagles (*Aquila chrysaetos canadensis*) migrating through Pennsylvania, USA. To do this, we designed a computer model to simulate migratory flights of eagles to estimate what proportion of the population is *available* (i.e., within visible range or close enough) to be counted at hawk-count sites in Pennsylvania. We then conducted a multi-state mark-recapture analysis to estimate *detection probability* (i.e., the rate at which birds within visible range are observed) of migrating eagles. Finally, we used availability rates and detection probabilities to adjust raw hawk-count data to produce estimates of population size. Our models suggest that 24% (± 14 ; mean $\pm$ SE) of migrating golden eagles are available to be counted at hawk-count sites, and that 55% (± 1.6) of the available eagles are detected by hawk-count observers. We estimate that 5122 (± 1338) golden eagles migrate annually through Pennsylvania. Our analysis provides the first quantitative estimate of the size of the eastern golden eagle population, and we demonstrate the utility of one approach to use citizen-science data to address a pressing conservation goal—population size estimation.

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1. Introduction

Estimating the size of wildlife populations is fundamental to conservation and management. However, estimating population size is rarely straightforward. For example, the vagility of many organisms can influence population-level monitoring, affecting survey methods and demographic estimates (Katzner et al., 2007; Yoccoz et al., 2001). Measurement of demographic parameters is also difficult and sometimes inefficient when animals are broadly distributed (Lewis and Gould, 2000; Link and Nichols, 1994). For instance, secretive and low-density raptors are hard to study in that monitoring of their populations can be both expensive and logistically demanding (Dunn and Hussell, 1995; Zalles and

Bildstein, 2000). However, such monitoring is often critical because raptors are apex predators indicative of the health of ecosystems (Sergio et al., 2006).

Monitoring programs are most effective and likely to be long-lasting when they are low-cost and simultaneously gather large amounts of reliable information on populations (Good et al., 2007; Kéry, 2008). There are many examples of enduring and relatively inexpensive monitoring programs that use citizen-science volunteers to collect data (Braschler, 2009; Cohn, 2008; Devictor et al., 2010; Katzner et al., 2005; Mulder et al., 2010; Silvertown, 2009). These include the Breeding Bird Surveys (BBS) and Christmas Bird Counts (CBC), which occur across North America and which gather massive amounts of information, especially about passerines, at relatively low-cost yet also without accounting for detection probabilities (Dunn et al., 2005; Thogmartin et al., 2006). Nevertheless, owing to their small population sizes and low detection probabilities, in general, most raptors are poorly monitored by BBSs and CBCs (Bildstein, 2006; Zalles and Bildstein, 2000).

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Numerous raptors migrate, and counts during migration are useful to monitor raptor species of conservation concern (Ainslie et al., 2014; Bildstein, 1998; Farmer et al., 2010; Sattler and Bart, 1984). Worldwide, hawk-count data are collected at sites where geography concentrates migrant raptors in large numbers (Zalles and Bildstein, 2000). In North America, these data are collected, stored digitally in the HawkCount database (www.hawkcoun.org), and made available by the Hawk Migration Association of North America (HMANA; [Hawk Migration Association of North America](http://www.hawkmigration.org), 2014). Because volunteers staff most sites, collection costs of hawk-count data are typically minimal to the monitoring organizations and scientific community at large.

Hawk-count data are inherently variable, and some sources of variation among hawk-count sites include: (a) poor standardization of counting coverage; (b) different local landscape traits and their impacts on detection; (c) variable numbers of observers; (d) disparity among observers' proficiencies; (e) weather effects on detection; and (f) temporal sampling variation (Bildstein et al., 2008a; Dunn and Hussell, 1995; Dunn et al., 2008; Heath and Nolte, 2009; Lewis and Gould, 2000; Margalida et al., 2011). In spite of this variability, a great deal of effort has gone into analyzing population trajectories over time (Bednarsz et al., 1990; Broun, 1935; Hoffman and Smith, 2003; Farmer and Smith, 2010; Farmer et al., 2008a, 2008b; Hull et al., 2010; Nagy, 1977). However, fewer studies have attempted to assess observer ability to detect migrating raptors (Allen et al., 1996; Berthiaume et al., 2009; Farmer et al., 2007, 2010; Heath and Nolte, 2009; Nolte, 2012). Hawk-count observers sample all visible migrants using a systematic approach, and detecting a migrant includes two components. Birds that are *available* to be counted represent the proportion of the population within visible range (or close enough to be observed) at hawk-count sites. *Detection probability* is the rate at which those birds within the visible range are actually observed (counted) at hawk-count sites.

Golden eagles (*Aquila chrysaetos canadensis*) are rare in eastern North America and little is known about their demography, movements, or behavior (Katzner et al., 2012; Kochert and Steenhof, 2002). The species breeds throughout northeastern Canada, and it is thought that the majority of the population migrates through the central Appalachian Mountains to overwinter in the eastern United States (Brodeur et al., 1996; Katzner et al., 2012; Millsap and Vana, 1984). In western North America, migratory populations may be in decline (Hoffman and Smith, 2003; Smith et al., 2008), whereas resident populations are stable (Millsap et al., 2013). In contrast, the eastern population likely increased through the late 20th century (Farmer et al., 2008a). Estimates of the size of the eastern population ranges between 1000 and 5000 individuals (Katzner et al., 2012; Ombalski and Brandes, 2010), less than a quarter of the number of golden eagles in western North America—i.e., 19,000–35,000 (Good et al., 2007; Millsap et al., 2013; Nielson et al., 2011). Eastern golden eagles are counted in the hundreds at hawk-count sites in the central Appalachians. We integrated these citizen-science data with modeling efforts to better understand their demography. Our process involved three steps. First, we estimated the proportion of golden eagles that migrate near hawk-count sites and that are available to be counted by observers. We modeled southbound autumn migration of golden eagles to estimate this parameter. Second, we estimated what proportion of available golden eagles is detected at hawk-count sites. We used a mark–recapture analysis to estimate this second parameter. Third, we combined parameters of eagle availability and detection with historic hawk-count data to estimate population size for eastern golden eagles. Finally, we compared past to present estimates of population size in the context of golden eagle conservation in eastern North America.

2. Materials and methods

2.1. Study area

We focused our research on an area of the central Appalachian Mountains roughly outlined by the state of Pennsylvania, USA (Fig. 1a). We chose to focus our research in Pennsylvania because eastern golden eagles move through this area in autumn in large numbers, and because it extends from the Great Lakes to the Atlantic Ocean, a large portion of eastern migrants must cross the state during their travels. Topography in Pennsylvania includes many long-linear ridges, lowland valleys, forested highlands, and mountain foothills (United States Forest Service, 2007). Local autumn weather is temperate, overcast, and characterized by westerly winds that interact with the steep topography of the ridge and valley regions to generate uplift (Miller et al., 2014). Of 32 established hawk-count sites, approximately 12 are active and regularly staffed in Pennsylvania, although others once operated intermittently. Peak migration of golden eagles through Pennsylvania occurs in November (Katzner et al., 2012).

2.2. Hawk-count data

HMANA volunteers and others collect, organize, and post hawk-count data from sites across North America ([Hawk Migration Association of North America](http://www.hawkmigration.org), 2014). Hawk-count data are the property of the individual monitoring sites while the HMANA web site acts as a data storage repository. At a subset of sites, hawk-count observers collect but do not post additional data on age and timing of movements of individual eagles. With permission of the individual sites, we downloaded posted data from Novembers 2002–2011 from 32 hawk-count sites and we requested detailed unposted data, when available.

2.3. Modeling golden eagle migration

To understand what proportion of migrant eagles are available to be counted at hawk-count sites (i.e., our first objective), we designed a computer model (migration model; implemented in Visual C# 4.0; Microsoft Corporation, 2010), to simulate migratory movements of golden eagles in the central Appalachian Mountains. The model was necessary because (a) hawk-count sites do not randomly sample the migrant eagle population (if they did, then we would only need detection rates to estimate population size) and (b) because telemetry data (Miller et al., 2014) are too sparse to use to estimate this parameter. We briefly describe the migration model here. Its decision steps are described in greater detail elsewhere (Dennhardt et al., *in press*).

Each simulated flight route begins at a randomly selected starting position on the north–northeastern Pennsylvania border between the easternmost and westernmost routes used by telemetered eagles (Miller, 2012). The migration model estimates uplift in five grid-cells (i.e., east, west, southeast, southwest, and south; 90-m resolution) surrounding each eagle's position based on weather conditions from a random sample of 33 November days between 2002 and 2011 from the North American Regional Reanalysis dataset (Mesinger et al., 2006). Movement of the simulated eagle into one of the five grid cells is based on a directed random walk determined in part by relative strength of uplift in those cells. This process is repeated until the simulated eagle reaches the southernmost border of the modeling region to complete its migration.

The following rules govern movements in this migration model:

1. Eagle movement decisions are based only on the interaction of topography and weather (i.e., uplift).

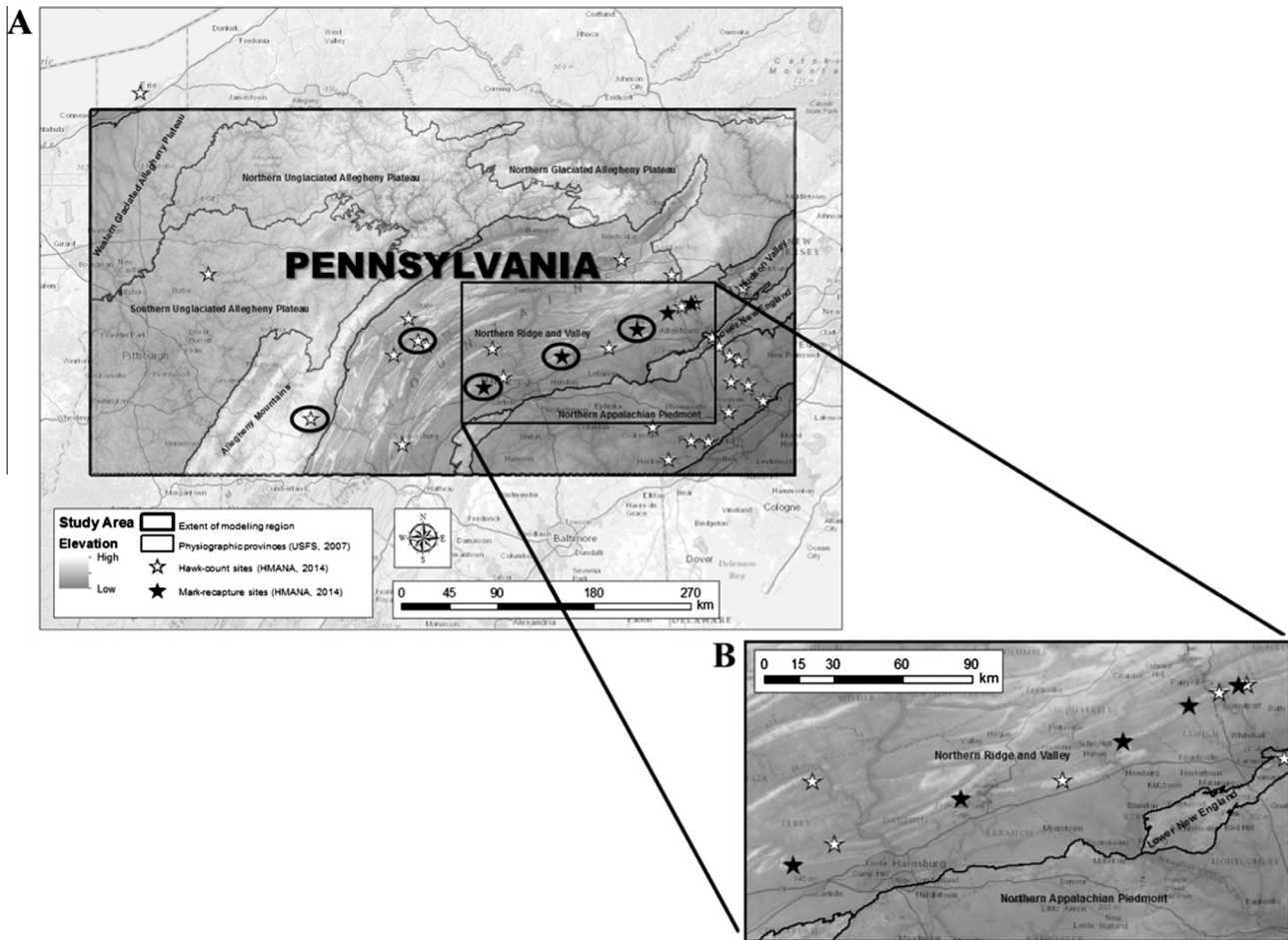


Fig. 1. (a) Simulation modeling area: the central Appalachian Mountain range in Pennsylvania, USA. (b) Mark-recapture modeling area: the Kittatinny Ridge. Mark-recapture sites (black stars), from northeast to southwest, are: Little Gap, Bake Oven Knob, Hawk Mountain Sanctuary, Second Mountain, and Waggoner's Gap. Local populations that are summed to obtain a regional population estimate (black ellipses) are (from east to west): Hawk Mountain Sanctuary, Second Mountain, Waggoner's Gap, Stone Mountain, and Allegheny Front.

2. Eagles accurately perceive strength of uplift in cells that they have not yet visited.
3. Eagles use only slope-soaring and thermal-soaring and gliding while on migration.
4. Eagles do not stop to forage or roost (i.e., flights are continuous and uninterrupted) and migrate across the study area within a 24-h time period.
5. Weather conditions (e.g., wind speed, wind direction, thermal activity) change after each 100 km of modeled flight.
6. Eagle movements are governed by a combination of deterministic patterns (based on available uplift) and stochasticity (directed random walk).
7. Eagles always migrate regardless of the weather conditions.

2.4. Data analysis and interpretation

From the perspective of observers at hawk-count sites, there are three different types of migrant eagles. There are eagles that are available to be counted and that are detected by observers (i.e., fly within a distance of the hawk-count site so that they can be identified), there are those that are available, but that pass undetected (i.e., fly close enough to a site, but are not seen), and there are those that are unavailable, and thus go undetected (i.e., fly too far away from a site to be seen and identified; Fig. 2). Hawk-count data include only the first of these types of eagles (those available and detected). The first two research objectives we out-

line in the introduction characterize the rate at which eagles are available and are detected, and provide essential information to estimating numbers of the second (available and undetected) and third (unavailable) types of eagles at hawk-count sites. Finally, our third and primary objective combines these data to estimate population sizes of eastern golden eagles migrating through the study area.

2.5. Estimating rates of eagle availability

The *availability* rate (A) is the ratio of the total number of eagles available to be counted ($\hat{N}_{available}$) to the total eagles present at a given site, as follows:

$$A = \hat{N}_{available} / (\hat{N}_{available} + \hat{N}_{unavailable}) \quad (1)$$

We estimated availability at five hawk-count sites: Allegheny Front, Stone Mountain, Waggoner's Gap, Second Mountain, and Hawk Mountain Sanctuary. We selected these five sites because of their counting coverage (i.e., greatest number of observers and hours spent counting per season) in the November peak migration, their distance from each other (≥ 25 km), and the many records they have of migrating golden eagles (≥ 50) each autumn. At such sites, observers can see and identify raptors up to 3 km from an observation point (Ainslie et al., 2014; Farmer et al., 2010). Therefore, in our models, $\hat{N}_{available}$ is the number of simulated flight routes that passed within 3 km of a hawk-count site. $\hat{N}_{unavailable}$ is

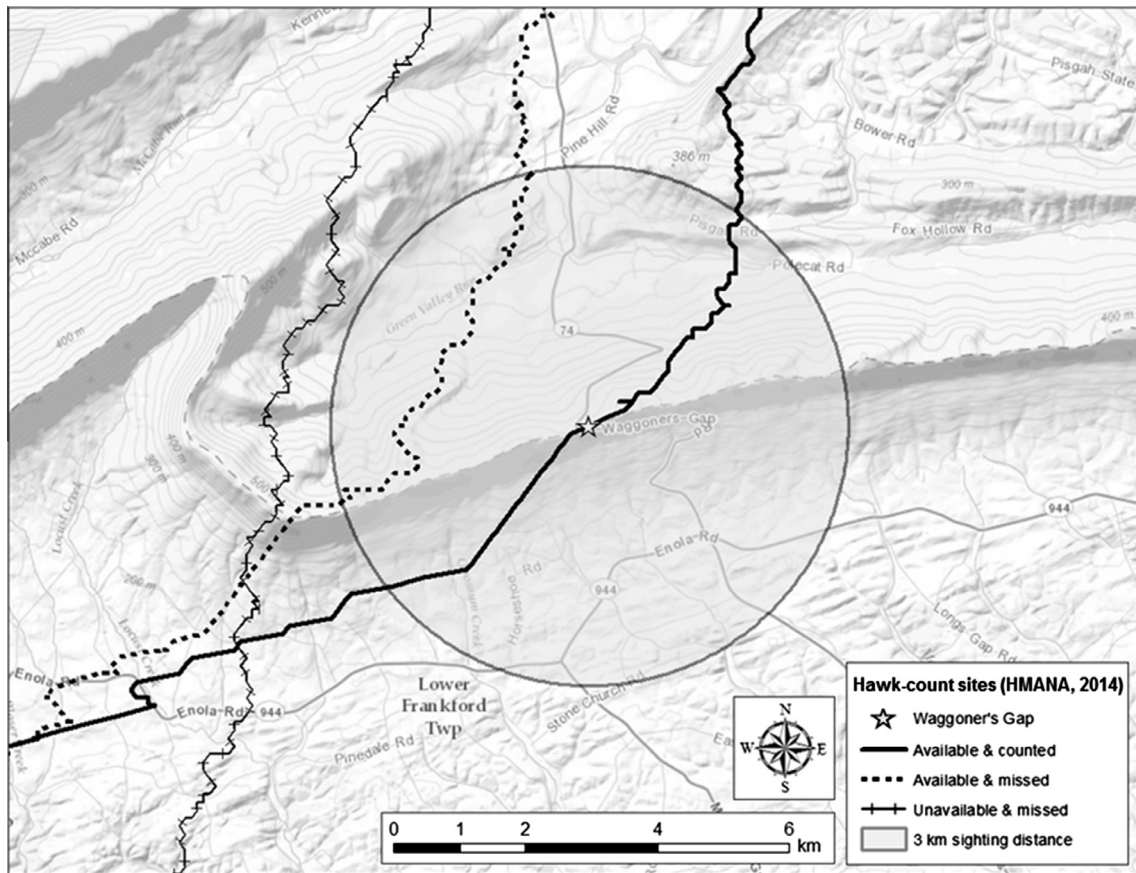


Fig. 2. Subset of simulated migration routes ($n = 3$) of golden eagles passing within 3 km (circular buffer) of an existing hawk-count site to illustrate availability v. detection. There are three types of eagles from the perspective of hawk-count observers with respect to eagle availability: an eagle that is both available to be counted and is counted (solid flight route), an eagle that is both available to be counted yet not seen and uncaptured (i.e., missed; dotted route), and an eagle that is both unavailable to be counted thus not seen and uncaptured (cross-hatched route). There are two types of eagles from the perspective of hawk-count observers with respect to eagle detection: an eagle that is detected (both detectable and counted; solid route) and an eagle that is undetected (both detectable yet not seen and uncaptured; dotted route). Detection does not let us account for eagles that are both undetectable and uncaptured (cross-hatched route), so we incorporate availability into our estimation procedure. In this example, for this site, eagle availability equals ~67% (2/3 available eagles), while eagle detection equals 50% (1/2 detectable eagles).

the number of simulated flight routes that passed >3 km-radius and <16 km-radius (half the average distances between hawk-count sites).

To account for weather effects on availability of eagles to observers, we evaluated hawk-count data on the 33 randomly chosen days on which we modeled eagle migration (Dennhardt et al., in press). To do this, we identified three categories of migration days (i.e., high, medium, and low counts) by natural breaks in the hawk-count data (i.e., ≥ 24 , 9, and 0 eagles counted on high-, medium-, and low-migration days, respectively). Finally, we estimated availability rates at each site for each of the three classes of days.

2.6. Estimating rates of eagle detection

We conducted a mark–recapture analysis on hawk-count data to estimate detection probabilities—the proportion of eagles available to be counted and actually seen by hawk-count observers. We focused this analysis on five sites along the Kittatinny Ridge (Little Gap, Bake Oven Knob, Hawk Mountain Sanctuary, Second Mountain, and Waggoner's Gap; Fig. 1b) because they present opportunities for birds to be repeatedly observed (e.g., “marked” and “recaptured”). In our formulation, a mark-and-recapture series represents a unique golden eagle that is potentially or actually counted at more than one hawk-count site on the ridge.

We built virtual capture histories based on hawk-count data, recorded during all days in November 2002–2011, the same period

used in the migration model. To do this, we identified cases where observations of eagles at successive hawk-count sites likely represented occasions where the same individual migrated along the ridge. We established three rules for this process (implemented in Visual C#; Microsoft Corporation, 2010). Our rules were that: (a) eagle recaptures had to be on the same day as captures; (b) a recapture could only occur when an eagle passed a subsequent site within a time window predicted by eagle flight speed; and (c) eagles that passed subsequent sites within the appropriate time window must also match in age class.

To estimate eagle flight times between sites, we measured ridgeline distance between sites and assumed that eagles travelled 10.90 ± 0.88 m/s (mean $\pm$ SE) using orographic (ridge) lift (Duerr et al., 2012). We repeated the analysis to evaluate potential variability in flight times for time windows classified by one, two, four, and six SEs around this mean speed. For each of the four classes of time windows (i.e., those with one, two, four, and six SEs), we built separate sets of capture histories with age class data included and then built separate sets without age classes. We generated eight sets of capture histories in total.

We used multi-state mark–recapture models implemented in Program MARK to estimate detection probabilities (Brownie et al., 1993; Cooch and White, 2014; Kendall and Nichols, 2002; White and Burnham, 1999). For this analysis, we substituted sites for capture occasions. Thus, for a given capture occasion, a one was recorded if an eagle was observed at the corresponding site and a

zero recorded if it was not observed. To allow all eagles to enter the study area, we added a pseudo-site at the beginning of each capture history. Without this pseudo-site, exit from the Kittatinny Ridge prior to the first (real) capture occasion is not estimable. In addition, we also assumed that transitions between states would be either random or a first-order Markov process in which the probability of transitioning between occasion i and $i + 1$ is dependent only on the state at i (Kendall, 1999; Nichols and Kendall, 1995).

Multi-state models that include unobservable states provide estimates of three parameters: transition or movement between states (Ψ), survival (Φ), and recapture probability (p ; Fig. 3; Fujiwara and Caswell, 2002). Transition is the probability of movement between different states. We modeled two states for golden eagles: migrating on the ridgeline and observable, state i , and migrating away from the ridgeline and unobservable, state B . We constrained survival to one because eagles are unlikely to die within a day (i.e., maximum time for an eagle to traverse the study area). Finally, recapture probability is the rate at which hawk-count observers detect available golden eagles. We fixed recapture probability to zero for the unobservable state (Kendall and Nichols, 2002; Kendall, 2004).

We defined a set of four candidate models, a priori (Table 1). There is clear evidence that detection probabilities vary among hawk-count sites (Farmer et al., 2010; Heath and Nolte, 2009; Nolte, 2012) and thus we allowed recapture probability to differ among sites in all candidate models. We set transitions between states as site-dependent or constant and as random or (first-order) Markovian movement, where an eagle's state at the next capture

Table 1

Candidate model set and parameters in multi-state mark–recapture models. Models were built in the context of eagle migration. Site-dependent parameters are designated by (i), whereas constant parameters are designated by (.). We did not estimate survival; instead, we constrained it one because eagles are unlikely to die within a day (i.e., maximum time for an eagle to traverse the study area). In all candidate models, detection probability (p) always varied with site.

Multi-state candidate models	
Fully site-dependent Markovian	$p(i)\Psi_{\text{Markovian}(i)}$
Site-dependent random transitions	$p(i)\Psi_{\text{Random}(i)}$
Constant Markovian transitions	$p(i)\Psi_{\text{Markovian}(.)}$
Constant random transitions	$p(i)\Psi_{\text{Random}(.)}$

occasion is dependent on its current state. Given combinations of either site-dependent or constant and random or Markovian settings on transitions between states, we have four candidate models in total. We fit all multi-state models with a logit-link function (White and Burnham, 1999), and we used Akaike's Information Criterion corrected for small sample sizes (AICc) to compare models (Burnham and Anderson, 2002).

2.7. Estimating regional population size

We estimated the regional population size by correcting raw hawk-count data (i.e., unadjusted for temporal coverage) from five hawk-count sites—Allegheny Front, Stone Mountain, Waggoner's Gap, Second Mountain, and Hawk Mountain Sanctuary (Fig. 1). We applied three correction factors to estimate population size from the count data. First, we used the detection probability from

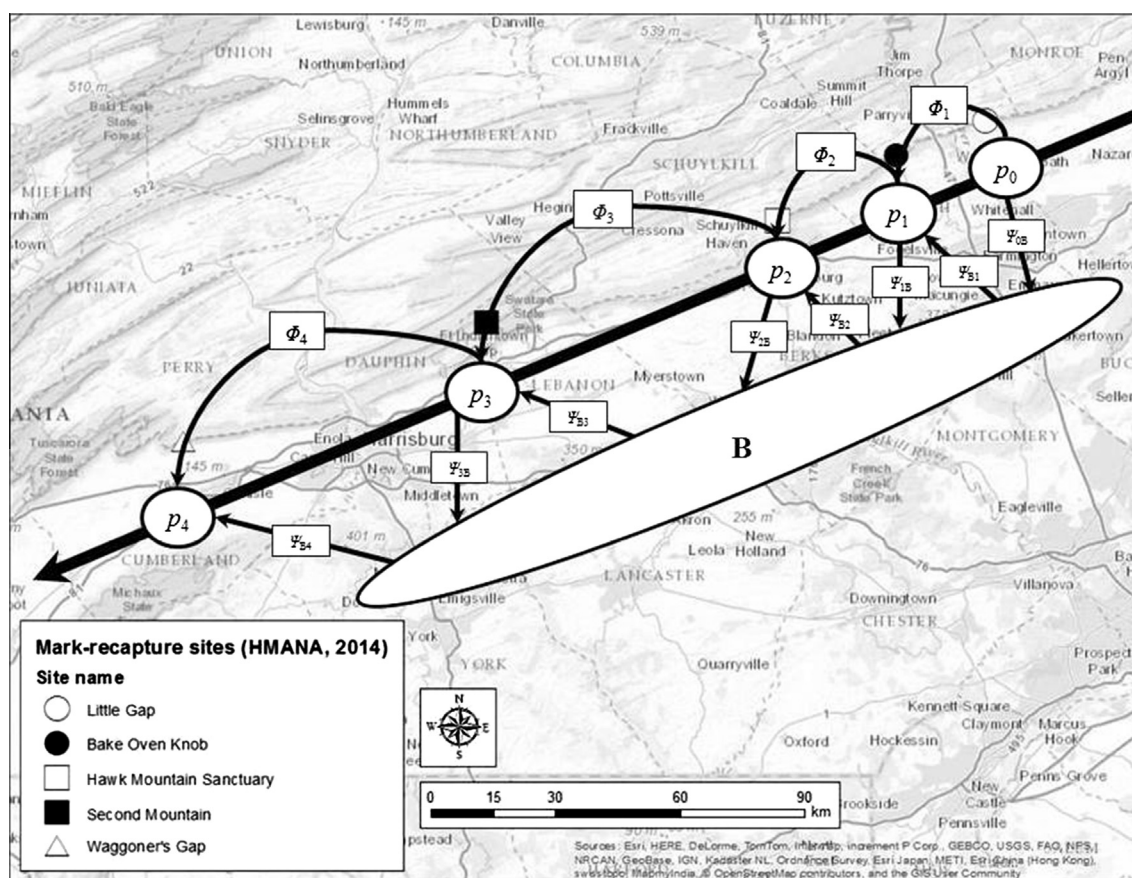


Fig. 3. Multi-state mark–recapture model overlaid on select hawk-count sites (i) in the Kittatinny Ridge, where: Φ_i is the probability of survival over the interval between sites, p_i is the probability of recapture (detection) at each site, and Ψ_{ij} is the probability of transition between states (whether from the observable state, i , on the ridgeline, or from the unobservable state, B , away from the ridgeline).

mark–recapture to adjust the count of golden eagles recorded in November at each of the five sites. Second, we adjusted the availability rate at each of the sites to account for eagles that are potentially counted at more than one of the sites. We termed this a *hypothetical double-count rate*, to avoid confusion with the term “double-counting” similar to that in mark–recapture analyses (Graham and Bell, 1989). We estimated hypothetical double-count rates between sites by counting the proportion of simulated flight routes that passed within half the average nearest neighbor distance (16 km) of more than one of the five sites. We then reduced availability by the proportion of birds potentially double-counted (hypothetical double-count rate) per site in order to derive the number of birds available to each site. Third, we corrected the count of golden eagles in November by the availability (corrected for hypothetical double-counting) to calculate the number of eagles available to be counted at each site. Mathematically, this proceeds as follows:

$$\hat{N}_{detectable} = N_i / \hat{p} \quad (2)$$

$$\hat{N}_{available} = \hat{N}_{detectable} / (A_i * d_i), \quad (3)$$

where N_i is the raw count of golden eagles in November at site i , $\hat{p}$ is the estimated detection probability from mark–recapture, $\hat{N}_{detectable}$ is the estimated number of eagles that were detectable at site i , and d_i is the hypothetical double-count rate at site i . A_i is the estimate of eagle availability at site i (Eq. (1)), and $\hat{N}_{available}$ is the number of eagles available to be counted at site i . Finally, we sum local population size from each hawk-count site together to estimate $\hat{N}_{total}$, the size of the total population that migrates through Pennsylvania, which is:

$$\hat{N}_{total} = \sum_{i=1}^n \hat{N}_{available}, \quad (4)$$

where $\hat{N}_{available}$ is summed for all hawk-count sites, i through n .

We modeled population size using ten years of hawk-count data and several combinations of eagle availability and detection probabilities. We produced population estimates for each year with or without an adjustment for hypothetical double-counting of eagles among sites, with detection probabilities estimated from capture histories with or without reported age class information, with availability rates based on each of the three classes of migration days noted previously, and with four different time windows (i.e., based on one, two, four, and six SEs). Thus, we generated 36 ten-yr estimates of population size with three availability rates, four detection probabilities, and three forms of each detection probability (i.e., high, mean, and low based on SEs of modeled estimates).

2.8. Estimating regional population size with detection probabilities from literature

We compared our population estimates with additional size estimates that involved published detection probabilities from other studies on migrating raptors (Berthiaume et al., 2009; Nolte, 2012; Sattler and Bart, 1984). In addition to the detection rates from our mark–recapture analysis, we used detection probabilities from the literature to estimate population size from the raw hawk-count data (i.e., unadjusted for temporal coverage). We based these estimates on the three published detection probabilities, three variations (i.e., high, mean, and low) of each rate, and three classes of migration days (i.e., high, medium, and low) with respect to eagle availability at each hawk-count site; therefore, producing 27 additional ten-yr estimates of population size to compare with our original 36 ten-yr estimates.

3. Results

3.1. Rates of eagle availability and hypothetical double-counts

We simulated 6094 eagle flight routes through Pennsylvania (Dennhardt et al., in press). Forty percent of these passed within 3 km of the historically active hawk-count sites in Pennsylvania. Mean ($\pm$ SE) availability of eagles to our five focal hawk-count sites was $24 \pm 14\%$ (range: 4–44). No simulated paths passed within 3 km of multiple sites, suggesting that double-counting is infrequent among the five sites. In order to evaluate the potential for hypothetical double-counting to affect population estimates, we used the 16 km-radius around sites to calculate hypothetical double-count rates, which represent absolute maxima. Hypothetical double-count rates for simulated flights varied from 80% (i.e., 80% of birds that would have been counted at Hawk Mountain Sanctuary also would have been counted at Second Mountain), 60% (of those at Second Mountain counted at Waggoner's Gap), 38% (of those at Hawk Mountain Sanctuary counted at Waggoner's Gap), and 59% (of those at Stone Mountain counted at Allegheny Front).

3.2. Building capture histories for eagles

We constructed capture histories from 3069 observations of migrant golden eagles along the Kittatinny during November from 2002 to 2011. Of these, 224 were counted at Little Gap, 543 at Bake Oven Knob, 650 at Hawk Mountain Sanctuary, 407 at Second Mountain, and 1245 at Waggoner's Gap. We did not control for year effects among our capture histories; it is therefore possible that some capture histories may represent the same individual eagle observed in more than one year. Based on capture histories built using the aging criterion and the four sets of timing criteria (i.e., one, two, four, and six SEs), we estimated that the mean ($\pm$ SE) number of individuals counted was 2705 (± 87 ; range: 2592–2775). This suggests that 400 eagles were seen repeatedly (“recaptured”) at more than one site. When capture histories did not use the aging criterion and were based on the same timing criteria as above, we estimated that the mean number of individuals counted was 2491 (± 116 ; range: 2347–2586).

3.3. Rates of eagle detection

Half of our model sets from the multi-state mark–recapture analysis produced reliable estimates of detection probability. The model sets based on capture histories with one SE timing criterion (with or without aging criterion) and the model sets including the aging criterion and either two SE or four SE timing criterion produced estimates of detection rates with SEs larger than means, indicating inflated error. We present results only for those four (of eight total) capture history sets with detection probabilities that were interpretable (i.e., only four of the eight different sets of capture histories).

For each model set, there was support for only models that included movement rates that depended on the hawk-count site (i.e., site-dependent transitions; Table 2). For three of these model sets, the best model included site-dependent movement rates with random transitions (six SE timing with aging and four and six SE timing without aging; Table 2a, c and d). The other model had site-dependent movement rates with Markovian transitions. The model set that included capture histories based on four SEs estimated time between sites without the aging criterion had two models supported by the data (Table 2c), both of which were fully site-dependent, although there was greater support for the model with random movement (AICc weight = 0.81) than for the model

Table 2

Model summaries and ranks for different, multi-state model sets. The capture history type corresponds to both how we estimated time windows (“timing criterion,” using ridgeline distance and mean flight speed for slope-soaring eagles) and whether or not we included age class information (“aging criterion,” from historic hawk-count data) to match individual eagles and construct unique capture histories. We modeled the parameters either constant (.) or variable (i) with respect to hawk-count site or state. All candidate models included detection probability (p) varying with site. Results for capture histories built with the aging criteria for one, two, and four SEs timing criteria were excluded from this analysis due to uninterpretable estimates of detection produced therein.

Capture history type	Model description	Delta AICc	AICc weight	Model likelihood	No. parameters
(A) 6 SE timing criterion With aging criterion	$\Psi(i)$ Random transitions	0.0	1.000	1.000	10
	Fully site-dependent Markovian	164.7	0.000	0.000	15
	$\Psi(.)$ Markovian transitions	553.6	0.000	0.000	7
	$\Psi(.)$ Random transitions	638.6	0.000	0.000	6
(B) 2 SE timing criterion Without aging criterion	Fully site-dependent Markovian	0.0	1.000	1.000	15
	$\Psi(i)$ Random transitions	69.0	0.000	0.000	10
	$\Psi(.)$ Markovian transitions	478.9	0.000	0.000	7
	$\Psi(.)$ Random transitions	605.5	0.000	0.000	6
(C) 4 SE timing criterion Without aging criterion	$\Psi(i)$ Random transitions	0.0	0.809	1.000	10
	Fully site-dependent Markovian	2.9	0.191	0.236	15
	$\Psi(.)$ Markovian transitions	422.7	0.000	0.000	7
	$\Psi(.)$ Random transitions	472.0	0.000	0.000	6
(D) 6 SE timing criterion Without aging criterion	$\Psi(i)$ Random transitions	0.0	1.000	1.000	10
	Fully site-dependent Markovian	33.2	0.000	0.000	15
	$\Psi(.)$ Markovian transitions	433.9	0.000	0.000	7
	$\Psi(.)$ Random transitions	450.9	0.000	0.000	6

with Markovian movement (AICc weight = 0.19). Multi-state models that included a constant transition probability were not supported by the data.

We generated our lowest estimate of detection probability ($52\% \pm 3.2$; mean $\pm$ SE) with capture histories that included the six SE timing criterion for flight speed and information on eagle age classes (Table 2a). Our highest estimate of detection probability ($63\% \pm 1.2$) was produced with capture histories that included the two SE timing criterion and excluded information on eagle age classes (Table 2b). Mean detection (i.e., per capture history type) was estimated at $56\% (\pm 5.2 \text{ SE})$; with age included and two SEs' time, $52\% (\pm 3.2)$; with age and six SEs' time, $63\% (\pm 1.2)$; without age and two SEs' time, $55\% (\pm 1.1)$; without age and four SEs' time, and $57\% (\pm 0.7)$; without age and two SEs' time). Grand mean detection (i.e., over all capture history types) was $55\% (\pm 1.6)$.

3.4. Number of eagles migrating

Estimated number of migrants through Pennsylvania was 5122 (± 1338 ; range: 2797–11,846; Fig. 4). The lowest estimates occurred when we modeled population size with site-specific availability, accounted for hypothetical double-counts of eagles, and set detection probabilities to ignore eagle age and with two SEs' time around the mean flight speed. The highest population estimates occurred when we modeled population size without accounting for hypothetical double-counts of eagles for all availability and detection probabilities.

3.5. Number of eagles based on detection probabilities from literature

We compared our estimates of population size with those built using published detection probabilities for migrating raptors in recent literature (pooled detection for bald (*Haliaeetus leucocephalus*) and golden eagles, $89\% \pm 10$, Berthiaume et al., 2009; for golden eagles, $87.5\% \pm 7.5$, Nolte, 2012; for red-tailed hawks, *Buteo jamaicensis*, $78\% \pm 4$, Sattler and Bart, 1984). Using these detection rates, mean population size for Pennsylvania migrants was 3471 (± 332 ; range: 2843–4644).

4. Discussion

We produced the first quantitative estimate of golden eagles migrating through Pennsylvania by combining citizen-science data

with a model of eagle movements. Citizen-science data are collected globally with a variety of goals in mind, and using these data presents challenges. For example, one major challenge of using count data from citizen-science is accounting for multiple errors such as estimates of double-counts that might lead to overestimating population size. With our approach, we accounted for multiple biases related to hawk-counts (e.g., availability, hypothetical double-counting, and detection rates) to estimate population size. Our approach shows the value of using one type of citizen-science data, in combination with models of animal movement, to account for potential biases in estimation of the size of migratory raptor populations.

4.1. Evaluating estimates of population size

Continent wide, there are an estimated 50,000–80,000 golden eagles in North America (Farmer et al., 2008a; Global Raptor Information Network, 2014; Hawk Mountain Sanctuary, 2014). Of these, an estimated 19,000–35,000 golden eagles reside in the western contiguous United States (Good et al., 2007; Millsap et al., 2013; Nielson et al., 2011).

Our models suggest that approximately 5000 golden eagles pass through the Appalachian migration corridor in Pennsylvania. Previously published estimates for this population are 1000–2500 (Katzner et al., 2012) and 3000–5000 (Ombalski and Brandes, 2010). Even when using detection probabilities from recent literature, population estimates (2843–4644; i.e., based in part on our migration model) overlap with previous numbers.

An additional 300–500 migrant golden eagles are observed outside of Pennsylvania, including Cape May Observatory (New Jersey), Detroit River Hawkwatch-Lake Erie Metropark (Michigan), and Hawk Ridge (Minnesota; Hawk Migration Association of North America, 2014). Thus, it is likely that the true population size of golden eagles in eastern North America is larger than previously recognized. That said, numbers of golden eagles in the east are small relative to their numbers in the west.

4.2. Golden eagle conservation in eastern North America

Between 1974 and 2004 numbers of golden eagles counted in eastern North America increased slowly but consistently (Farmer et al., 2008b). Such a pattern could be explained by one of several possible changes—e.g., increases in the temporal coverage of hawk-

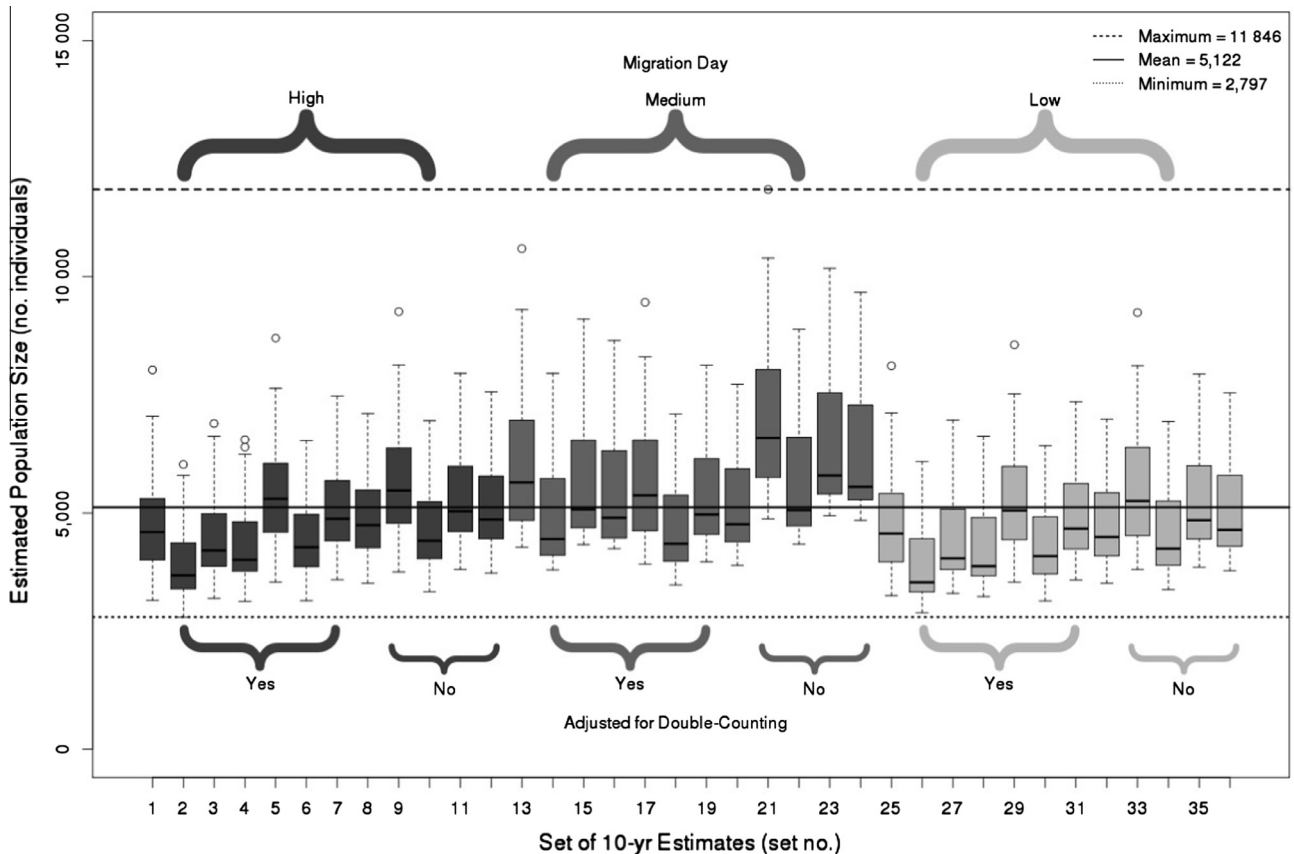


Fig. 4. Variation in ten-yr sets ($n = 36$) of estimated population size of golden eagles during November 2002–2011 in Pennsylvania. To estimate population size, we used November data from the following hawk-count sites: Allegheny Front, Stone Mountain, Waggoner's Gap, Second Mountain, and Hawk Mountain Sanctuary (Hawk Migration Association of North America, 2014). We modeled population size with numerous separate assumptions about eagle availability and detection. We classified hawk-count data by types of migration days ("high," "medium," and "low") using natural breaks in the golden eagle count data. In addition, we either adjusted ("yes") or did not adjust ("no") population estimates by rates of double-counting. Mean ($\pm$ SE) population size was 5122 ($\pm$ 1338). Lowest estimates of population size involved highest estimates of detection, adjustments for hypothetical double-counting and site-specific estimates of availability based on classes of migration days.

count sites (e.g., increased late season coverage during peak eagle migration time), an increase in the number of eagles, or a change in eagle migratory flight behavior that affects general spatial patterns of their movements and increases detectability or availability of eagles. There is no evidence in our data to suggest that eagle migration patterns are changing. However, it is reasonable to assume that the concurrent effects during this period of global climate change and increases in numbers of white-tailed deer (*Odocoileus virginianus*) in the Appalachians may act to increase winter survival of golden eagles. When combined with reductions in pesticide (e.g., DDT) use and persecution, it seems reasonable that numbers of eastern golden eagles increased from 1970 to 2004. However, trends from hawk-count sites over the past ten years (Raptor Population Index, 2013) suggest that golden eagle counts may no longer be increasing in eastern North America. These trends may indicate that the population is limited by factors such as nest site availability or mortality due to threats such as lead poisoning, direct persecution, incidental trapping, or other causes (Katzner et al., 2012).

Monitoring the population status and flight behavior of golden eagles in eastern North America is a conservation priority due to potential threats to individual survival (Katzner et al., 2012). Our migration model indicates that a portion of the eagle population is not observed at hawk-count sites. In Pennsylvania, this probably occurs outside of the Ridge and Valley physiographic province where there are few active hawk-count sites. Away from prominent ridgelines eagles depend more heavily on a thermal-soar and glide strategy, a faster and more direct mode of transportation

than slope-soaring (Duerr et al., 2012). When eagles are engaged in thermal-soaring and gliding flight, both availability and detectability of eagles to hawk-count observers is reduced compared to when eagles are engaged in slope-soaring flight and are flying closer to hawk-count sites.

4.3. Considerations for applicability

Our study demonstrates the feasibility of using citizen-science data in general to inform estimates of population size. Considering the strengths and weaknesses of our approach is useful for interpreting the results and also to future applications that may use other citizen-science data in this manner.

Our approach is likely applicable to population estimation for a wide range of other species. Hawk-count data are collected globally for large numbers of migratory raptors, and, as long as flight behavior is moderately well understood, the movement models we developed are broadly adaptable. In particular, we believe that our approach will be useful in areas where hawk-count sites are grouped as they were in this study. There are few other cases where citizen-science data are collected that are of quality high enough quality for use in similar applications. BBS and CBC data are two cases where such an approach may be useful. Likewise citizen-science counts of other aggregated organisms (fruit bats, ungulates) could be developed in a manner that allows similar population estimation. A significant benefit of this approach is that multiple years of population estimates can be produced at relatively low-cost. This is largely because the citizen-science data

on eagle migration were collected through existing networks and provided to us at no charge. This approach seems especially economical when contrasted with other work on golden eagles. For instance, annual aerial surveys are conducted for breeding and overwintering golden eagles in the western (conterminous) United States. Aerial surveys are considerably more expensive than the work we present here (current costs are ~\$320,000/year; [United States Government, 2014](#)). Although the output data are different, these two approaches provide similar information of similar conservation utility yet one year of aerial data collection and analysis is many times the cost of our entire study.

In spite of these strengths, there also are a number of limitations relevant to applying this technique in other settings. The data we used to estimate population size required spatial structures in hawk-count sites that is, to our knowledge, not replicated elsewhere. First, the organization of hawk-count sites along the Kittatinny Ridge made it feasible to develop capture histories for eagles. Second, the high density of hawk-count sites throughout the Appalachian migration corridor in Pennsylvania is well suited for assessing population size in a small area. Thus, some modification would be required to apply our approach to other areas with different distributions of count sites.

In addition, a number of elements of our data interpretation and analysis could be refined in subsequent studies. Our estimates of availability rates and hypothetical double-counts were derived through use of a simulation model that was not trivial to create. For certain species, there are sufficient telemetry data to estimate these parameters without the assumptions required in modeling. Likewise, our estimates of detection probabilities were invariant with regard to distance, land-cover, or topography. We were constrained in this manner because hawk-count data typically do not include estimates of distance from observer to the detected bird. An improved mark–recapture framework would use data that account for these characteristics. Furthermore, our detection probabilities are lower than previously published estimates ([Berthiaume et al., 2009](#); [Nolte, 2012](#)), a trend that increases some of our population estimates (i.e., >5000). However, our use of multiple sites to estimate detection is a strength (e.g., the previous studies were conducted only at one site), and future studies designed explicitly to estimate detection rates may further improve these estimates.

Finally, our need to use broad error distributions around the time windows for flight between hawk-count sites suggests that a more structured mechanism for creating capture histories along the Kittatinny Ridge could also improve our population estimates. This could be achieved if observers at hawk-count sites were in better communication with each other. Under such a scenario, it may be possible to create capture histories that are less likely to violate assumptions about tag loss or gain (i.e., to correctly track individual birds; [Cooch and White, 2014](#)). However, communication between sites would likely artificially increase detection probabilities, and this would need to be accounted for in estimates of population trend. A study that accounted for such biases could improve precision in detection estimates and subsequent population estimates ([Arnason and Mills, 1981](#); [Margalida et al., 2011](#)).

4.4. Research implications

Hawk-count data are useful because their collection is standardized and they are available at relatively low-cost ([Bildstein et al., 2008b](#); [Dunn et al., 2008](#); [Hawk Migration Association of North America, 2006](#)). Previous research has used these raw data to evaluate demographic trends. This study demonstrates the value of using these citizen-science data toward population estimation. Such data can be used retrospectively as we have here, or even as they are collected, to assess complex demographic phenomena.

The convergence of the 36 population estimates we generated speak to the robust nature of both this particular estimate and the value of our approach in general.

Future work with hawk-count data might focus on further standardization of their collection and greater spatiotemporal coverage in counts and number of observers in order to maximize the efficiency of our proposed approach. Additional evaluations of this approach are also important next steps, especially in which data on other migrant raptor species are used. New study designs that allow for better estimation of availability, double-count rates, and detection probabilities are also beneficial to our approach and others, particularly where integrated models are used to estimate population size.

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