Applying citizen-science data and mark–recapture models to estimate numbers of migrant Golden Eagles in an Important Bird Area in eastern North America

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RESEARCH ARTICLE

Applying citizen-science data and mark–recapture models to estimate numbers of migrant Golden Eagles in an Important Bird Area in eastern North America

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ABSTRACT

Estimates of population abundance are important to wildlife management and conservation. However, it can be difficult to characterize the numbers of broadly distributed, low-density, and elusive bird species. Although Golden Eagles (*Aquila chrysaetos*) are rare, difficult to detect, and broadly distributed, they are concentrated during their autumn migration at monitoring sites in eastern North America. We used hawk-count data collected by citizen scientists in a virtual mark–recapture modeling analysis to estimate the numbers of Golden Eagles that migrate in autumn along Kittatinny Ridge, an Important Bird Area in Pennsylvania, USA. In order to evaluate the sensitivity of our abundance estimates to variation in eagle capture histories, we applied candidate models to 8 different sets of capture histories, constructed with or without age-class information and using known mean flight speeds $\pm$ 1, 2, 4, or 6 SE for eagles to travel between hawk-count sites. Although some abundance estimates were produced by models that poorly fitted the data ($\hat{c} > 3.0$), 2 sets of population estimates were produced by acceptably performing models ($\hat{c} \leq 3.0$). Application of these models to count data from November, 2002–2011, suggested a mean population abundance of 1,354 $\pm$ 117 SE (range: 873–1,938). We found that Golden Eagles left the ridgeline at different rates and in different places along the route, and that typically <50% of individuals were detected at the hawk-count sites. Our study demonstrates a useful technique for estimating population abundance that may be applicable to other migrant species that are repeatedly detected at multiple monitoring sites along a topographic diversion or leading line.

Keywords: Aquila chrysaetos, citizen-science data, Golden Eagle, Kittatinny Ridge, mark–recapture, raptor migration, Pennsylvania, population estimation

Aplicación de datos de ciencia ciudadana y modelos de captura-recaptura para estimar el número de migrantes de *Aquila chrysaetos* en un Área Importante para las Aves en el este de América del Norte

RESUMEN

Las estimaciones de abundancia poblacional son importantes para el manejo y la conservación de la vida silvestre. Sin embargo, puede ser difícil caracterizar las abundancias de las especies de aves ampliamente distribuidas, de baja densidad y esquivas. Aunque *Aquila chrysaetos* es una especie rara, difícil de detectar y ampliamente distribuida, está concentrada durante su migración de otoño en los sitios de monitoreo en el este de América del Norte. Usamos datos de conteos de halcones colectados por científicos ciudadanos en un análisis modelado de marca-recaptura virtual para estimar los números de otoño de individuos de *A. chrysaetos* que migran a lo largo de la Cresta Kittatinny, un Área Importante para las Aves en Pensilvania, EEUU. Con el fin de evaluar la sensibilidad de nuestros estimaciones de abundancia para la variación en las historias de captura de las águilas, aplicamos modelos de candidatos a 8 sets diferentes de historias de captura, construidos con o sin información de clases de edad y usando velocidades medias conocidas $\pm$1, 2, 4, o 6 EE para águilas que viajan entre sitios de conteo de halcones. Aunque algunas estimaciones de abundancia fueron producidas por modelos que se ajustaron pobremente a los datos ($\hat{c} > 3.0$), dos sets de estimaciones poblacionales fueron producidos por modelos de desempeño aceptable ($\hat{c} \leq 3.0$). Las aplicaciones de estos modelos a los datos de conteo desde noviembre de 2002 a 2011 sugieren una abundancia poblacional media de 1,354 ($\pm$ 117 [EE]; rango: 873–1,938). También encontramos que *A. chrysaetos* deja la línea de cresta a diferentes tasas y en lugares diferentes a lo largo de la ruta y que típicamente <50% de los individuos son detectados en los sitios de conteo de halcones. Nuestro estudio aporta una técnica útil para estimar la abundancia poblacional que puede ser aplicable a otras especies migratorias que son detectadas repetidamente en múltiples sitios de monitoreo a lo largo de una derivación topográfica o línea principal.

INTRODUCTION

Estimates of population abundance are important to wildlife management and conservation. However, it is difficult to survey species that are broadly distributed, occur at low densities, or tend to avoid areas influenced by human activities (Link and Nichols 1994, Lewis and Gould 2000, Margalida et al. 2011). It is also the case that broad-scale estimates of population abundance for wide-ranging species are rarely used in conservation actions at local scales. This is usually due to the fact that such estimates, by their nature, lack specific information at finer scales, especially in regard to species' seasonal uses of a particular area (e.g., migratory movements). Instead, broad-scale population trajectories are the most common foundation for local management decisions. However, many of the problems that apply to broad-scale estimates of population abundance are also relevant to local migratory population estimates. As such, there is an important need to develop methods to estimate the size of at-risk migratory populations, especially with respect to wind energy development and the impacts on bird populations (e.g., Predatory Bird Research Center 1997, Predatory Bird Research Group 1999, Hunt 2002, Barrios and Rodríguez 2004).

The size of raptor populations is rarely well estimated by traditional broad-scale monitoring programs (e.g., the North American Breeding Bird Survey and Christmas Bird Count; Zalles and Bildstein 2000, Bildstein 2006). However, counts of raptors passing by a single location are recorded at leading lines for migration (Kerlinger 1989). Kittatinny Ridge, in the central Appalachian Mountains in Pennsylvania, USA, is a migration hotspot recognized as an Important Bird Area (Lebbin et al. 2010, National Audubon Society 2013), and, like many other ridges in the region, it is the focus of wind energy development (Audubon Pennsylvania 2010). Increased wind energy development creates not only the potential for conflict with wildlife, but also new conservation attention, because many raptor species frequent the Appalachians during their semiannual migrations (www.hmana.org). This puts many raptors at risk of potential collision with turbines, especially when both are found along mountain ridgetops (Kerlinger 1989, Newton 2008, Miller et al. 2014).

Raptors are counted at several hawk-count sites along Kittatinny Ridge because their migrations are concentrated there due to its topography and the updrafts that are generated by the ridge (Sattler and Bart 1984, Bildstein 1998, Farmer et al. 2010, Ainslie et al. 2014). Although the oldest hawk-count sites in North America occur along this

ridgeline, there are no empirically based estimates of the numbers of individuals of any species that migrates there. One of the rarest and highest-priority migrant species for conservation that frequents the area during both autumn and spring is the Golden Eagle (*Aquila chrysaetos*; Kochert and Steenhof 2002, Katzner et al. 2012a). There is a great deal of interest in estimating the numbers of eagles nationally (Millsap et al. 2013) and regionally (Dennhardt et al. 2015a), but it would also be useful if ridge-specific estimates of eagle numbers could be generated. Golden Eagles are regularly cited in management decisions about wind energy in the United States (see USFWS 2013). However, to date, no population estimates of migrating eagles have been produced to help inform management along specific mountain ridgelines in the Appalachians.

To address this information gap, we developed a technique to estimate the number of Golden Eagles moving along Kittatinny Ridge during autumn migration. Our approach was to apply a mark–recapture analysis to historical hawk-count data collected from 2002 to 2011 by citizen scientists at several sites along the ridge during autumn migration. We then used these data to draw inferences about (1) eagle flight behavior (i.e. their fidelity to the ridgeline during migration), (2) the effectiveness of hawk-count observers for detecting migrants, and (3) the numbers of Golden Eagles migrating along Kittatinny Ridge each autumn. Because similar hawk-count data exist for a variety of other migrant species, we also discuss the utility of our approach for estimating the population abundance of other species for which such knowledge may benefit ecological research and conservation management.

METHODS

Study Area

We focused our mark–recapture analysis on Kittatinny Ridge in Pennsylvania (Figure 1A) because it contains multiple autumn hawk-count sites along a single geographical feature, and thus presents opportunities for individuals to be repeatedly observed (i.e. "marked" and "recaptured"). Kittatinny Ridge is the easternmost ridge in a central Appalachian Mountain chain that begins in southeastern New York, USA, proceeds through northwestern New Jersey, and ends in south-central Pennsylvania. The local weather in autumn is temperate, often cloudy and overcast, and dominated by westerly and northwesterly winds that interact with the steep topography to generate orographic (ridge) uplift that migrating birds use to subsidize the energetic costs of long-distance flight (Katzner et al. 2012b, 2015, Duerr et al. 2015).
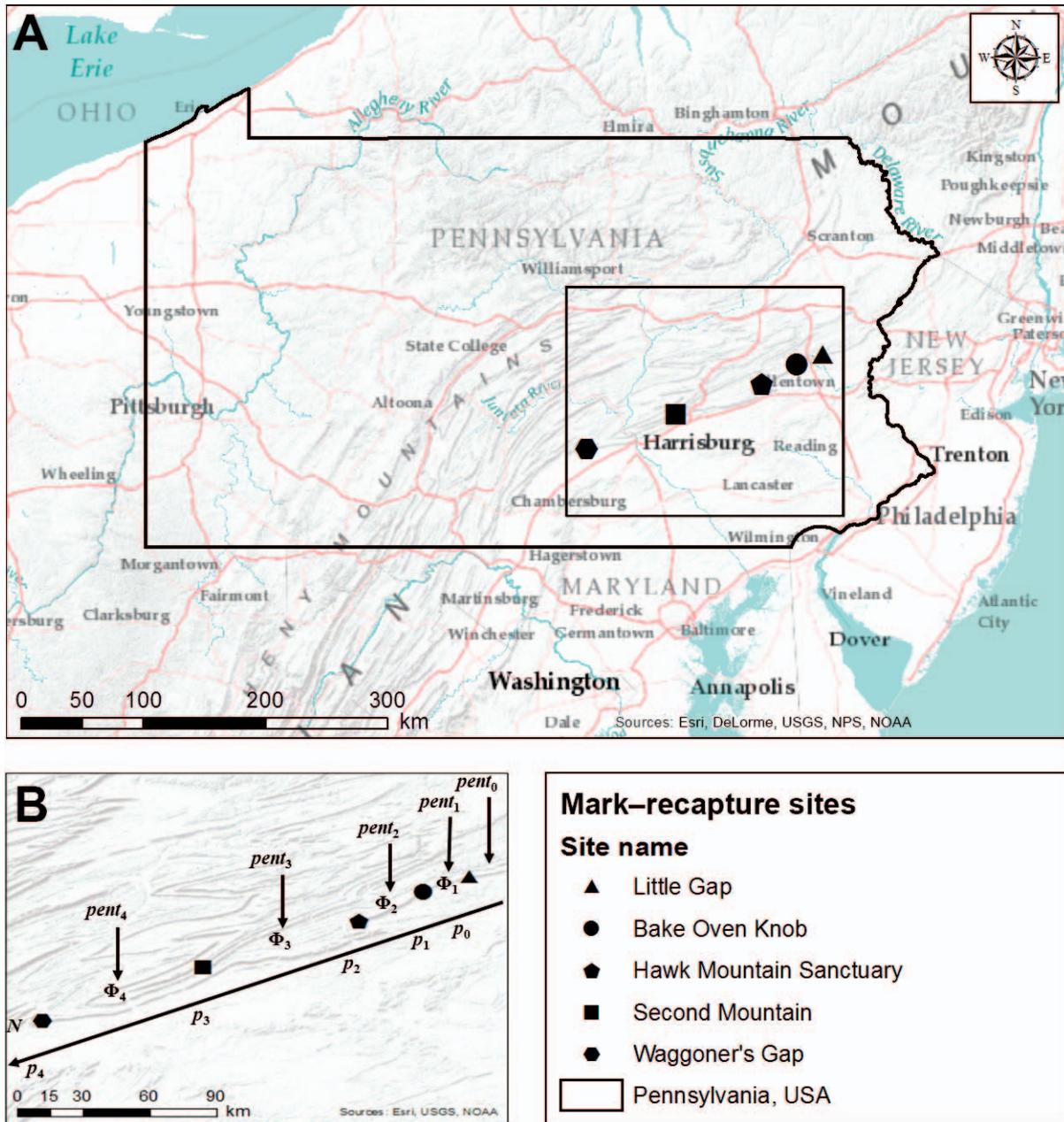
FIGURE 1. (**A**) The Kittatinny Ridge study area in Pennsylvania, USA. Individual hawk-count sites represent different sampling sites in our mark–recapture experiment to estimate the numbers of Golden Eagles that migrated along Kittatinny Ridge each autumn in 2002–2011. Observers at each site encountered Golden Eagles during late autumn as the eagles migrated through the area from northeast to southwest. (**B**) Population Analysis (POPAN) Jolly-Seber model parameters overlaid on Kittatinny Ridge, where $pent_i$ is the probability of entry (an influx of new eagles) before each site (*i*), Φ_i is the probability of apparent survival (eagle adherence to the ridgeline) when migrating between sites, p_i is the probability of recapture (detection) at each site, and N is the estimated population size over the entire study area. Solid black arrows represent the basic flow of eagles in the study area.

Because large numbers of raptors follow Kittatinny Ridge during fall migration (i.e. August 1–December 31, annually), monitoring has occurred there for decades (Broun 1935). Hundreds of Golden Eagles are counted migrating along the ridge each autumn, and their peak migration occurs in November (mean unadjusted propor-tion of the total autumn flight: 54%; range: 37–68%; www.hmana.org). Raw count data from 2002 to 2011 (unad-justed for sampling effort and imperfect detection) suggest that the average number of Golden Eagles encountered daily per site was 2 (range: 1–3) during November and 4 (range: 3–5) over the entire autumn migration season.

Hawk-count Data

Citizen-scientist volunteers collect hawk-count data from across North America (www.hmana.org), and then organize and post the data on the internet (www.hawkcount.org). However, some ancillary data to the hawk counts are not available in the online database. For example, at a subset of hawk-count sites, observers collect, but do not post, data on raptor age (usually based on plumage characteristics), as well as the time that observations were made (i.e. to the minute) for individual birds. With permission from data owners, we downloaded data on Golden Eagle migration collected during November, 2002–2011, at the 5 main Kittatinny Ridge sites: Little Gap, Bake Oven Knob, Hawk Mountain Sanctuary, Second Mountain, and Waggoner's Gap (Figure 1A). We also requested and incorporated detailed data on the age of Golden Eagles and timing of observations, when available. No information was available, however, on observer proficiencies in terms of identifying species or aging birds.

Capture Histories

In our study design, a mark-and-recapture sequence represented an individual eagle that was potentially or actually counted at more than one hawk-count site along the ridgeline. Although we did not physically capture, release, and recapture eagles, our virtual (resighting) approach avoided costly physical marking efforts in the field (McClintock 2016) and has been previously demonstrated to be applicable to Golden Eagles (Dennhardt et al. 2015a). Golden Eagle migration in autumn is stereotyped, in that individuals usually migrate alone and follow Appalachian ridgelines closely (e.g., typically <5 km in horizontal distance from and above count sites). In general, observers used (1) binoculars and spotting scopes to locate and investigate migrating birds, (2) local knowledge, experience, onsite training, and field guides to identify birds to the species level, and (3) local knowledge, experience, onsite training, and other guides to age migrating birds in flight, based on species-specific plumage characteristics (Liguori 2004, 2011). Consequently, we sought to test that historical records of eagles could be matched between hawk-count sites, based on firm and consistent rules.

We constructed Golden Eagle capture histories in a computing environment using November hawk-count data recorded at the 5 Kittatinny Ridge sites during 2002–2011. Starting with Golden Eagles observed ("marked") at the northernmost count site (Little Gap), we identified potential recaptures for each eagle from the set of Golden Eagle observations made at the more southerly count sites. We coded 3 rules to identify recaptures: (1) "recaptured" eagles had to be recorded as the same age as during the original capture (i.e. classified as either "Adult" or "Immature," the latter of which included both subadults

and juveniles); (2) an eagle had to be counted on the same day for initial capture and all later recaptures; and (3) an eagle could only be recaptured when it passed a site downstream from a more northerly site within a specified time period. We calculated that time period based on straight-line ridge distances between sites measured with GIS (ArcMap 10.0; ESRI, Redlands, California, USA) and measures of flight speed for eagles engaged in slope-soaring (mean $\pm$ 1, 2, 4, or 6 SE; see Sensitivity Analysis and Model Performance). Flight speed was measured for 5 migratory Golden Eagles equipped with GPS-GSM telemetry devices (10.90 $\pm$ 0.87 m s^{-1} [$\pm$ 1 SE]; see Duerr et al. 2012).

To illustrate these rules, for example, consider an eagle that was detected at an upstream site on a particular day. The time of detection (to the nearest minute) and age-class of the eagle were recorded by the observer(s) at that site. If a new observation of a similarly aged eagle was recorded at a site downstream within an allotted time period, then we would match these records as 2 observations of a single eagle. For the capture history of this bird, we would then record 2 ones in a sequence. Finally, the completed capture history would comprise a sequence of ones and zeros denoting presence (1) or absence (0) of the bird at each of the 5 sites along Kittatinny Ridge.

We characterized all eagles observed at the northernmost site (Little Gap) as captures. However, not all eagles were detected at Little Gap. For each unpaired eagle observation at the next count site to the south (i.e. those that did not match up with an eagle counted at Little Gap), we restarted the pairing process (i.e. we matched remaining eagle records from upstream sites to downstream ones, based on estimated flight times between sites), until all eagle observations for a given day had been identified as either a capture or a recapture. The capture history for each eagle consisted of a "1" at the site of initial capture and subsequent recaptures and a "0" when recaptures did not occur within the appropriate time period at subsequent count sites.

We wrote a program in Visual C# (Microsoft Corporation, Redmond, WA, USA) to measure the time between observations at hawk-count sites along Kittatinny Ridge and to create complete capture histories (i.e. sequences of ones and zeros) for every eagle observed. We created 2 sets of capture histories for each year of data that we considered (2002–2011), one that incorporated age-class data and another without those data. Grouping capture histories by year thus allowed us to generate multiple population abundance estimates for each year of the analysis. When we excluded age-class data from this process, our program to create capture histories only employed rules (2) and (3) from above. We hypothesized that capture histories with age data would be improved because recaptures would be more likely to be accurately

TABLE 1. Candidate models, parameter descriptions, and biological interpretations of parameters in Population Analysis (POPAN) Jolly-Seber mark–recapture models of Golden Eagles migrating southward along Kittatinny Ridge, Pennsylvania, USA, 2002–2011. Site-dependent parameters are designated by (i) and constant parameters are designated by (.). In each candidate model, we allowed recapture probability (p) to vary with site and year.

Model description	Apparent survival (Φ)	Probability of entry ($pent$)	Population size (N)
Fully site-dependent: $\Phi(i)pent(i)N(i)$	Site-dependent: Eagles leave the ridgeline at different rates between sites	Site-dependent: Eagles enter the system at different rates between sites	Site-dependent: Local abundance estimates vary among sites
Constant apparent survival: $\Phi(.)pent(i)N(i)$	Constant: Eagles stay on the ridgeline at the same rate between sites	Site-dependent: Eagles enter the system at different rates between sites	Site-dependent: Local abundance estimates vary among sites
Constant probability of entry: $\Phi(i)pent(.)N(i)$	Site-dependent: Eagles leave the ridgeline at different rates between sites	Constant: Eagles enter the system at the same rate between sites	Site-dependent: Local abundance estimates vary among sites
Constant survival, entry, and population size: $\Phi(.)pent(.)N(.)$	Constant: Eagles stay on the ridgeline at the same rate between sites	Constant: Eagles enter the system at the same rate between sites	Constant: Local abundance estimates do not vary among sites

identified. However, such an approach incorporates an additional source of uncertainty, in that aging eagles is difficult and inconsistently applied at hawk-count sites (Liguori 2004, 2011). As a result, fewer capture histories included age data. Consequently, the variance associated with the resulting population estimate based on such data is likely to be larger than that for estimates based on capture histories without age-class data.

Mark–Recapture Analyses

We estimated the number of Golden Eagles migrating along Kittatinny Ridge using the Population Analysis (POPAN) parameterization of a Jolly-Seber mark–recapture model (Jolly 1965, Seber 1965, Schwarz and Arnason 2016) in program MARK 8.0 (White and Burnham 1999). The POPAN Jolly-Seber model estimates 4 variables: apparent survival (Φ), recapture (detection) probability (p), probability of entry into the system ($pent$), and site-level population abundance (i.e. the number of eagles at each hawk-count site, N_i; Figure 1B). We assumed that eagles did not die within a single migration day. Thus, we used apparent survival (Φ) to represent the probability that an eagle remained on Kittatinny Ridge between sites, and $1 - \Phi$ was the probability that an eagle left the ridgeline. Recapture probability (p) was the rate at which hawk-counters detected Golden Eagles at each site. Thus, this parameter represents the proportion of visible eagles that were actually seen and recorded by observers. We did not consider how the distance between eagles and observers influenced estimated detection rates in our models; this would have been difficult because the majority of the data that we used lacked information on these distances. Probability of entry ($pent$) was the likelihood that an eagle entered the ridge system between hawk-count sites. Finally, superpopulation size ($\hat{N}^*$) represented the estimated total number of Golden Eagles, both counted and uncounted, that migrated along Kittatinny Ridge each autumn.

Before fitting our candidate models, we categorized capture histories by year. As a result, the output from our modeling provided 10 population estimates, one for each year. For each candidate model, we set the recapture probability (p) as site-specific ($p(i)$; Farmer et al. 2010). We considered the parameters apparent survival, probability of entry, and site-level population abundance as either site-dependent (i) or constant (.) (Table 1). In these models, the parameters Φ and $pent$ influenced estimates of N such that whenever Φ or $pent$ differed by site, so too did N. Consequently, this parameterization limited our candidate set to 4 different models in total, rather than the 8 parameter combinations possible had all 3 parameters (i.e. Φ, $pent$, and N, because p was always site-dependent) each had 2 states that varied independently. We fit all models using a logit link for $\hat{\Phi}$ and $\hat{p}$, multinomial logit links for $\widehat{pent}$ (i.e. group-specific link functions, one for each year of data), and an identity link for $\hat{N}$ (White and Burnham 1999). We used Akaike's information criterion corrected for small sample sizes (AIC_c) to evaluate model performance, and we model-averaged estimates of population abundance across candidate sets that included multiple supported models (Buckland et al. 1997).

Sensitivity Analysis and Model Performance

We conducted a sensitivity analysis to understand how population estimates changed as a consequence of adjusting the rules for constructing eagle capture histories. To do this, we constructed additional capture histories (with and without age-class information) for eagle flight times of 2, 4, and 6 SE around the mean flight speed of eagles. This gave us 8 different sets of capture histories and allowed us to evaluate how sensitive the estimates of population abundance and other parameters were to our methodology.

To assess the reliability of our estimates and relative model performance, we used program RELEASE (Burnham et al. 1987) within package RMark in R 3.2.0 to estimate the variance inflation factor, $\hat{c}$, of the models (Laake 2013, R Core Team 2015). We estimated $\hat{c}$ for the saturated model (i.e. fully site-dependent model: $\Phi(i)p(i)$-$pent(i)N(i)$) using the results from a series of tests on raw capture histories as described below. In RMark, the command release.gof() produces results for 3 separate tests, TEST2, TEST3, and Total. TEST2 evaluates whether the probability of an eagle being seen at site $i + 1$ is a function of whether or not it was seen at site i, given that it survived from i to $i + 1$, i.e. equal catchability of marked eagles. TEST3 tests the assumption that all marked eagles alive at site i have the same probability of surviving to site $i + 1$, i.e. equal survivability of marked eagles. To assess relative model performance, we used the equation $\hat{c} \cong \chi^2/$df, where χ^2 and df signify the model deviance test statistic and degrees of freedom, respectively, as an estimator of variance inflation due to extrabinomial noise in the saturated (fully site-dependent) model that enlarged uncertainty around estimated parameters (Cooch and White 2016). This allowed us to evaluate which assumptions of the Jolly-Seber model may have been violated in our mark–recapture analysis.

We interpreted models with estimates of $\hat{c} \leq 3.0$ from the Total test as reliable models of eagle population abundance (Lebreton et al. 1992), and then adjusted our model-selection tables and parameter estimates to incorporate uncertainty due to model specification (Cooch and White 2016). We then used quasi-AIC_c ($QAIC_c$) statistics to conduct multimodel inference in the same manner as we did with AIC_c scores. Because estimates of superpopulation size ($\hat{N}^*$) are not corrected for $\hat{c}$ in program MARK (White and Burnham 1999), we report grand mean ($\pm$ SE) estimates of eagle population abundance. We also report abundance estimates generated by each of the model sets that used capture histories with 1, 2, 4, or 6 SE of eagle flight time between sites and with or without eagle age-class information (8 model sets in total). However, we considered population estimates to be reliable only from those model sets that met our performance criterion (i.e. $\hat{c} \leq 3.0$).

RESULTS

Building Capture Histories
We built capture histories using 3,069 observations of Golden Eagles counted along Kittatinny Ridge during November, 2002–2011. These included 224 at Little Gap, 543 at Bake Oven Knob, 650 at Hawk Mountain Sanctuary, 407 at Second Mountain, and 1,245 at Waggoner's Gap. Among these observations, ~40% were classified as adults, ~43% as immatures, and ~17% as unaged birds. Using

capture histories built with age-class data, our time-varying analysis (based on mean flight speed $\pm$ 1, 2, 4, or 6 SE) suggested that 294, 296, 389, or 477 eagles, respectively, were counted at least twice, and that the 3,069 observations represented 2,775, 2,773, 2,680, or 2,592 individual eagles, respectively. Using capture histories built without age-class data, our time-varying analysis suggested that 483, 486, 621, or 722 eagles, respectively, were counted at least twice, and that the 3,069 observations represented 2,586, 2,583, 2,448, or 2,347 individual eagles, respectively.

Jolly-Seber Model Sets
When age-class data informed capture histories, there was support ($QAIC_c$ weight > 0.0) only for models that included site-dependent estimates of population abundance (Table 2, Appendix Table 4). The model set with age-class information and eagle flight time between sites set at the mean speed $\pm$ 1 SE had a single model (site-specific survival, probability of entry, and population abundance) supported by the data ($QAIC_c$ weight $\cong$ 1.00; Table 2A). The model set with age-class information and eagle flight time between sites set at the mean speed $\pm$ 2 SE had the same top-ranked model (Table 2B). The fully site-dependent model was also the best-supported model in all other model sets that included age-class information (mean flight time $\pm$ 4 and 6 SE: $QAIC_c$ weights > 0.94). In model sets without age-class data, the best-supported model ($QAIC_c$ weights > 0.97) was always the model with constant survival, probability of entry, and population abundance (Appendix Table 4).

Jolly-Seber Model Parameter Estimates
Model-averaged estimates of apparent survival, probability of entry, and recapture probabilities were variable between candidate model sets that included age-class data and mean flight speed $\pm$ 1 or 2 SE (Table 3). In the top-ranked model in both candidate sets, probabilities of ridgeline adherence (apparent survival, $\hat{\Phi}$) were estimated as site-specific and model-averaged estimates were high (sometimes 1.0). Probabilities of eagle entry onto the ridgeline ($\widehat{pent}$), also estimated as site-specific in both models sets, were variable. In the first model set ($\pm$ 1 SE flight time, with age-class data), estimates ranged from 0% to 58% of the population entering the ridgeline before a given site (Table 3A). In the second model set ($\pm$ 2 SE flight time, with age-class data), the probability of eagle entry onto the ridgeline ranged from 0% to 57% (Table 3B). Finally, probabilities of eagle recapture ($\hat{p}$), also estimated as site-specific, were highly variable and averaged 10% in both model sets (Table 3). These estimates suggest that ~1 out of every 10 eagles that migrates along Kittatinny Ridge is actually detected at a hawk-count site. The highest and lowest detection rates in the first model set were found at

TABLE 2. Model summaries and ranks for 2 Population Analysis (POPAN) Jolly-Seber model sets to estimate the size of Golden Eagle populations using different simulated flight speeds during autumn migration along Kittatinny Ridge, Pennsylvania, USA, 2002–2011. Models were ranked by differences in quasi-Akaike's information criterion corrected for small sample size ($\Delta QAIC_c$), quasi-Akaike weights ($QAIC_c$ weight), and model likelihoods. K is the number of model parameters, and Deviance is the model deviance. The capture history type corresponds to the allotted flight speed (mean $\pm$ 1 or 2 SE) and whether or not we used age-class data from hawk counts to match individual eagles and construct unique capture histories across 5 sites along the ridge. Parameters in the POPAN Jolly-Seber models for each capture history type are the probability of apparent survival (Φ), probability of entry ($pent$), recapture probability (p), and population size (N). We modeled these parameters as either constant (.) or variable (i) at each hawk-count site. All candidate models allowed recapture probability (p) to vary with site and year. Both model sets are corrected for the variance inflation factor ($\hat{c}$) of the saturated (i.e. fully site-dependent) model, which was 2.996 and 3.013 for model set (**A**) and (**B**), respectively. We used the top-ranked model in each model set to produce what we interpreted from our sensitivity analysis as the most reliable estimates of population abundance and parameters describing the eagle migration process along Kittatinny Ridge. Capture histories were grouped by year to produce annual estimates of population abundance.

Capture history type	$\Delta QAIC_c$	$QAIC_c$ weight	Model likelihood	K	Deviance
(**A**) 1 SE, with age data					
$\Phi(i)pent(i)N(i)$	0.0 [a]	0.999	1.000	20	−2,217.804
$\Phi(i)pent(.)N(i)$	14.8	0.001	0.001	19	−2,200.959
$\Phi(.)pent(i)N(i)$	161.5	0.000	0.000	18	−2,052.210
$\Phi(.)pent(.)N(.)$	216.0	0.000	0.000	8	−1,977.560
(**B**) 2 SE, with age data					
$\Phi(i)pent(i)N(i)$	0.0 [b]	0.999	1.000	20	−2,200.729
$\Phi(i)pent(.)N(i)$	14.4	0.001	0.001	19	−2,184.283
$\Phi(.)pent(i)N(i)$	160.5	0.000	0.000	18	−2,036.193
$\Phi(.)pent(.)N(.)$	214.1	0.000	0.000	8	−1,962.440

[a] Top-ranked model $QAIC_c = 896.041$.
[b] Top-ranked model $QAIC_c = 893.262$.

TABLE 3. Summary statistics for parameters estimated from 2 Population Analysis (POPAN) Jolly-Seber model sets used to estimate the size of Golden Eagle populations using different simulated flight speeds (mean $\pm$ 1 or 2 SE) between hawk-count sites during autumn migration along Kittatinny Ridge, Pennsylvania, USA, 2002–2011. Values represent model-averaged estimates of the probability of apparent survival ($\widehat{\phi}$; probability of remaining along the ridgeline), probability of entry ($\widehat{pent}$; probability of entering the ridge system between sites), and probability of recapture ($\hat{p}$; rate of detection by hawk-count observers). Estimates paired with parenthetical values denote the parameter's mean ($\pm$ SE) over the study period. Parameters not separately estimable in either model set are denoted with NA and were not used to summarize these statistics. Dashes (—) indicate that there was no sampling occasion or the parameter was not estimated. All estimates are corrected for the variance inflation factor ($\hat{c}$) of the saturated (i.e. fully site-dependent) model, which was 2.996 and 3.013 for model sets (**A**) and (**B**), respectively. Capture histories were grouped by year to produce annual estimates of population abundance. Detection probabilities ($\hat{p}$) were allowed to vary with site and year.

Capture history type	From site	To site	$\widehat{\phi}$	$\widehat{pent}$	$\hat{p}$*
(**A**) 1 SE, with age data [†]	—	Little Gap	—	NA [a,b,c]	NA [a,b]
	Little Gap	Bake Oven Knob	NA [a]	NA [a,c]	0.094 (0.016)
	Bake Oven Knob	Hawk Mountain Sanctuary	0.630 (0.137)	0.575 (0.067)	0.179 (0.047)
	Hawk Mountain Sanctuary	Second Mountain	1.000 (0.000)	0.000 (0.000)	0.036 (0.006)
	Second Mountain	Waggoner's Gap	NA [d]	—	NA [e]
(**B**) 2 SE, with age data [‡]	—	Little Gap	—	NA [a,b,c]	NA [a,b]
	Little Gap	Bake Oven Knob	NA [a]	NA [a,c]	0.094 (0.016)
	Bake Oven Knob	Hawk Mountain Sanctuary	0.630 (0.136)	0.574 (0.067)	0.180 (0.048)
	Hawk Mountain Sanctuary	Second Mountain	1.000 (0.000)	0.000 (0.000)	0.036 (0.006)
	Second Mountain	Waggoner's Gap	NA [d]	—	NA [e]

* Estimates correspond to individual hawk-count sites listed under 'To site.'
[†] Model-averaged estimates of the parameters are based on candidate models summarized in Table 2A.
[‡] Model-averaged estimates of the parameters are based on candidate models summarized in Table 2B.
[a] Initial probability of apparent survival is not separately estimable from the initial probability of entry, second probability of entry, and initial recapture probability.
[b] Initial probability of entry is not separately estimable from the initial recapture probability.
[c] Second probability of entry cannot be cleanly estimated because the initial probability of entry is inestimable.
[d] Final probability of apparent survival is not separately estimable from the final recapture probability.
[e] Final recapture probability is not separately estimable from the final probability of apparent survival.

Hawk Mountain Sanctuary and Second Mountain, respectively (Table 3A). The highest and lowest detection rates in the second model set were also estimated for these sites (Table 3B).

Sensitivity Analysis and Model Performance
Estimates of population abundance changed substantially with increasing simulated variation in eagle flight speed (Figure 2B). As the variation in flight speeds increased, variability of the population abundance estimates decreased (i.e. precision increased); however, poor performance of these models ($\hat{c} > 3.0$; Appendix Table 5) suggests that these estimates were inaccurate. Only 2 models, those based on capture histories constructed with ± 1 or 2 SE flight time between sites and with age-class information, had acceptable performance ($\hat{c} \cong 2.996$ and 3.013, respectively; Appendix Table 5). In both cases, after adjusting the models by their values of $\hat{c}$, the saturated (fully site-dependent) model carried virtually all of the QAIC$_c$ weight (>0.999) and model likelihood (1.000; Table 2). Our sensitivity analysis and model performance tests with Program RELEASE suggested that this may have been because capture histories constructed with unaged birds or based on assumptions of more variable flight speeds (± 4 or 6 SE) violated the essential Jolly-Seber model assumptions of equal catchability and survivability of marked eagles (Appendix Table 5).

Number of Eagles Migrating along Kittatinny Ridge
On average, hawk counters recorded ~307 observations of Golden Eagles per year. Capture histories built without age-class data resulted in estimates of population abundance that were smaller and less variable than age-inclusive estimates (Figure 2), but were based on poorly performing models. The mean of the estimates from the 2 best-fitting models ($\hat{c} \leq 3.0$) of the number of Golden Eagles migrating was 1,354 ± 117 SE. These 2 model sets used capture histories built with age-class data and flight speeds of 10.90 ± 0.87 m s^{-1} (using ± 1 SE) or 10.90 ± 1.74 m s^{-1} (using ± 2 SE) between hawk-count sites. Estimated abundance varied annually from 875 ± 76 to 1,942 ± 138 individuals over the study period for flight time ± 1 SE models and from 871 ± 75 to 1,934 ± 137 for flight time ± 2 SE models (Figure 2, Appendix Table 6).

DISCUSSION

Estimates of population abundance are important for the management of many species of conservation concern. Here, we have produced the first quantitatively based estimates for rarely seen Golden Eagles migrating along a single ridgeline in eastern North America. Although admittedly imprecise, these estimates allow us to generally appraise, for the first time, the scale of eagle migration along this ridgeline. Furthermore, these estimates are more robust to variability in eagle migration than estimates generated simply from count data and observer effort without accounting for imperfect detection. Because the type of citizen-science data that we used is common and publicly available, our nontraditional mark–recapture analysis has potential applicability to counts of other migrant species observed at hawk-count sites along topographic diversions or leading lines worldwide.

How Many Golden Eagles Migrate along Kittatinny Ridge?
The fact that our 2 most robust population abundance estimates (i.e. 1,357 ± 117 and 1,350 ± 117 for models including age-class information and ± 1 or 2 SE eagle flight times, respectively, between sites) were almost identical to one another has several implications for interpreting our results. First, these estimates suggest that the hawk-count sites were far enough apart that the adjustment from ± 1 to ± 2 SE of eagle flight time did not affect the likelihood that we would count a Golden Eagle observation as a recapture. Second, the relative strengths of our models with ± 1 or 2 SE of eagle flight time suggest that eagles migrate at a steady rate (i.e. only 0.87–1.74 m s^{-1} around the mean flight speed) and likely in more straight-line, rather than complicated, flight paths. This is consistent with recent GPS telemetry data showing extensive use of orographic updrafts during autumn migration through Pennsylvania (Duerr et al. 2012, 2015, Katzner et al. 2015). Third, we place greater confidence in our age-inclusive population estimates than those produced by models that excluded eagle age-class data. In general, models without age-class data consistently poorly fitted the data ($\hat{c} > 3.0$; Appendix Table 5). Despite this fact, our best models, those with age-class data and ± 1 or 2 SE of eagle flight time between sites, produced estimates of eagle population abundances that were 2 to 3 times larger than unadjusted counts (Appendix Table 6).

Although less robust, our population estimates from models excluding age-class data were consistently less variable than those from their age-inclusive counterparts (Figure 2). Consequently, we believe that aging eagles in flight likely represents a substantial source of interobserver error in the sampling process. Golden Eagles are challenging to age when in flight, especially at considerable distances (e.g., >5 km; Liguori 2004, 2011). In-flight aging relies on (1) birds being close enough for observers to see the flight feathers, and (2) observers having the skill set and timing to accurately characterize those feathers.

It is important to put our population estimates into a context that recognizes both the broad-scale population abundance of Golden Eagles in eastern North America and the threats that Kittatinny Ridge faces. Previous research has suggested that there are ~5,000 Golden Eagles on the
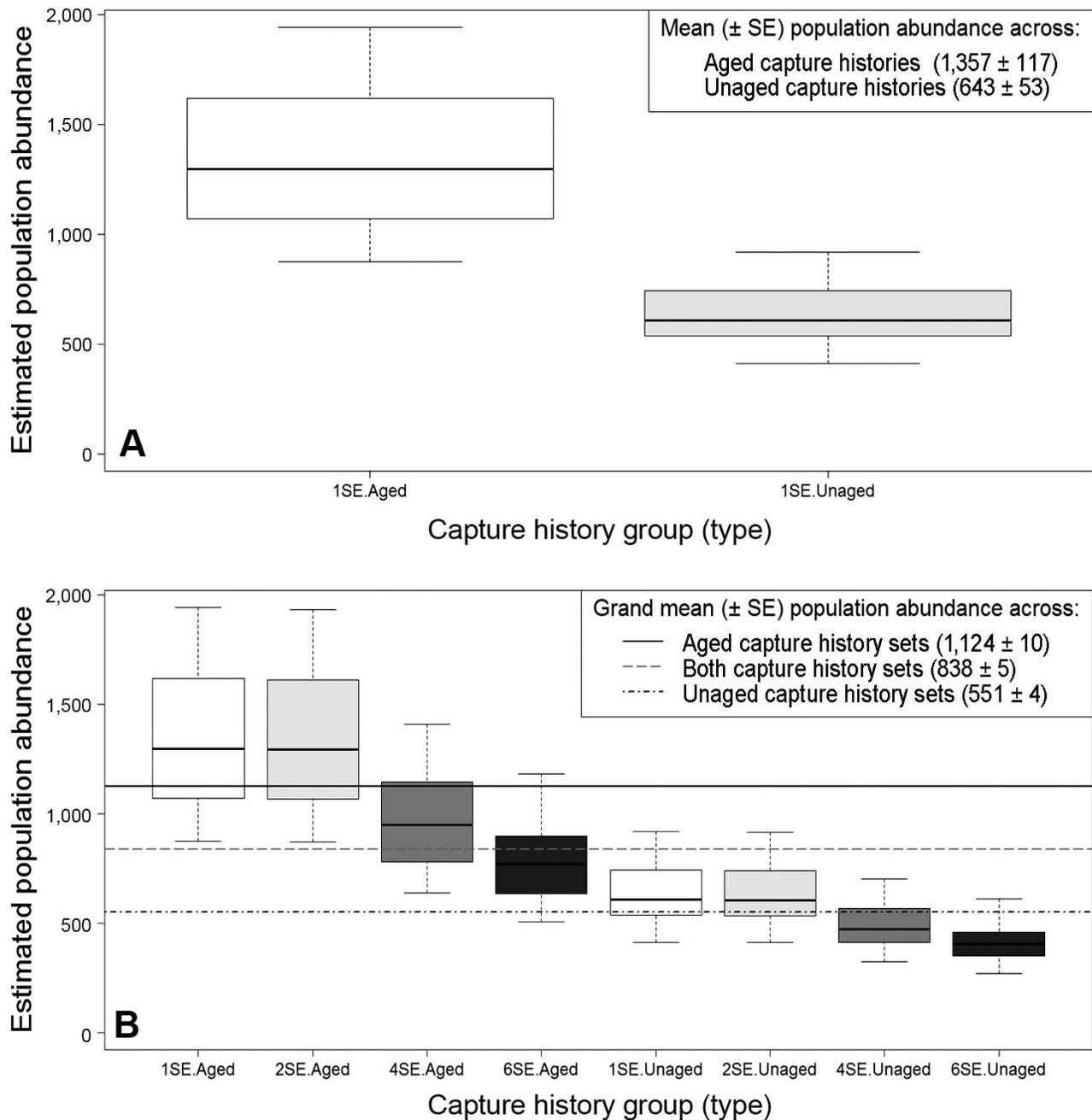
FIGURE 2. Estimated numbers of Golden Eagles migrating annually along Kittatinny Ridge, Pennsylvania, USA, during November, 2002–2011. Estimates are derived from Population Analysis (POPAN) Jolly-Seber mark–recapture models with or without age-class data used to construct capture histories. (**A**) Variation in population estimates based on 1 SE eagle flight time between sites, and (**B**) sensitivity of population estimates to different simulated flight speeds of eagles between hawk-count sites (mean $\pm$ 1, 2, 4, or 6 SE). Both panels summarize estimated mean population abundance within aged, unaged, or both groups. Bold lines show the median, boxes represent the 25th and 75th quartiles, and whiskers represent 1.5 times the interquartile range.

breeding grounds in Québec, Canada, and about that many passing through Pennsylvania, USA, each autumn (Dennhardt et al. 2015a, Morneau et al. 2015). Our analysis here suggests that ~17–27% of this larger population (i.e. 871 and 1,354 individuals divided by 5,000 total eagles for

grand minimum and mean population estimates, respectively) migrates along Kittatinny Ridge during November. Since only 54% of eagles counted along this ridge are seen in November, the total number migrating along Kittatinny Ridge is likely larger than the estimates that we present.

Other key ridgelines to the west of Kittatinny Ridge that are heavily used in Pennsylvania include Bald Eagle, Tussey, and Stone mountains, as well as the Allegheny Front (Dennhardt et al. 2015b). Count data from sites at these other ridgelines are more sparse than those collected along Kittatinny Ridge, and so producing population estimates for these other areas is more challenging. However, if each of these other ridgelines accounts for a similar proportion of migrants as Kittatinny Ridge, then these 5 ridges likely support the migration of >50% of the total eastern Golden Eagle population that passes through Pennsylvania. As such, their conservation is immediately relevant to eagle management (see Miller et al. 2014). Such conservation measures may be especially important in light of the increased consideration for wind energy development along these ridges (USDOE 2016).

Annual variability in the number of eagles is indicative of several important migratory processes. First, the population of Golden Eagles in eastern North America exhibits characteristics of partially migrant populations. Telemetry observations suggest that a few individuals, especially those that breed at more southerly latitudes in eastern Canada, may occasionally overwinter on their breeding grounds (Miller 2012). Likewise, records from a long-term camera-trapping program suggest substantial interannual variation in the numbers of eagles overwintering in New York State, far north of the Kittatinny Ridge hawk-count sites (T. E. Katzner personal observation). The telemetry and camera-trap data together are consistent with eagles showing a migratory response to weather conditions and/or prey availability, which is likely reflected in our models as interannual variation in population estimates.

Applicability, Limitations, and Next Steps
Although our approach produced plausible estimates of population abundance, there are some limitations that should be considered in new applications of our technique. Most importantly, the POPAN parameterization of the Jolly-Seber design produced lower estimates of eagle recapture probabilities than we initially expected (Table 3). Although detection rates for eagles may be low, it is also possible that our time-varying analysis (i.e. based on changing SEs around the mean flight speed) may have resulted in individuals "gaining" or "losing" virtual tags (Arnason and Mills 1981), thus biasing estimates of detection rates. Tag gain and loss violate an important assumption of mark–recapture models; this problem is especially likely in the case of capture histories built using data including incorrectly aged birds. In fact, this bias could only exist in capture histories (1) for birds that were matched or could have been matched when observations between sites included age-class data, or (2) if observers at downstream sites failed to detect birds "marked" or

"recaptured" at upstream sites (likely a rare occurrence, given that eagle migratory flights are often concentrated close to ridgelines during autumn). Furthermore, the aging bias would likely be less of a problem if age-class data were not collected at all sites at all times; if ages are not recorded, we can assume that unaged birds are successfully matched when their flights fall within travel time intervals between sites. Regardless, many of the tests in our sensitivity analysis pointed to violated model assumptions of equal catchability and survivability of marked eagles between sites (Appendix Table 5; Cooch and White 2016). Such violations can significantly bias estimates of population abundance.

It is also possible that Golden Eagles may have frequently left and later returned to the ridgeline (i.e. temporarily emigrated), which would have biased rates of apparent survival. In fact, eagles may frequently leave Kittatinny Ridge to stop over, forage, or roost, and then return later to resume migration. This is commonly seen in studies of other raptor species (Klaassen et al. 2008, Newton 2008). Such behaviors are presumed to influence broad-scale models of eagle migration (Brandes and Ombalski 2004, Brandes 2009, Dennhardt et al. 2015b) and associated estimates of detection rates (Farmer et al. 2010, Dennhardt et al. 2015a). These behaviors would also have influenced our final estimates of population abundance, likely biasing them high, because such temporary emigration could have caused a single eagle to be recorded as 2 different eagles in our capture histories. Use of multistate mark–recapture models may help to address this issue (Dennhardt et al. 2015a).

Because it is possible to identify the age classes of only a few migrant raptor species, future applications of this approach should incorporate a greater understanding of species-specific age information in the construction of models. In addition, modifications of our approach could focus on evaluating (1) the accuracy of the mean and variance of measured flight speeds for different species, (2) heterogeneity in observer proficiency, (3) double-observer sampling methods, (4) observer communication between monitoring sites, (5) sampling designs that help to account for temporary emigration events, (6) rates of tag loss via misclassifications of bird age or timing of detection, and (7) the abundance of low-density species contrasted with that of high-density species, especially in light of possible data violations to key mark–recapture assumptions (e.g., no tag loss). These modifications to our method would improve estimates of key model parameters, thus improving model performance and refining resultant population estimates.

Although hawk-count data are primarily used to assess raptor population trends (Farmer et al. 2008), our approach demonstrates their additional utility to estimation of population abundance. In theory, the mark–

recapture framework that we have developed could be applied in any situation in which raptors or other soaring birds migrate, as long as there is a high likelihood of correctly converting raw count data to individual capture histories. In practice, estimating recapture rates may be easiest where diversions or leading lines (e.g., peninsulas, ridges, or lakeshores) cause raptors to travel sequentially along a narrow front (Kerlinger 1989). Because our approach required long-term effort by hundreds of citizen scientists over time, it is also important to note ways in which these efforts could be more effectively designed to estimate population abundance. In particular, these data would be even more useful to modeling abundance if there were efforts to (1) further standardize citizen-science data collection (Dunn et al. 2005, Silvertown 2009), (2) ensure long-term viability of these monitoring programs (Linden-mayer and Likens 2009), and (3) increase the number and spatiotemporal coverage of count sites along ridgelines, in Important Bird Areas, and in other locations of conservation concern.

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APPENDIX TABLE 4. Model summaries and ranks for 6 additional Population Analysis (POPAN) Jolly-Seber model sets used to estimate the size of populations of Golden Eagles using different flight times (mean $\pm$ 1, 2, 4, or 6 SE) between hawk-count sites along Kittatinny Ridge, Pennsylvania, USA, 2002–2011. Models were ranked by differences in quasi-Akaike's information criterion corrected for small sample size ($\Delta QAIC_c$), quasi-Akaike weights ($QAIC_c$ weight), and model likelihoods. K is the number of model parameters, and Deviance is the model deviance. The capture history type corresponds to the allotted flight time and whether or not we used age-class data from hawk-count data to match individual eagles and construct unique capture histories. Parameters in the POPAN Jolly-Seber models for each capture history type are the probability of apparent survival (Φ), probability of entry (*pent*), probability of recapture (p), and site-level population size (N). We modeled these parameters as either constant (.) or variable (i) at each hawk-count site. All candidate models allowed recapture probability (p) to vary with site and year. All model sets are corrected for the variance inflation factor ($\hat{c}$) of the saturated (i.e. fully site-dependent) model. Due to their problematic diagnostics ($\hat{c} > 3.0$; Appendix Table 5), we considered estimates from these models unreliable for use in eagle management.

Capture history type	$\Delta QAIC_c$	$QAIC_c$ weight	Model likelihood	K	Deviance
4 SE, with age data					
$\Phi(i)pent(i)N(i)$	0.0 [a]	0.974	1.000	20	−1,392.972
$\Phi(i)pent(.)N(i)$	7.3	0.026	0.027	19	−1,383.650
$\Phi(.)pent(i)N(i)$	109.9	0.000	0.000	18	−1,283.976
$\Phi(.)pent(.)N(.)$	127.1	0.000	0.000	8	−1,241.656
6 SE, with age data					
$\Phi(i)pent(i)N(i)$	0.0 [b]	0.942	1.000	20	−1,068.659
$\Phi(i)pent(.)N(i)$	5.7	0.054	0.058	19	−1,060.920
$\Phi(.)pent(.)N(.)$	11.2	0.000	0.000	8	−1,033.239
$\Phi(.)pent(i)N(i)$	86.6	0.000	0.000	18	−977.999
1 SE, without age data					
$\Phi(.)pent(.)N(.)$	0.0 [c]	0.971	1.000	8	−932.567
$\Phi(i)pent(.)N(i)$	7.6	0.021	0.022	19	−947.141
$\Phi(i)pent(i)N(i)$	9.6	0.008	0.008	20	−947.201
$\Phi(.)pent(i)N(i)$	100.8	0.000	0.000	18	−851.978
2 SE, without age data					
$\Phi(.)pent(.)N(.)$	0.0 [d]	0.972	1.000	8	−928.071
$\Phi(i)pent(.)N(i)$	7.8	0.020	0.021	19	−942.513
$\Phi(i)pent(i)N(i)$	9.7	0.008	0.008	20	−942.577
$\Phi(.)pent(i)N(i)$	101.2	0.000	0.000	18	−847.072
4 SE, without age data					
$\Phi(.)pent(.)N(.)$	0.0 [e]	0.996	1.000	8	−654.547
$\Phi(.)pent(i)N(i)$	12.0	0.003	0.022	18	−660.772
$\Phi(i)pent(.)N(i)$	14.0	0.001	0.008	19	−660.772
$\Phi(i)pent(i)N(i)$	16.0	0.000	0.000	20	−660.872
6 SE, without age data					
$\Phi(.)pent(.)N(.)$	0.0 [f]	0.999	1.000	8	−508.980
$\Phi(.)pent(i)N(i)$	14.0	0.001	0.001	18	−515.140
$\Phi(i)pent(.)N(i)$	16.0	0.000	0.000	19	−515.140
$\Phi(i)pent(.)N(i)$	18.1	0.000	0.000	20	−515.151

[a] Top-ranked model $QAIC_c = 698.090$.
[b] Top-ranked model $QAIC_c = 637.853$.
[c] Top-ranked model $QAIC_c = 558.562$.
[d] Top-ranked model $QAIC_c = 558.498$.
[e] Top-ranked model $QAIC_c = 481.850$.
[f] Top-ranked model $QAIC_c = 434.382$.

APPENDIX TABLE 5. Summary diagnostics for 8 Population Analysis (POPAN) Jolly-Seber models used to estimate the size of populations of Golden Eagles using aged or unaged eagles and different simulated flight times (mean ± 1, 2, 4, or 6 SE) between hawk-count sites along Kittatinny Ridge, Pennsylvania, USA, 2002–2011. Program RELEASE reports the results of 3 tests (TEST2, TEST3, and Total), which reveal whether or not capture histories violated the assumptions of the mark–recapture models. TEST2 evaluated the equal catchability of marked eagles, while TEST3 evaluated the equal survivability of marked eagles, both of which were key assumptions under POPAN Jolly-Seber. Capture history types (columns 2–9) correspond to those displayed in Figure 2B and indicate the allotted eagle flight time between sites (1, 2, 4, or 6 SE) and whether or not age-class information (with = Aged, without = Unaged) was used to construct the capture history. Types with values of $\hat{c} > 3.0$ indicate the capture histories that failed the corresponding diagnostic test (TEST2, TEST3) or for which the saturated (fully site-dependent) model poorly fit the capture history data altogether (Total).

Diagnostic [a]	1SE.Aged	2SE.Aged	4SE.Aged	6SE.Aged	1SE.Unaged	2SE.Unaged	4SE.Unaged	6SE.Unaged
TEST2								
χ^2	31.790	32.737	65.223	69.885	168.986	169.811	215.849	234.592
df	14	14	16	17	22	22	23	22
$\hat{c} \cong \chi^2/df$	2.271	2.338	4.076	4.111	7.681	7.719	9.385	10.663
TEST3								
χ^2	67.088	66.689	96.603	153.647	102.287	102.302	198.280	275.817
df	19	19	20	24	20	20	26	26
$\hat{c} \cong \chi^2/df$	3.531	3.510	4.830	6.402	5.114	5.115	7.626	10.608
Total								
χ^2	98.878	99.426	161.826	223.532	271.273	272.114	414.129	510.409
df	33	33	36	41	42	42	49	48
$\hat{c} \cong \chi^2/df$	2.996	3.013	4.495	5.452	6.459	6.479	8.452	10.634

[a] Diagnostic tests correspond to those available for use in package RMark (Laake 2013), which are also discussed at length in Cooch and White (2016).

APPENDIX TABLE 6. Estimates of the number of Golden Eagles ($\hat{N}^*$) migrating along Kittatinny Ridge, Pennsylvania, USA, each autumn from 2002 to 2011, derived from 2 Population Analysis (POPAN) Jolly-Seber model sets, compared with total raw counts of eagles recorded at 5 hawk-count sites along the ridge. Estimates paired with values in parentheses denote the parameter's mean (± SE) during the study period. Autumn counts were not adjusted for annual variation in observer effort and did not vary with capture history type (see Appendix Table 5 for descriptions).

Capture history type	Year	$\hat{N}^*$	Autumn count
(**A**) 1 SE, with age data [†]	2002	1,071 (87)	568
	2003	1,913 (136)	697
	2004	1,135 (91)	480
	2005	1,409 (107)	656
	2006	1,619 (119)	779
	2007	1,189 (94)	514
	2008	1,942 (138)	649
	2009	875 (76)	379
	2010	1,414 (107)	650
	2011	1,008 (84)	622
	$\bar{N}^*$	1,357 (117)	
(**B**) 2 SE, with age data [‡]	2002	1,066 (87)	
	2003	1,903 (135)	
	2004	1,130 (90)	
	2005	1,402 (106)	
	2006	1,612 (118)	
	2007	1,183 (94)	
	2008	1,934 (137)	
	2009	871 (75)	
	2010	1,402 (106)	
	2011	998 (83)	
	$\bar{N}^*$	1,350 (117)	

[†] Model-averaged estimates across candidate models in Table 2A.
[‡] Model-averaged estimates across candidate models in Table 2B.