

## **Golden Eagle Abundance in Alaska: Migration Counts and Movement Data Generate a Conservative Population Estimate**

Authors: Booms, Travis L., Paprocki, Neil A., Eisaguirre, Joseph M., Barger, Chris P., Lewis, Stephen B., et al.

Source: Journal of Raptor Research, 55(4) : 496-509

Published By: Raptor Research Foundation

URL: <https://doi.org/10.3356/JRR-20-81>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# GOLDEN EAGLE ABUNDANCE IN ALASKA: MIGRATION COUNTS AND MOVEMENT DATA GENERATE A CONSERVATIVE POPULATION ESTIMATE

TRAVIS L. BOOMS<sup>1</sup>

*Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701 USA*

NEIL A. PAPROCKI<sup>2</sup>

*HawkWatch International, 2240 South 900 East, Salt Lake City, UT 84106 USA*

JOSEPH M. EISAGUIRRE<sup>3</sup>

*Department of Biology & Wildlife and Department of Mathematics and Statistics, University of Alaska Fairbanks, 982 North Koyukuk Drive, Fairbanks, AK 99775 USA*

CHRIS P. BARGER

*Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701 USA*

STEPHEN B. LEWIS

*US Fish and Wildlife Service, 3000 Vintage Boulevard, Suite 201, Juneau, AK 99801 USA*

GREG A. BREED

*Institute of Arctic Biology, University of Alaska Fairbanks, 982 North Koyukuk Drive, Fairbanks, AK 99775 USA*

**ABSTRACT.**—Estimating species density and abundance is challenging but important for establishing conservation and management strategies. Significant progress has been made toward estimating Golden Eagle (*Aquila chrysaetos*) abundance in the conterminous United States of America (USA) but much less is known about eagle abundance in Alaska. Here, we paired migration count and GPS-tracking data collected near Gunsight Mountain, Alaska, in a Bayesian framework to estimate the number of Golden Eagles in south-central Alaska. We estimated 1204 (95% credible interval: 866, 1526) potentially breeding ( $\geq 4$  yr old) Golden Eagles annually moved through the Gunsight Mountain migration corridor and summered over an area of 150,325 km<sup>2</sup> in south-central Alaska, equating to a density of 0.80 potentially breeding eagles/100 km<sup>2</sup>. By extrapolating across the species' nesting range in Alaska (1,180,489 km<sup>2</sup>) and incorporating published productivity and age-specific survival rates for eagles  $< 4$  yr old into our hierarchical model, we estimated 12,717 (95% credible interval: 9043, 16,349) Golden Eagles of all ages occur in Alaska, annually. We propose this as a conservative statewide population estimate because we used methods that likely underestimated population size. Even so, our estimate is three to five times larger than previous estimates and likely represents about one quarter of the USA's population.

**KEY WORDS:** *Golden Eagle; Aquila chrysaetos; abundance; Alaska; availability; density; migration; telemetry.*

---

<sup>1</sup> Email address: travis.booms@alaska.gov

<sup>2</sup> Present address: Idaho Cooperative Fish and Wildlife Research Unit, College of Natural Resources, 875 Perimeter Drive, Moscow, ID 83844 USA.

<sup>3</sup> Present address: US Fish and Wildlife Service, Marine Mammals Management, 1011 East Tudor Road, Anchorage, AK 99503 USA.

ABUNDANCIA DE *AQUILA CHRYSAETOS* EN ALASKA, EEUU: LOS CONTEOS DURANTE LA MIGRACIÓN Y LOS DATOS DE MOVIMIENTO GENERAN UNA ESTIMACIÓN CONSERVADORA DE SU POBLACIÓN

RESUMEN.—Estimar la densidad y abundancia de una especie es un desafío, pero es importante para establecer estrategias de conservación y manejo. Se han hecho significativos progresos para estimar la abundancia de *Aquila chrysaetos* en la parte contigua de Estados Unidos de América (EEUU), pero mucho menos se sabe sobre la abundancia de esta especie en Alaska. Con el fin de estimar el número de individuos de *A. chrysaetos* en el sur-centro de Alaska, combinamos los conteos migratorios y los datos de seguimiento con GPS recopilados cerca de la Montaña Gunsight en un marco de trabajo bayesiano. Estimamos que 1204 individuos (intervalo creíble del 95%: 866, 1526) con potencial reproductivo ( $\geq 4$  años de edad) se desplazaron anualmente a través del corredor migratorio de la Montaña Gunsight y veranearon en un área de 150,325 km<sup>2</sup> en el sur-centro de Alaska, representando una densidad de 0.80 individuos con potencial reproductivo cada 100 km<sup>2</sup>. Mediante la extrapolación a través del rango de distribución reproductiva de la especie en Alaska (1,180,489 km<sup>2</sup>) e incorporando en nuestro modelo jerárquico la productividad publicada y las tasas de supervivencia específica por edad para las águilas de <4 años de edad, estimamos que anualmente 12,717 individuos de *A. chrysaetos* de todas las edades (intervalo creíble del 95%: 9043, 16,349) están presentes en Alaska. Proponemos este valor como una estimación conservadora de la población de todo el estado, ya que usamos métodos que probablemente subestimaron el tamaño poblacional. Incluso así, nuestra estimación es tres a cinco veces mayor que las estimaciones previas y probablemente la población de Alaska representa cerca de un cuarto de la población de *A. chrysaetos* de los EEUU.

[Traducción del equipo editorial]

INTRODUCTION

Estimating the abundance of animal populations has been a central undertaking in wildlife ecology (Burnham and Overton 1979, Buckland et al. 1993, Collier et al. 2013) and such estimates are important components of conservation and management strategies (Dzul et al. 2013, Millsap et al. 2013, Dennhardt et al. 2015). Abundance can be relatively straightforward to estimate for sessile organisms occurring within a restricted range (Dzul et al. 2013); however, estimating abundance of mobile organisms with wide geographic distributions is more difficult (Whitehead 2002, Dennhardt et al. 2015). Geographically broad sampling strategies designed to estimate abundance over large areas can be expensive (Millsap et al. 2013, Nielson et al. 2014), require large numbers of people (Miller et al. 2016), and can be logistically difficult or near impossible to implement across remote landscapes (Dunn et al. 2005). These factors have collectively limited researchers from rigorously estimating densities and population sizes of many wildlife species in Alaska (Alaska Department of Fish and Game [ADFG] 2015), including the Golden Eagle (*Aquila chrysaetos*).

Golden Eagle abundance estimation has received substantial attention in the USA (US Fish and Wildlife Service [USFWS] 2009, Dennhardt et al. 2015, USFWS 2016), though most efforts have focused on estimates in the conterminous United

States. In 2009 and 2014, the total population size of Golden Eagles in the United States was estimated at 39,000 and 40,000 individuals, respectively (USFWS 2016). Abundance estimates for specific regions within the USA were derived using late summer aerial surveys combined with Breeding Bird Survey data for the western USA (USFWS 2016) and migration count data and flight simulations for the eastern USA (Dennhardt et al. 2015). To estimate the population size in Alaska, the USFWS (2016) used the difference between the average late-summer estimate derived from surveys since 2006 and the average winter aerial survey estimates obtained from 2 yr of winter surveys within the conterminous western USA to estimate the number of migrant eagles present during winter. This number was then proportionally split by land area to approximate the proportion of migrants originating from Alaska (24%) and Canada (76%; USFWS 2016). The resulting estimate ranged from 1000 to 4000 mid-winter Golden Eagles that presumably originated from Alaska (USFWS 2016). The larger estimate (4000) was considered a liberal estimate and the midpoint (2500) a conservative estimate. The USFWS (2009) had previously estimated Alaska's summer population to be 2400 individuals.

McIntyre and Lewis (2016) observed 1364 migrating Golden Eagles during 9 d (39.5 hr) of fall migration counts from a single location in eastern Alaska. However, Golden Eagle migration in Alaska

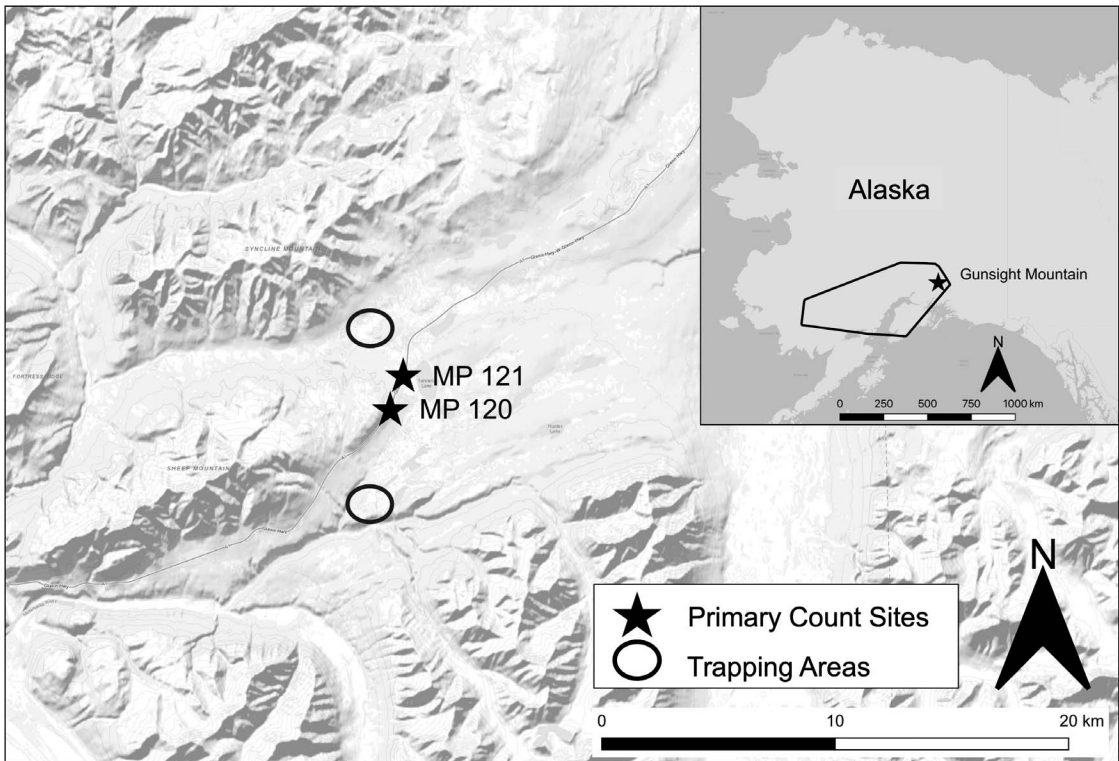


Figure 1. Spring Golden Eagle count (stars) and trapping site locations (circles) at Gunsight Mountain, Alaska, and the approximate area over which remotely tracked eagles summered (inset).

extends over a period of months (McIntyre et al. 2008, ADFG and USFWS unpubl. data) and the migration corridor through eastern Alaska covers an area much larger than what could be seen from a single count site (McIntyre and Lewis 2016, Bedrosian et al. 2018). Hence, McIntyre and Lewis (2016) suggested it was highly improbable that they counted approximately half of the state's estimated 2500 Golden Eagles from one site in 9 d, and the authors highlighted the need for a method to more accurately estimate eagle abundance in Alaska. Therefore, our goal was to provide a more plausible estimate by pairing migration count and GPS-tracking data from birds known to summer in Alaska, along with national demographic estimates, to coarsely estimate the total numbers of Golden Eagles that likely occur in Alaska.

#### METHODS

**Study Area.** We conducted spring migration counts and captured migrating Golden Eagles in south-central Alaska during 2014–2018 in the Gun-

sight Mountain area, near Eureka, AK, USA ( $61^{\circ}51.95'N$ ,  $147^{\circ}20.96'W$ ; Fig. 1). This area is approximately 155 km northeast of Anchorage, Alaska, in the Tahneta Pass between the Chugach and Talkeetna Mountain ranges. The two mountain ranges act as a natural funnel, concentrating migrating raptors moving westward through the pass where they can be counted by observers on the ground and sometimes captured. From this location, birds move westward to arrive on their summering grounds. We ultimately defined our study area as that over which Golden Eagles with satellite transmitters (hereafter, remotely tracked eagles) spent their summers (15 May–31 August) in south-central Alaska during 2014–2018 (Fig. 1 inset).

**Field Methods.** We conducted daily raptor migration counts from 7 March–15 May, 2016–2018 at pull-outs along the Glenn Highway near milepost 120 (March,  $61^{\circ}51.95'N$ ,  $147^{\circ}20.96'W$ ) and milepost 121 (April and May,  $61^{\circ}52.91'N$ ,  $147^{\circ}20.19'W$ ; Fig. 1). We moved to milepost 121 after March to better observe the primary migratory flight line as it shifted

seasonally. Counts were conducted by two experienced migration observers with at least several seasons of raptor migration experience; other HawkWatch International staff and local volunteers provided additional survey effort when available. Observers worked collectively to count migrating raptors; we did not use independent or double-observer methods. Weather permitting, we began observations at 0900 H and ended at 1700 H. We did not conduct counts on the five days when inclement weather (e.g., snow, fog) significantly obstructed views of the main migratory flight lines. All migrating raptors were identified to species, aged when possible, and tallied into 1-hr time intervals (e.g., 1000–1100 AKST). Local raptors (i.e., not actively migrating) were differentiated from migrants based on behavior (e.g., territorial displays), direction of flight, and unique characteristics (e.g., missing feathers, visible transmitters) and were excluded from counts.

We deployed 45-g solar-powered GPS/Argos platform transmitter terminals (Microwave Telemetry, Inc., Columbia, MD, USA) on 53 Golden Eagles ( $n = 15$  in 2014,  $n = 23$  in 2015, and  $n = 15$  in 2016). Transmitters from three eagles failed to provide summer range locations and were not included in these analyses. We captured eagles between 17 March and 6 April annually within 7 km of the count sites (Fig. 1) and considered these eagles part of the population being counted. We used remote-controlled net launchers over carrion bait and placed transmitters on all eagles captured without discrimination by age, sex, body condition, or other variables until no transmitters remained for that year. We attached transmitters to eagles using custom-fit backpack harnesses and programmed transmitters to report 4–14 GPS locations/d depending on season and year (Eisaguirre et al. 2019). We filtered the data for outliers by speed and visual inspection and removed any locations that indicated a movement rate of  $>20$  m/sec or appeared unreasonable. This removed only a few observations from our data set. All data were received through the Argos satellite system and managed in Movebank (<https://www.movebank.org/>); we used only GPS locations that had a reported horizontal error of approximately  $\pm 18$  m (Microwave Telemetry, Inc.) for our analyses. We used plumage to age eagles at time of capture (Liguori 2004), and all 50 eagles used for analyses were  $\geq 4$  yr old. Because eagles have been documented to first attempt breeding at 4 yr of age (Katzner et al. 2020) and because not all adults breed each year, we defined the population we

studied and quantified in south-central Alaska as potential breeders ( $\geq 4$  yr old).

**Study Area Abundance Estimation.** We implemented a Bayesian hierarchical model that integrated migration counts and observations of availability and detectability to estimate Golden Eagle abundance.

**Availability.** We defined availability as the proportion of remotely tracked eagles that likely were within view of the count site when observers were present (i.e., available to be counted). We mapped the observers' viewshed from count locations based on distances to landmarks and the maximum distance we could detect eagles with the naked eye or binoculars ( $< 11$  km; Fig. 2A). The boundaries of the viewshed were irregular and largely dictated by ridgetops of the surrounding mountains, which obscured eagles passing behind them. We used annual spring migration tracks from remotely tracked eagles that reported  $\geq 5$  GPS fixes/d on migration to assess availability of eagles at the count site. Not all transmitters provided adequate data to assess availability each year, and some were therefore excluded from our availability analysis. To account for uncertainty between discrete GPS locations of each eagle, we fit a dynamic Brownian bridge movement model to individual tracks for each spring migration (Farmer et al. 2010) in R (version 3.3.0) with the package *move* (Kranstauber et al. 2012, R Core Team 2016.).

To fit the model, we identified migration departure and arrival dates qualitatively. We defined the start migration point as the first point indicative of a northbound movement with no subsequent return to the individual's apparent winter area and the end migration point as the first point on the summer home range. The movement model was fit to these tracks plus approximately two margin lengths on each end to permit reasonable Brownian motion variance estimates for the entire migration track. The window and margin lengths, used for computing breakpoints in the dynamic Brownian motion variance (Kraunstauber et al. 2012), were set to an average of 3 d and 1 d, respectively, and calculated for each individual independently. We used 95% isopleths of the utilization distributions predicted by the movement models for each individual as estimates of the eagles' realized migratory movement corridors. We then overlaid movement isopleths along with location fix timestamps onto observer viewsheds and visually inspected for overlap.

We defined an eagle as available to be counted if it met two criteria: (1) the movement isopleth at least

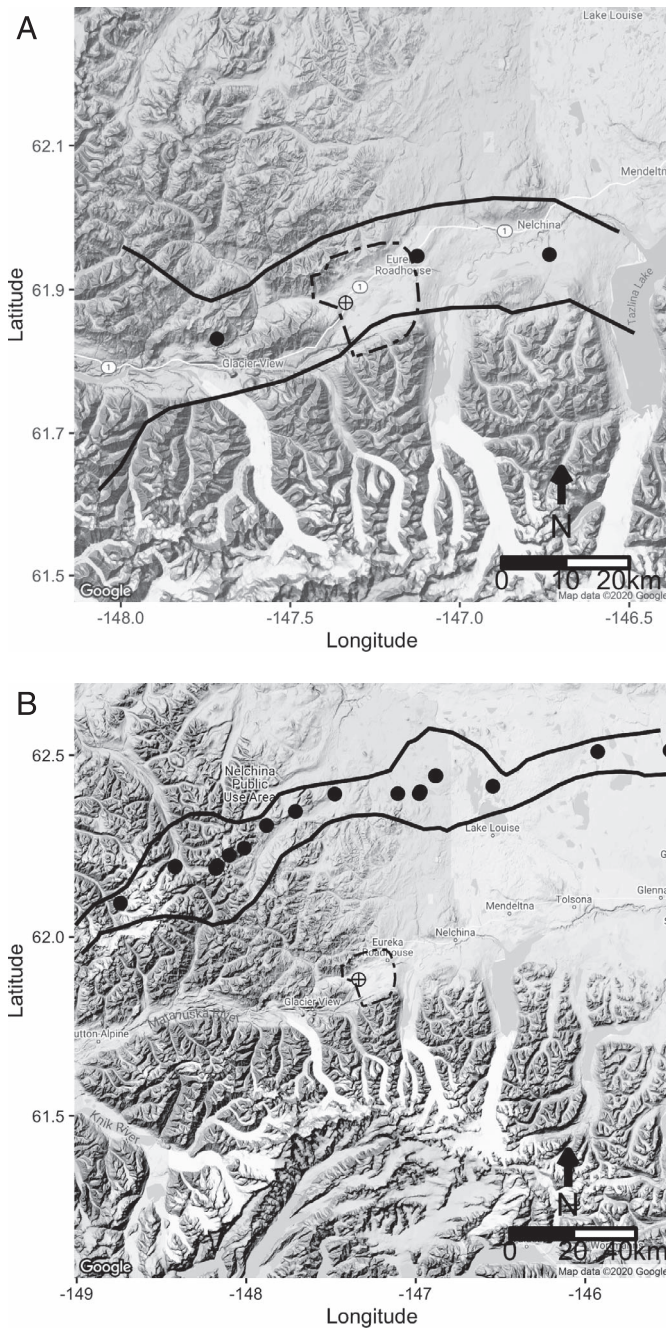


Figure 2. Example migration tracks, based on dynamic Brownian bridge movement models for spring 2016, of two Golden Eagles classified as (A) available and (B) unavailable to be counted based on the viewshed of observers on the ground (dashed line) near Gunsight Mountain, Alaska. Solid line denotes the 95% movement isopleth. Count site is identified by the crosshairs, and black dots indicate GPS locations of eagles during passage.

partially overlapped the observer viewshed (Fig. 2A); and (2) an observer was on duty for at least 1 hr during the possible passage window. If a movement isopleth did not overlap the observer viewshed (Fig. 2B) or no observer was on duty during the time of passage (including the 5 d when inclement weather precluded counts), we defined that eagle as unavailable to be counted.

**Detectability.** We assessed our subset of available eagles for their likelihood of being detected by on-the-ground observers. We defined detectability as the proportion of available eagles likely detected by observers. We classified a remotely tracked eagle as detected if observers counted any eagle during the interval when the movement isopleth passed the count site, irrespective of the recorded flight direction and locale of the available isopleth. We classified an eagle as undetected if observers saw no migrating eagles during that isopleth passage interval. We assumed the probability of eagle detection at a given count location and time was constant regardless of number or identity of observers, use of optics, age of eagles, weather, or flight conditions. We also used the average of two published detection probability estimates (Berthiaume et al. 2009 and Nolte et al. 2016) to create an informative prior in our hierarchical model of abundance (see below).

**Counts.** We adjusted eagle counts to exclude birds <4 yr old (hereafter, pre-breeders) because we did not collect movement data for these age classes and they can exhibit substantially different movements than potential breeders (Katzner et al. 2020). In 2017, highly experienced observers assigned ages to the greatest proportion of eagles counted at Gunsight Mountain in any year (89% of eagles aged; 86% of which we classified as potential breeders). We therefore multiplied each year's count by 0.86 and rounded it to the nearest integer to estimate the total number of potentially breeding eagles that migrated past Gunsight Mountain annually.

We assessed the independence of marked eagles using a Spearman test function in R (*coin* package) with a Monte Carlo distribution approximation to assess independence between our two samples: (1) average counts from 5-d passage windows; and (2) average daily passage of remotely tracked eagles from 5-d passage windows based on dynamic Brownian bridge movement models. We did not remove marked eagles from the count and compared marked eagles to all eagles. We used raw counts not corrected for availability or detection. We

chose a 5-d window *a priori* because 5-d windows are often used to smooth count data, given large, daily migration count fluctuations. We rejected the null hypothesis that the two samples were independent ( $Z=2.74$ ,  $P=0.002$ ) and concluded that our sample of remotely tracked eagles was congruent with our sample of eagles counted. By concluding this, we assumed that (1) our availability and detectability estimates from remotely tracked individuals were representative of the population of migrating eagles being sampled, and (2) remotely tracked eagles were a representative sample of potentially breeding eagles migrating past Gunsight Mountain. Had we failed to reject the null hypothesis, our interpretation of the representativeness of our sample would have been more equivocal.

**Hierarchical model.** We implemented a Bayesian hierarchical model that integrated the observations of availability  $y$  and detectability  $z$  as well as the (adjusted) counts  $C$  to estimate the probabilities of an eagle being available  $p_a$  and detected  $p_d$  and the abundance of potential breeders in the study area  $N_{ad}$ . For year  $t$  and individual  $i$ , the data model took the form:

$$y_i \sim \text{Bernoulli}(p_{a,t}),$$

$$z_i | y_i = 1 \sim \text{Bernoulli}(p_{d,t}),$$

$$C_t \sim \text{Binomial}(N_{ad,t}, p_{a,t} p_{d,t}),$$

and the process model took the form:

$$\text{logit}(p_a) = \mathbf{X}\beta,$$

$$\text{logit}(p_d) = \mathbf{X}\alpha,$$

$$\beta_t \sim \text{Normal}(\mu_\beta, \sigma_\beta^2),$$

$$\alpha_t \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2),$$

$$N_{ad,t} \sim \text{Poisson}(\lambda_t),$$

$$\lambda_t \sim \text{Normal}^+(\mu_\lambda, \sigma_\lambda^2),$$

where  $\mathbf{X}$  is a design matrix indicating the year;  $\mu_\beta$ ,  $\mu_\alpha$ , and  $\mu_\lambda$  are global availability, detectability, and potential breeder abundance, respectively; and  $\text{Normal}^+$  corresponds to the truncated (at zero) normal distribution. To complete the model hierarchy, we specified  $\mu_\beta \sim \text{Normal}(0, 1.75^2)$ ,  $\mu_\alpha \sim \text{Normal}(2, 0.5^2)$ ,  $\mu_\lambda \sim \text{Normal}^+(1000, 300^2)$ , and

InverseGamma(1,1) for all variances. The prior on  $\mu_x$  is strongly informative, centered on the average of two previous detection probabilities estimated for Golden Eagles (89% in Berthiaume et al. [2009] and 84% in Nolte et al. [2016]).

We estimated parameters in the model with a custom Markov chain Monte Carlo (MCMC) algorithm, composed of a combination of Gibbs and Metropolis-Hastings updates, in R. We obtained an MCMC sample from the posterior with three chains of 200,000 iterations (discarding the first 100,000 as burn in) and assessed convergence to the posterior with traceplots. We summarized and reported results from the hierarchical model with posterior means and 95% credible intervals throughout.

*Summer range.* We used kernel density estimates (KDEs) to estimate the summer range size for potentially breeding eagles that used the Gunsight migration corridor; KDE is an approach commonly used in wildlife biology to estimate individual animal home ranges (Worton 1989, Kernohan et al. 2001, Kie et al. 2010, Kie 2013). Burt (1943) defined an animal's home range as the space traversed by an individual in its normal activities of foraging, mating, and caring for young. For this analysis, we expanded this definition to the population level and defined the summering range of a population as the collective space used by marked individuals during the summering period. This approach has been used in other taxa to identify population-level seasonal home ranges (e.g., Nicholson et al. 2016, Viengkone et al. 2018). Based on remote-tracking data and our understanding of this population's behavior, we defined the summering period as 15 May to 31 August. We believe this period represents a conservative estimate of the time over which the population is established on its summer range and avoids including data from late arriving or early departing eagles. To avoid biasing the KDEs toward birds with multiple years of summer locations, we used only the first summer of data for each bird even though eagles returned to the same areas annually. Due to duty cycles' inconsistency among deployment years, the year a transmitter was deployed had an inherent effect on the number of GPS locations reported. We therefore randomly sampled the track of each bird to match the number of locations provided by the duty cycle programmed to collect the fewest locations for a summer (eight locations per day and 872 for the summer). If a transmitter provided fewer than this number, we used all the locations it reported. We combined all of the resulting points

from each eagle into one data set to estimate the collective summer range of the population. We summarized the mean number of fixes per bird  $\pm$  standard errors, with ranges shown in parentheses.

We generated KDEs of the population's summer range in R with the package *adehabitatLT* version 0.3.25 (Calenge 2006). We chose the 95% isopleth of the KDE (hereafter 95% KDE; bivariate normal kernel) as the most appropriate representation of the population's use of space across the summer range (Kernohan et al. 2001). Choice of the bandwidth, or smoothing parameter  $h$ , is important to estimating home ranges with KDEs (Silverman 1986, Worton 1989, 1995, Seaman and Powell 1996, Seaman et al. 1999, Kernohan et al. 2001, Kie 2013). We therefore used two methods to select a bandwidth. The first method was the reference bandwidth ( $h_{ref}$ ; Silverman 1986, Worton 1989), which can result in over smoothing of multi-modal data and a positive bias in home range size estimates (Wand and Jones 1993, Kie 2013). In the second method, we used an adaptation of the "rule-based ad hoc" approach (hereafter ad hoc method), proposed by Kie (2013), which involves sequential scaling of  $h_{ref}$  and visual assessment of the KDE until the KDE fits an *a priori* definition of home range. When the KDE fits the definition, the  $h$  used, and the KDE generated is accepted as the most appropriate for the animal's track. We defined *a priori* the summer range of this population as that which assigned the smallest continuous polygon for the primary range and a secondary polygon for a range comprised of two individuals that summered further west (i.e., smallest area that resulted in two polygons in the 95% KDE, Fig. 3). The ad hoc method resulted in a range much larger than the reference method, which itself is known to positively bias range size (Wand and Jones 1993, Kie 2013). Though we present results of both, we considered the ad hoc method more appropriate for cautiously estimating statewide abundance (a positive bias in our range size causes a negative bias in our statewide population estimate). We calculated eagles/100 km<sup>2</sup> by dividing the population size by range size and multiplying by 100.

We made the following assumptions for our summer range analysis: (1) remotely tracked eagles composed a representative sample of the migratory summering population of potentially breeding eagles; (2) all eagles in the adjusted counts summered within the calculated summering range; and (3) adjusted eagle counts represented the entire



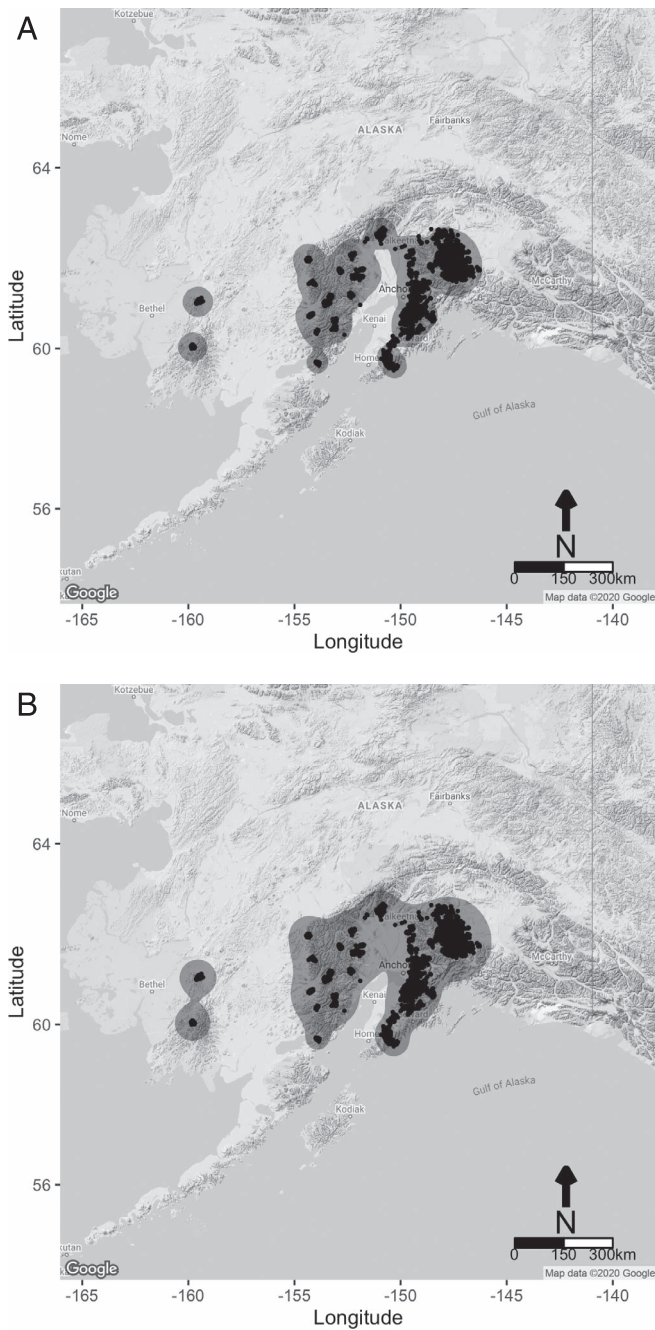


Figure 3. Golden Eagle summer range estimates based on the collective space used by remotely tracked eagles trapped at Gunsight Mountain, Alaska 2014–2016 ( $n=50$ ). Estimates created using two different 95% kernel density estimator (KDE) smoothing parameters: (A) Range One  $h_{ref}$  (B) Range Two  $h_{ad hoc}$ . Gray areas denote the 95% KDE summer range; black dots are eagle GPS locations.

population of potentially breeding migratory eagles summering within the calculated summer range.

**Statewide Abundance Estimation.** To arrive at a statewide estimate that includes eagles of all ages, we first quantified the area over which Golden Eagles nest in Alaska by overlaying the breeding range map from Kochert et al. (2002) onto a georeferenced map of Alaska in ArcGIS 10.7 (Esri, Redlands, CA, USA) and clipped the state map by the breeding range polygon. We then generated posterior realizations from our model, such that  $\lambda_{state}^{(k)} = A_{state}/A_{sample} \times \mu_{\lambda}^{(k)}$  for the  $k$ th MCMC iteration, where  $A_{state}$  is the area of the statewide summer range in Alaska and  $A_{sample}$  is the area of the summer range of the remotely tracked sample of eagles. This provided us an estimate of the number of potential breeders in Alaska. To arrive at posterior realizations of total abundance including all age cohorts, we assumed a stable age distribution and incorporated previously estimated parameters. We specified the statewide abundances for potential breeder, fledgling, first year, second year, and third year age groups as follows:  $N_{ad}^{(k)} \sim \text{Poisson}(\lambda_{state}^{(k)})$ ,  $N_{fl}^{(k)} \sim \text{Poisson}(0.5N_{ad}^{(k)}\psi^{(k)}\phi^{(k)})$ ,  $N_{1Y}^{(k)} \sim \text{Poisson}(s_1^{(k)}N_{fl}^{(k)})$ ,  $N_{2Y}^{(k)} \sim \text{Poisson}(s_2^{(k)}N_{1Y}^{(k)})$ ,  $N_{3Y}^{(k)} \sim \text{Poisson}(s_3^{(k)}N_{2Y}^{(k)})$ .

Here,  $\psi$  and  $\phi$  are the proportion of territorial eagles and productivity, respectively, and each  $s$  is age-specific survival. We used USFWS (2016) national estimates (1.13:1 floater to breeder ratio, 0.54 eagles fledged per occupied territory, and annual age-specific survival rates of 0.70, 0.77, and 0.84 for first-, second-, and third-year birds, respectively; survival rates were incorporated as Beta distributions parameterized by the USFWS), and we specified  $\psi \sim \text{Normal}(1/2.13, 0.01^2)$ ,  $\phi \sim \text{Normal}(0.55, 0.087^2)$ ,  $s_1 \sim \text{Beta}(353, 159)$ ,  $s_2 \sim \text{Beta}(287, 85)$ , and  $s_3 \sim \text{Beta}(243, 47)$ .

Finally, statewide total abundance was  $N_{tot}^{(k)} = N_{ad}^{(k)} + N_{fl}^{(k)} + N_{1Y}^{(k)} + N_{2Y}^{(k)} + N_{3Y}^{(k)}$ . All R code was archived at <http://doi.org/10.5281/zenodo.4474843>.

## RESULTS

We counted 1163, 705, and 1020 migrating Golden Eagles in 2016, 2017, and 2018, respectively, at Gunsight Mountain, Alaska. Our hierarchical model estimated availability and detectability as 0.68 (95% credible interval: 0.39, 0.89) and 0.95 (0.80, 0.99), respectively, although it suggested availability likely varied by year (Fig. 4). The model estimated 1204 (866, 1526) potentially breeding Golden Eagles migrated through the Gunsight

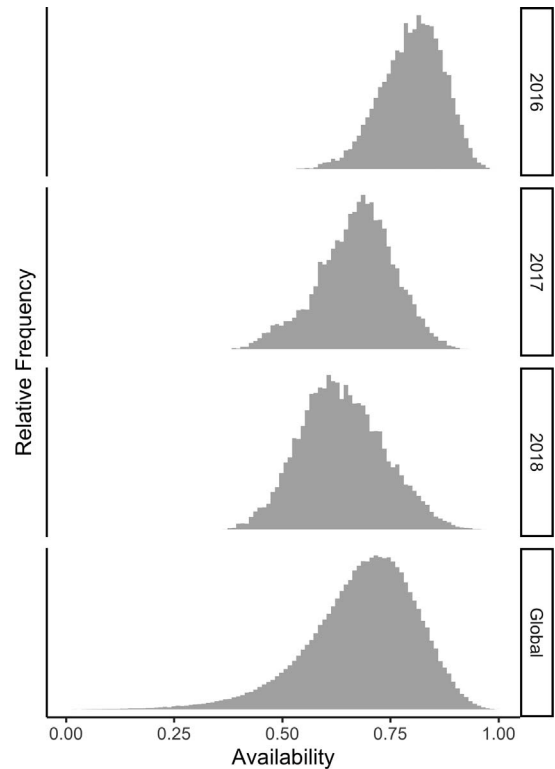


Figure 4. Probability distributions of eagle availability by year and summarized across years (global) for eagles migrating past Gunsight Mountain, Alaska, 2016–2018.

Mountain migration corridor and summered within our study area, annually (Fig. 5).

We collected a total of 52,658 GPS fixes from 15 May to 31 August from the 50 Golden Eagles in our study ( $1053 \pm 39.2$  per individual; range: 175–1518). Of those, we included 41,339 fixes ( $829 \pm 19.3$  per individual; range: 175–872) in our analyses. We estimated the total summer range for our south-central Alaska population at 108,945 km<sup>2</sup> (Range One) and 150,325 km<sup>2</sup> (Range Two; Fig. 3A and 3B, respectively) with resulting mean densities of 1.11 (0.79, 1.40) and 0.80 (0.58, 1.02) potentially breeding eagles/100 km<sup>2</sup>, respectively. The summer range consisted primarily of the western Alaska mountain range, as well as parts of the Talkeetna, Chugach, Kenai, and to a lesser extent, the Kuskokwim mountain ranges. These mountains support large areas of partially forested river valleys, shrub- and tundra-covered mountain slopes, alpine meadows, and barren rocky highlands. The summer range also included large areas of presumably lower

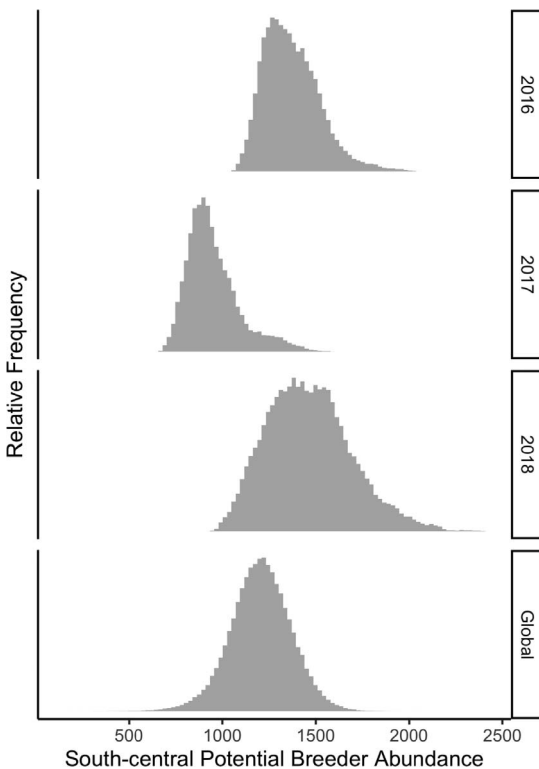


Figure 5. Probability distributions of potentially breeding Golden Eagle abundance in our study area in south-central Alaska from 2016–2018 and summarized across years (global).

quality eagle habitat including glaciers, ocean, and the lowland Susitna River valley.

We estimated the current breeding range of Golden Eagles in Alaska covers 1,180,489 km<sup>2</sup> (69% of Alaska's 1,717,856 km<sup>2</sup>). By applying the Range One (108,945 km<sup>2</sup>) and Two (150,325 km<sup>2</sup>) summer area estimates, the posterior realizations from the hierarchical model that included demographic estimates for pre-breeding eagles suggested a total statewide population size of 17,547 (12,476, 22,553) and 12,717 (9,043, 16,349) Golden Eagles of all age cohorts, respectively.

#### DISCUSSION

We combined Golden Eagle migration counts and movement data from remotely tracked eagles placed in a Bayesian hierarchical framework to conservatively estimate the number of potentially breeding Golden Eagles in our study area in south-central Alaska. We then applied this estimate to the

geographic extent of the Golden Eagle's breeding range in Alaska along with published productivity and age-specific survival rates to arrive at a statewide late summer population estimate of approximately 12,700 eagles of all age classes. We propose this as a coarse conservative statewide population estimate. Though coarse, this estimate represents a three to five-fold increase in the number of eagles in Alaska compared to current USFWS population estimates (2500–4000; USFWS 2016). Hence, our study contributes substantial support to a previous investigation by McIntyre and Lewis (2016) that suggested the number of Golden Eagles in Alaska is much higher than previously estimated. In fact, our estimate shows Alaska likely has the largest population of any regional Golden Eagle management unit in the USA and supports roughly one quarter of the USA population.

Throughout this study, we purposely chose approaches that should guard against overestimating abundance, and we recognize this approach may seem unconventional. However, we consider it the most prudent method given the extrapolations necessary for a statewide estimate, lack of precision in our estimates, the substantial logistical challenges that currently prohibit a more robust, unbiased estimate for Alaska, and the conservation implications of potentially overestimating abundance. We believe our estimate likely underestimates the true abundance of Golden Eagles for several reasons. First, we likely overestimated availability (which lowers adjusted counts) by considering an eagle with any portion of its movement isopleth overlapping the observers' viewshed as available even if only the periphery of the isopleth overlapped. Second, we assumed a remotely tracked eagle was detected if any eagle was counted during that eagle's passage window, even though most eagles passed at distances too far to see a transmitter. This likely artificially inflated our detection probability estimate and lowered adjusted eagle counts. It is noteworthy that our eagle detectability estimate (95%) was quite high despite the strong prior used in the model, which was informed by previous estimates (89% in Berthiaume et al. 2009 and 84% in Nolte et al. 2016). Third, we assumed a constant eagle detection rate regardless of observer identity, weather, and flight conditions even though these factors are known to affect detectability (Berthiaume et al. 2009, Nolte et al. 2016). Accounting for these factors likely would have only reduced detection probability relative to our estimate and hence, raised adjusted counts.

Fourth, we assumed all eagles in our population migrate and were accounted for in our migration counts. However, an unknown but potentially consequential proportion of Golden Eagles, including some tagged in this study, forego migration and overwinter in Alaska in some years (Kessel 1988; T. Booms, S. Lewis, unpubl. data). Any such eagles were not included in our counts and would again cause our population estimate to be biased low. Fifth, we selected the larger of two summer home range estimates, both of which were derived from methods known to be biased high (which result in lower density and population estimates because of the larger denominator). Lastly, we assumed no eagles arriving from other migration routes summered in our study area, which may be unlikely.

Our sample size of 50 remotely tracked Golden Eagles represents an immense effort and is much larger than any previous study of breeding-age Golden Eagles in Alaska (and many other locations), but it is still small compared to the size of the regional and statewide populations we estimated. Small sample sizes and population-level inference are known limitations of remote-tracking work, typically due to financial and logistical constraints (Hebblewhite and Haydon 2010), and are reasons that we chose methods that, if anything, likely underestimate abundance. We attempted to assess how representative our sample was by comparing the timing of passage between marked and all eagles, and we found no statistical difference. Additionally, past studies attempting to assess the number of remotely tracked individuals needed to quantify group-level space use concluded that tens of individuals were needed to approach an asymptote in median area estimates (Gutowsky et al. 2015). Relatively smaller sample sizes ( $n=30$ ) were needed to calculate space use during more sedentary periods of the annual cycle (e.g., breeding season as done here; Thums et al. 2018, reviewed in Sequeira et al. 2019). We therefore concluded that our sample of 50 tagged eagles represented a sufficient sample from the overall population of eagles that uses the Gunsight Mountain migration corridor.

We chose to not exclude substantial areas of water (including ocean) or glaciers from the south-central summer range estimate because one tracked eagle spent long periods of time on the coast and, given the discrete-time nature of tracking data, there is no way of knowing for certain that eagles do not make at least short forays over water or ice. Further, areas of presumably low-quality habitat are likewise included

in the estimated statewide breeding range of the species. Thus, our approach should at least partially account for the variable nature of habitat quality and hence, eagle abundance, in a similar fashion to the large-scale delineation of the nesting range in Alaska.

We purposely excluded pre-breeding Golden Eagles from our study area population and density estimates because (1) we did not have GPS data with which to quantify their summer movements, (2) pre-breeding eagles often exhibit substantially different summer movements than potential breeders (McIntyre et al. 2008, Katzner et al. 2020), and (3) many pre-breeding eagles move outside the study area and Alaska's breeding range (e.g., coastal plain of northern Alaska) during their pre-breeding years (McIntyre and Lewis 2018). It is therefore not surprising that the proportion of potentially breeding eagles in our study area as estimated by the age composition of the count data (86%) was higher than what the national estimates at equilibrium would have predicted (78%, USFWS 2016). Our methods would not have been appropriate to estimate densities for pre-breeding eagles because an unknown portion of them do not occur in our study area or the statewide breeding distribution. Instead, we used national demographic rates (USFWS 2016) to calculate how many younger eagles are produced, survive, and occur in each pre-breeding age class in Alaska. We decided to use national estimates instead of local ones because few such estimates are available for Alaska, and our goal was to use approaches consistent with USFWS (2016) whenever possible. In the longest and most comprehensive study of Golden Eagles in Alaska, McIntyre and Schmidt (2012) estimated average Golden Eagle productivity in Denali National Park (just north of our study area) at 0.62 fledglings per occupied nesting territory, which is higher than the national estimate we used (0.54 fledglings). Using the Alaskan estimate would have increased our statewide population estimate by 300 eagles to a total of approximately 13,000 eagles.

Our density estimate (0.80 potentially breeding eagles/100 km<sup>2</sup>) is at the low end of other North American eagle density estimates, lending support to our conclusion that it is both reasonable and conservative in nature. Millsap et al. (2013) calculated late-summer Golden Eagle densities using western United States aerial survey data and presented the following mean densities within select Bird Conservation Regions (BCR; converted from

eagles/km<sup>2</sup> to eagles/100 km<sup>2</sup>): Southern Rockies/Colorado Plateau (BCR 16) = 0.8; Great Basin (BCR 9) = 0.9; Northern Rockies (BCR 10) = 1.5; and Badlands and Prairies (BCR 17) = 2.7. One important caveat to this comparison is that the Millsap et al. (2013) estimates were calculated from data collected after the breeding season and therefore include recently fledged young and other pre-breeding eagles. Our study area density estimate only includes potentially breeding birds (i.e.,  $\geq 4$  yr old). If pre-breeding eagles had been included, our estimate would have been slightly higher.

Estimating availability and its potential interannual variation at raptor migration sites is important to estimating actual population size as done here. It is also critically important in evaluating broader population indices derived from migratory count data to assess population change over time (Bildstein et al. 2008, Nolte et al. 2016). Importantly, our study is among the first to assess interannual variation in availability of birds at a count site (Fig. 4). Both Farmer et al. (2010) and Dennhardt et al. (2015) quantified availability of migrating birds at count sites but neither estimated how these measures change over time, which is inherently important to ascribing cause to changes. Without such an understanding, it is difficult to differentiate between population-induced changes in counts versus changes in bird availability at count sites. Our data suggest that availability may be influencing changes in raw count data, at least for one migration site.

We recognize that our estimates are based on key assumptions and that we extrapolate beyond our study area to arrive at a coarse estimate of Golden Eagle abundance in Alaska. The size, remoteness, and diversity of habitats in Alaska represent substantial challenges to using more rigorous methods to estimate statewide abundance. The current lack of resources to overcome these challenges leaves few or no feasible alternatives with which to reasonably estimate Golden Eagle abundance for the management community. Though based on relatively simple count and movement data, we contend our approach is logical, reasonable, and based on the best available science. Additionally, even without extrapolating beyond our study area, our corrected migration count of approximately 1200 potentially breeding golden eagles that summer on about 9% of the Alaska's total land mass is almost half of the current USFWS conservative population estimate for all of Alaska. If the USFWS estimate is accurate, then the other half of Alaska's eagles would be distributed

over the remaining 91% of Alaska at extraordinarily low densities—a conclusion we find unlikely. Finally, based on our collective firsthand experience surveying and working with Golden Eagles across Alaska (TLB, 15 yr; SBL, 10 yr; JME, 7 yr), we consider our estimate more plausible and reflective of what we see in the field than previous population estimates. The true Golden Eagle population size in Alaska remains uncertain but given the information we present here and our field experiences, it is likely larger, possibly much larger, than even our conservative estimate of 12,700 eagles.

#### ACKNOWLEDGMENTS

Funding was provided by the Alaska Department of Fish and Game through the Federal Aid State Wildlife Grant Program, Anchorage Audubon Society, Eppley Foundation for Research, HawkWatch International, and the US Fish and Wildlife Service. We thank hawk migration counters R. Rubenthaler, C. Davis, D. Crowson, F. Nicoletti, F. Simone, and S. Nelson for their hard work collecting data, and C. McIntyre, J. Schmidt, G. Pendleton, B. Millsap, J. Pagel, G. Zimmerman, and D. Oleyar who contributed valuable perspectives and suggestions in the development of this manuscript. We also thank A. Duerr and an anonymous peer reviewer for providing additional helpful suggestions. J. Roach assisted with the GIS analysis. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service.

#### LITERATURE CITED

- Alaska Department of Fish and Game (ADFG) (2015). Alaska Wildlife Action Plan. Alaska Department of Fish and Game, Juneau, AK, USA.
- Bedrosian, B. E., R. Domenech, A. Shreading, M. M. Hayes, T. L. Booms, and C. P. Barger (2018). Migration corridors of adult Golden Eagles originating in northwestern North America. *PLoS ONE* 13: e0205204. <https://doi.org/10.1371/journal.pone.0205204>.
- Berthiaume, É., M. Bélisle, and J.-P. Savard (2009). Incorporating detectability into analysis of population trends based on hawk counts: A double-observer approach. *The Condor* 111:43–58.
- Bildstein, K. L., J. P. Smith, E. R. Inzunza, and R. R. Veit (2008). State of North American's Birds of Prey. Nuttall Ornithological Club and American Ornithologist's Union, Washington, DC, USA.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake (1993). *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, London, UK.
- Burnham, K. P., and W. S. Overton (1979). Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60:927–936.

- Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24:346–352.
- Calenge, C. (2006). The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.
- Collier, B. A., S. L. Farrell, A. M. Long, A. J. Campomizzi, K. B. Hays, J. L. Laake, M. L. Morrison, and R. N. Wilkins (2013). Modeling spatially explicit densities of endangered avian species in a heterogeneous landscape. *The Auk* 130:666–676.
- Dennhardt, A. J., A. E. Duerr, D. Brandes, and T. E. Katzner (2015). Integrating citizen-science data with movement models to estimate the size of a migratory Golden Eagle population. *Biological Conservation* 184:68–78.
- Dunn, E. H., B. L. Altman, J. Bart, C. J. Beardmore, H. Berlanga, P. J. H., Blancher, G. S. Butcher, D. W. Demarest, R. Dettmers, W. C. Hunter, E. E. Iñigo-Elias, et al. (2005). High priority needs for range-wide monitoring of North American landbirds. In *Partners in Flight Technical Series No. 2*. <http://www.partnersinflight.org/pubs/ts/02-monitoringneeds.pdf>.
- Dzul, M. C., S. J. Dinsmore, M. C. Quist, D. B. Gaines, K. P. Wilson, M. R. Bower, and P. M. Dixon (2013). A simulation model of the Devils Hole pupfish population using monthly length-frequency distributions. *Population Ecology* 55:325–341.
- Eisaguirre, J. M., M. Auger-Methe, C. P. Barger, S. B. Lewis, T. L. Booms, and G. A. Breed (2019). Dynamic-parameter movement models reveal drivers of migratory pace in a soaring bird. *Frontiers in Ecology and Evolution* 7:317. <https://doi.org/10.3389/fevo.2019.00317>.
- Farmer, C. J., K. Safi, D. R. Barber, I. Newton, M. Martell, and K. L. Bildstein (2010). Efficacy of migration counts for monitoring continental populations of raptors: An example using the Osprey (*Pandion haliaetus*). *The Auk* 127:863–870.
- Gutow, S. E., M. L. Leonard, M. G. Connors, S. A. Shaffer, and I. D. Jonsen. (2015). Individual-level variation and higher-level interpretations of space use in wide-ranging species: An albatross case study of sampling effects. *Frontiers in Marine Science* 2:1–17.
- Hebblewhite, M., and D. T. Haydon (2010). Distinguishing technology from biology: A critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 2303–2312.
- Katzner, T. E., M. N. Kochert, K. Steenhof, C. L. McIntyre, E. H. Craig, and T. A. Miller (2020). Golden Eagle (*Aquila chrysaetos*). In *Birds of the World* (P. G. Rodewald and B. K. Keeney, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.goleag.02>.
- Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh (2001). Analysis of animal space use and movements. In *Radio Tracking and Animal Populations* (J. J. Millspaugh and J. M. Marzluff, Editors). Academic Press, San Diego, CA USA. pp 125–166.
- Kessel, B. (1988). *Birds of the Seward Peninsula, Alaska: Their Biogeography, Seasonality, and Natural History*. University of Alaska Press, Fairbanks, AK, USA.
- Kie, J. G. (2013). A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry* 1:13. <http://www.animalbiotelemetry.com/content/1/1/13>.
- Kie, J. G., J. Matthiopoulos, J. Fieberg, R. A. Powell, F. Cagnacci, M. S. Mitchell, J.-M. Gaillard, and P. R. Moorcroft (2010). The home-range concept: Are traditional estimators still relevant with modern telemetry technology? *Philosophical Transactions of the Royal Society of London B* 365:2221–2231.
- Kochert, M. N., K. Steenhof, C. L. McIntyre, and E. H. Craig (2002). Golden Eagle (*Aquila chrysaetos*). In *The Birds of North America* (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.
- Kranstauber, B., R. Kays, S. D. Lapoint, M. Wikelski, and K. Safi (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology* 81:738–746.
- Liguori, J. (2004). How to age Golden Eagles. *Birding* 36:278–283.
- McIntyre, C. L., D. C. Douglas, and M. W. Collopy (2008). Movements of Golden Eagles (*Aquila chrysaetos*) from interior Alaska during their first year of independence. *The Auk* 125:214–224.
- McIntyre, C. L., and S. B. Lewis (2016). Observations of migrating Golden Eagles (*Aquila chrysaetos*) in eastern interior Alaska offer insights on population size and migration monitoring. *Journal of Raptor Research* 50:254–264.
- McIntyre, C. L., and S. B. Lewis (2018). Statewide movements of non-territorial Golden Eagles in Alaska during the breeding season. Information for developing effective conservation plans. *Alaska Park Science* 17:65–73.
- McIntyre, C. L., and J. H. Schmidt (2012). Ecological and environmental correlates of territory occupancy and breeding performance of migratory Golden Eagles (*Aquila chrysaetos*) in interior Alaska. *Ibis* 154:124–135.
- Miller, R. M., N. Paprocki, M. J. Stuber, C. E. Moulton, and J. D. Carlisle (2016). Short-eared Owl (*Asio flammeus*) surveys in the North American Intermountain West: Utilizing citizen scientists to conduct monitoring across a broad geographic scale. *Avian Conservation and Ecology* 11:3. <http://dx.doi.org/10.5751/ACE-00819-110103>.
- Millsap, B. A., G. S. Zimmerman, J. R. Sauer, R. N. Nielson, M. Otto, E. Bjerre, and R. Murphy (2013). Golden Eagle population trends in the western United States: 1968–2010. *Journal of Wildlife Management* 77:1436–1448.
- Nicholson, K. L., S. M. Arthur, J. S. Horne, E. O. Garton, and P. A. Del Vecchio (2016). Modeling caribou

- movements: Seasonal ranges and migration routes of the central Arctic herd. *PLoS ONE* 11(4):e0150333. <https://doi.org/10.1371/journal.pone.0150333>.
- Nielson, R. M., L. Mcmanus, T. Rintz, L. L. McDonald, R. K. Murphy, W. H. Howe, and R. E. Good (2014). Monitoring abundance of Golden Eagles in the Western United States. *Journal of Wildlife Management* 78:721–730.
- Nolte, E. G., J. Bart, B. P. Pauli, G. S. Kaltenecker, and J. A. Heath (2016). Detectability of migrating raptors and its effect on bias and precision of trend estimates. *Avian Conservation and Ecology* 11:9. <http://dx.doi.org/10.5751/ACE-00894-110209>.
- R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen (1999). Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- Seaman, D. E., and R. A. Powell (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.
- Sequeira, A. M. M., R. M. Heupel, M.-A. Lea, V. M. Eguíluz, C. M. Duarte, M. G. Meekan, M. Thums, H. J. Calich, R. H. Carmichael, D. P. Costa, L. C. Ferreira, et al. (2019). The importance of sample size in marine megafauna tagging studies. *Ecological Applications* 29:1344–1360.
- Silverman, B. W. (1986). *Density Estimation for Statistics and Data Analysis*. Monographs on Statistics and Applied Probability, Chapman and Hall, London, UK.
- Thums, M., J. Rossendell, M. Guinea, and L. Ferreira. (2018). Horizontal and vertical movement behaviour of adult flat-back turtles and spatial overlap with industrial development. *Marine Ecology Progress Series* 602:237–253.
- US Fish and Wildlife Service (USFWS) (2009). *Final Environmental Assessment: Proposal to Permit Take as Provided under the Bald and Golden Eagle Protection Act*. USDI Fish and Wildlife Service, Division of Migratory Bird Management, Washington, DC, USA.
- US Fish and Wildlife Service (USFWS) (2016). *Bald and Golden Eagles: Population Demographics and Estimation of Sustainable Take in the United States, 2016 Update*. USDI Fish and Wildlife Service, Division of Migratory Bird Management, Washington, DC, USA.
- Viengkone, M., A. E. Derocher, E. S. Richardson, M. E. Obbard, M. G. Dyck, N. J. Lunn, V. Sahanatien, B. G. Robinson, and C. S. Davis (2018). Assessing spatial discreteness of Hudson Bay polar bear populations using telemetry and genetics. *Ecosphere* 9:e02364. 10.1002. <https://doi.org/10.1002/ecs2.2364>.
- Wand, M. P., and M. C. Jones (1993). Comparison of smoothing parameterizations in bivariate kernel density estimation. *Journal of the American Statistical Association* 88:520–528.
- Whitehead, H. (2002). Estimates of the current global population size and historical trajectory for sperm whales. *Marine Ecological Press Series* 242:295–304.
- Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.
- Worton, B. J. (1995). Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59:794–800.

Received 4 June 2020; accepted 3 February 2021