## **RESEARCH ARTICLE**



# Estimating abundance in unmarked populations of Golden Eagle (Aquila chrysaetos)

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#### Abstract

- 1. Estimates of species abundance are of key importance in population and ecosystem level research but can be hard to obtain. Study designs using camera traps are increasingly being used for large-scale monitoring of species that are elusive and/or occur naturally at low densities.
- 2. Golden eagle (Aquila chrysaetos) is one such species, and we investigate whether existing large-scale monitoring programs using baited camera traps can be used to estimate the abundance of golden eagles, as an alternative to traditional labour-intensive searches for active territories and nest sites during the breeding period.
- 3. The camera-trap data allowed two measures of abundance to be estimated within each of four main study areas in mid and northern Norway; occupancy was measured as the probability of camera site use, and population size was measured as the number of individuals using camera sites within a study area. Spatial and temporal patterns in occupancy and population size were explored and evaluated against independent estimates of breeding pair density in the study areas.
- 4. Annual estimates of golden eagle occupancy showed low precision, while estimates of population size were more precise in relation to both estimated and anticipated abundance fluctuations. Estimates of population size may therefore be suitable for monitoring within-study area temporal abundance trends, while estimates of occupancy seem unsuitable for such for golden eagles. Across study areas, patterns in both average occupancy and average population density estimated from population size were consistent with the spatial pattern in average breeding pair densities (r = 0.99, and r = 0.89, respectively). This suggests that camera-trap-based estimates of occupancy and population density, both reflect territory density at large spatial scales. In conclusion, our results suggest that baited camera traps can be a cost-effective strategy for monitoring the abundance of golden eagles.

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#### KEYWORDS

Aquila chrysaetos, camera traps, estimating abundance, golden eagle, monitoring

## 1 | INTRODUCTION

Estimates of species occurrence and abundance are of key importance in nature management (e.g. Nichols, 2014) and appropriate sampling designs and statistical analyses are needed to provide unbiased and robust estimates (Murray & Sandercock, 2020; Royle & Dorazio, 2008; Yoccoz et al., 2001). Species that have large home ranges, cryptic behaviour and/or large floater populations provide an extra challenge in terms of study design, logistics and finances. Investigating the use of data from multiple existing monitoring programs is therefore appealing as it may enable improved estimation at a low cost (Rich et al., 2017; Steenweg et al., 2017).

Automated monitoring stations are increasingly used in sampling designs requiring large temporal and spatial scales (Burton et al., 2015; Henden et al., 2014; Jachowski et al., 2015; Weingarth et al., 2015). Automated monitoring stations reduce human presence to a minimum and may therefore reduce biases associated with invasive count sampling and observer effects (e.g. Caravaggi et al., 2017). An increasing number of analytical methods are available for analysing data obtained from such automated sampling designs, including methods accounting for non-perfect detection in unmarked populations (e.g. see review in Bailey et al., 2014) and mark capture-recapture models that take unique natural markings of individuals into account (e.g. Denes et al., 2015; Hostetter et al., 2019; Karanth et al., 2004; McClintock, 2015; Méndez et al., 2019).

Golden eagles (Aquila chrysaetos) have a wide distribution in the northern hemisphere, but are typically found at low breeding population densities and are cryptic for large periods of the year and inhabit areas that are often difficult to access (Katzner et al., 2020; Nygård et al., 2016; Watson, 2010). Both migratory and non-migratory populations have been documented (Katzner et al., 2020), home ranges may vary seasonally and in their first years of life individuals join a floater population with extended geographic space use (e.g. Brown et al., 2017; McIntyre et al., 2008; Nygård et al., 2016; Poessel et al., 2016). Monitoring programs typically focus on the density and productivity of the breeding population, through monitoring of territories and nest sites (e.g. Derlink et al., 2018; Gjershaug et al., 2018; Jachowski et al., 2015; Katzner et al., 2020; Mabille et al., 2015; Tovmo et al., 2020; Tveraa et al., 2014; Watson, 2010). Diet varies widely both temporally and spatially in relation to availability, and golden eagles are both predators and carrion consumers (Katzner et al., 2020; Mattisson et al., 2017; Watson, 2010). They are frequent visitors to baits during the winter months, and this suggests that baited camera traps may be an efficient approach to monitoring their abundance (Hamel et al., 2013; Henden et al., 2014; Jachowski et al., 2015). Furthermore, considerable plumage variation exists between individuals (e.g. Ellis, 1979; Orrhult, 2017), but whether it can be used to estimate variation in the abundance of golden eagles using camera traps has received little attention (e.g. Vukovich et al., 2015; Vukovich et al., 2021).

# We used data from two existing large-scale multi-annual camera monitoring programs in Norway (Henden et al., 2014; Killengreen et al., 2012; Rød-Eriksen, 2020) to investigate whether automated camera monitoring at baits can be used to estimate spatio-temporal variation in the abundance of golden eagles. We used occupancy modelling (MacKenzie et al., 2017; Royle & Dorazio, 2008) to estimate camera site probability of occupancy during the sampling period. In addition, we used mark-recapture analysis (McClintock, 2015) to estimate golden eagle population sizes in the study areas covered by the camera-trap monitoring programs, using the natural asymmetrical patterns in eagle plumage as individual markers. We compared the pattern of between-year variation in these two measures of abundance (occupancy and population size) and investigated their relationship with independent estimates of the density of territories in the study areas based on the national monitoring scheme for breeding golden eagles in Norway (e.g. Tovmo et al., 2020).

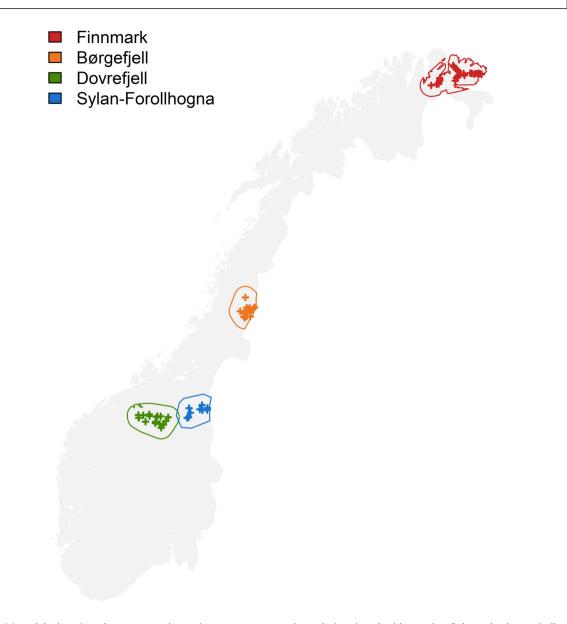
## 2 | MATERIALS AND METHODS

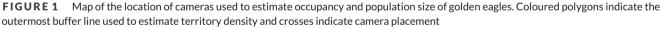
#### 2.1 | Monitoring data

The data used were obtained from two regional research projects targeted towards the conservation of the nationally endangered arctic fox (*Vulpes lagopus*) (COAT, 2021; Rød-Eriksen, 2020). Both projects use baited camera traps (RECONYX©) during late winter with the primary goal to monitor arctic fox abundances as well as other potentially competitive species in the scavenger community, including golden eagles. Data from the COAT monitoring program originate from the north-eastern part of Finnmark County (70°N and 26–30°E) in the low arctic tundra bioclimatic zone, and mountain plateaus typically < 400 m a.s.l. (Killengreen et al., 2007; Figure 1). Data from the second monitoring program originate from three areas in mid-Norway (Rød-Eriksen, 2020), Dovrefjell (62°22'N and 9°03'E) and Sylan-Forollhogna (63°00'N and 12°09'E) in the low alpine bioclimatic zone, and Børgefjell (65°15' and 13°46') in the north boreal to low alpine bioclimatic zone and with peaks between 1000 and 1900 m a.s.l.

#### 2.2 | Study design

In each study area, between seven and 25 camera traps were deployed each year with placements designed to cover the gradient from the boreal to the tundra biome (Table 1). Polygons made by the convex hull connecting the outer camera traps within each study area covered from





970 to 3200 km<sup>2</sup> (Table 1). Each camera trap consisted of a camera (RECONYX HyperFire Professional P800 IR) positioned half a meter above ground and 5 m from a 15–20 kg frozen reindeer offal block. Blocks were replaced non-systematically between two and four times during each survey period depending on the site. Pictures of the offal blocks were taken at 10-min intervals. Poor quality images occurred due to adverse weather or snow covering the lens and only days with a minimum of 50 good quality pictures were included in analyses.

In Finnmark, we used data from the inception of the monitoring design in 2005(e.g. Killengreen et al., 2012 for a full description of monitoring design) until 2015. Preliminary investigation revealed that there was too little variation to investigate occupancy, abundance and eagle territory density at finer spatial scales within the Finnmark study

area. In mid-Norway, cameras have been programmed to take images at predetermined time intervals since 2011 at Dovrefjell, Børgefjell and Sylan-Forollhogna. At Dovrefjell, monitoring was terminated in 2013. At Børgefjell and Sylan-Forollhogna, we used data from 2011 to 2014.

Territory holders of golden eagles in Scandinavia show both yearround attendance and migratory movements outside the breeding season (Moss et al., 2014; Stien et al. unpub. data; Tikkanen et al., 2018). In all study areas, the camera traps were operational in late winter to spring (February–early June; Table 1). The study design therefore covers the breeding season, as territory defence, display and nest building commence in February, and the data are therefore likely to include individuals holding active territories nearby.

<b>TABLE 1</b> Summary of study designs and data obtained from the camera traps in Finnmark, Børgefjell, Dovrefjell and Sylan-Forollhogna. Mean distance and max distance refer to mean and
maximum distances between nearest cameras. For Finnmark, distance between mountain chains varied between 16 and 50 km. Range of operating days refers to the number of days cameras
recorded more than 49 images. Daily presence is the number of days at least one golden eagle was recorded at a camera and percent presence expresses daily presence over the total number of
operational days

Finnmark 11 3206 1	cameras	Mean distance (km)	Max distance (km)	Max range operating days	Range of operating days	Daily presence	Total sampling days	% presence
	15-25	6.0	14	Mid Feb-late Apr	33-70	371	7118	0.05
Børgefjell 4 1228 1	14	14.7	33	Early Feb-early Jun	76-114	44	2735	0.02
Dovrefjell 3 1655 8	8-13	15.8	34	Late Feb-late May	68-87	81	1530	0.05
Sylan-Forollhogna 4 968 7	7-9	21.9	49	Mar-mid Jun	19-48	17	1293	0.01

### 2.3 | Occupancy estimation

We aggregated the information on the camera images to simple detection/non-detection (1/0) of at least one golden eagle for each day and camera trap before occupancy analyses. We analysed the daily data on golden eagle presence/absence at each camera trap using the single season closed occupancy model by MacKenzie et al. (2002), using zero-inflated binomial models (MacKenzie, 2006; Royle & Dorazio, 2008), and fitted using the R package unmarked (Fiske & Chandler, 2011; R Core Team, 2020). Occupancy models estimate occupancy as the probability of occurrence (w) adjusted by an estimated probability of detection (b) (Royle & Dorazio, 2008).

Probability of detection was modelled as a function of presence/absence of bait (0/1), presence/absence of a golden eagle at the camera trap the previous day (0/1), and year fitted as a factor. Occupancy was modelled as a function of year fitted as a factor. Data from the four study areas were analysed separately. To obtain estimates of the overall average occupancy within an area, that is, pooled year estimates, we used only the two predictor variables presence of bait and eagle the previous day in the model for the probability of detection, and the intercept alone to model occupancy.

# 2.4 | Abundance estimation and density of individuals

Golden eagles moult annually and have both age-specific and withinage individual variation in their plumage (Watson, 2010). Moult is incomplete, bilaterally asymmetrical and can occur between March and November, so that within a season individual specific plumage patterns can often be reliably recognized when individuals are seen repeatedly (Ellis, 1979; Tjernberg, 1977). Moult patterns can also be used to give a coarse indication of age. We identified age based on keys in Orrhult (2017) and Leksands Fågelklubb (2021) and used the estimates of age to evaluate whether individuals were likely to be territorial or non-territorial. Golden eagles are long-lived and typically do not hold a territory before they are 4 years old or more (Watson, 2010). In the present study, we chose to include individuals 3 years old (4th winter plumage) or more. This was done because there is substantial uncertainty in the ageing of eagles close to 4 years old due to high variation in their plumage characteristics (e.g. Orrhult, 2017). We have no knowledge of the age and turnover rates of territorial individuals locally in the study areas, and individuals less than 4 years old have been recorded as territory holders in some study systems (Haworth et al., 2006; Sánchez-Zapata et al., 2000; Steenhof et al., 1983), suggesting that our youngest age class may also include territory holders. By including individuals aged as 4th winter plumage we included two individuals at baits in Finnmark, six individuals in Børgefjell and seven individuals in Dovrefjell. Whether we included or excluded individuals with 4th winter plumage when estimating population sizes did not affect the general conclusions of the study.

We identified eagles to individual level from individual plumage characteristics observed on the left- or right-hand side only, or from both sides. The latter was possible for ringed individuals and consecutive images indicating the same individual had turned round. Incorrect identification of naturally marked individuals is a potential bias in camera identified individuals (Johansson et al., 2020). To reduce the chance of incorrect identification, images were classified in two rounds with several months between rounds. During each round, images were first labelled in chronological order and thereafter in random order within known sites. Where individual identification differed between viewings, the images were reviewed. In some cases, identity could not be identified due to poor picture quality or poor visibility of crucial feathers. In addition, false identification at multiple sites was reduced by ensuring images related to the same individual did not occur at multiple cameras too close in time, assuming the average flight speed for golden eagles to be 18 m/s (Lanzone et al., 2012). In the analyses, we did not include individuals with plumage indicating that they were 2 years old or less (first to third winter plumage). These individuals are unlikely to hold a territory (Watson, 2010) and lacked individual defining feather plumage.

Estimation of population size was undertaken using the library multimark (McClintock, 2015) in R (R Core Team, 2020). Although natural marks may be unique to an individual, they may be bilaterally asymmetrical. Multimark facilitates the joint analysis of only partly known (type 1 – known left hand side encounter  $\hat{Y}_1$ , type 2 – known right hand side encounter  $\hat{Y}_2$ ) and known encounter histories ( $\hat{Y}_{known}$  – type 3 encounter), while accounting for uncertainty in the number of unique individuals encountered. Latent encounter histories (Y) generate the observed encounter histories ( $\hat{Y}_1$ ,  $\hat{Y}_2$ ,  $\hat{Y}_{known}$ ) and the analysis estimates the set of latent encounter histories that are feasible given the observed encounter histories so that capture-recapture models can be fitted (McClintock et al., 2013). Models were fitted separately to data from Finnmark (2011-2015), Børgefjell (2011-2014) and Dovrefjell (2011-2013) for each year as moult histories from 1 year to the next are unknown. As in McClintock et al. (2013), observations that could not be assigned identity were excluded from the analysis. In total there were n = 29 encounter his from Finnmark (23 seen more than once), n = 16 for Børgefjell (9 seen more than once) and n = 30 for Dovrefjell (23 seen more than once). There were too little data to allow the model to be fitted to the data from Sylan-Forollhogna, that is, in 2011, there was only one eagle detected and no recaptures; in 2012, there were two eagles detected and no recaptures; in 2013, there were three individuals and no recaptures; and in 2014, there were three individuals and only one of these with one recapture.

Individual daily encounter histories were coded using: 0 = no encounter, 1 = left-hand side encounter, 2 = right-hand side encounter and 3 = known non-simultaneous left and right-hand side encounter histories. Preliminary exploration of the data indicated that models could only be fitted with an intercept to estimate abundance and detection probabilities. Models were fitted using 50,000 MCMC iterations with burn in of 25,000 iterations. Conditional probabilities for left- and

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right-hand encounters were allowed to vary. Model diagnostics that assessed chain convergence and effective sample size were obtained using the R package coda. Model selection was carried out by inspecting the estimates and their 95% credibility intervals. Eagle density was estimated by dividing the estimated population size within a study area by an estimate of the study area and scaled to give an estimate of the density of eagles per 1000 km<sup>2</sup>. The area that the camera traps covered was defined using a convex hull (R package rgeos) covering the geographical coordinates of the camera traps and is hereafter referred to as the camera site area with buffer = 0 km (Figure S1 and Table S1).

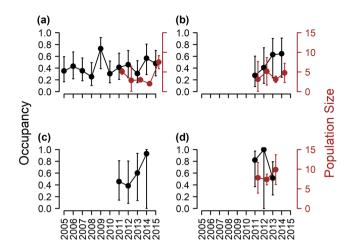
#### 2.5 | Territory density estimation

The bait monitoring period (February–mid June) overlapped the breeding period for golden eagles which is February–end of August in Norway. All camera traps were in the vicinity of one or more known golden eagle territories (Dahl et al., 2015, https://rovdata.no) and territory holders are expected to be more numerous than non-territorial birds (Nilsen et al., 2015). We therefore expected abundance estimates to be positively related to the density of territory holding golden eagles in the study areas.

We estimated golden eagle territory densities using co-ordinates from known nest sites recorded in the national database for golden eagle territories (https://rovdata.no). A territory is defined as a specific area having one or more known nests (https://rovdata.no/Konge%C3% B8rn/Instrukser.aspx) and is in agreement with the non-ambiguous terminology recommended in Steenhof et al. (2017). Where multiple nests were recorded within the same territory, we used the Euclidean mid-point of the nests as the territory co-ordinate. All territories within a study area were counted when estimating territory densities.

In the absence of empirical data on the space use of golden eagles, we used different definitions for the area covered by camera traps within each study area. The minimum study area was defined using the camera-trap locations as the border of the study area as given by the camera site area with buffer = 0 km. In addition, we added buffer zones around each camera trap with 5 km intervals up to a maximum distance of 30 km (Table S1 and Figure 1). This buffer range corresponds to the range of breeding territory areas (20–700 km<sup>2</sup>) reported in Scandinavia and Scotland (Moss et al., 2014; Singh et al., 2016; Tikkanen et al., 2018; Whitfield et al., 2001) assuming circular territories. Buffer zones are clipped to coastline and due to absence of nesting territory data from Sweden, the national border with Sweden.

Sampling effort in the monitoring of territories varied between years (Dahl et al., 2015). We used data from the time period corresponding to the camera monitoring period when calculating mean number of territories per area, that is, for Børgefjell and Sylan-Forollhogna 2011–2014, Dovrefjell 2011–2012, while for Finnmark we used the time-period 1995–2015. Territory densities were expressed as the number of territories per 1000 km<sup>2</sup>.



**FIGURE 2** Estimates of annual eagle occupancy (black points) and population size (brown points) at camera monitored baits in late winter and spring for (a) north-east Finnmark, (b) Børgefjell, (c) Sylan-Forollhogna and (d) Dovrefjell. Estimates are shown with 95% confidence intervals

### 3 | RESULTS

# 4 | Estimates of annual occupancy and annual abundance

In all study areas, annual estimates of golden eagle occupancy had low precision (Figure 2). The estimated confidence limits for annual estimates were large in relation to both the estimated and the theoretically possible variation in occupancy (0–1). This makes the estimates of occupancy unsuitable for evaluating temporal trends in abundance. The most precise estimates were obtained in Finnmark where occupancy estimates varied around 0.4 for most years, but with the estimated occupancy in 2009 being higher (0.73; Figure 2(a)). In the occupancy models, the probability of detection was in general estimated to be low, but was improved when a bait was present, and by the presence of a golden eagle the previous day (Table 2).

The precision of the estimates of golden eagle population size (Figure 2) varied depending on data quality with the narrowest 95% confidence intervals occurring when both sides of individuals were identified in most individuals. There was no strong correlation between annual estimates of occupancy and population size within the study areas where both statistics were estimable (Finnmark: r = -0.04; Børgefjell: r = 0.15).

# 4.1 | Study area level estimates of occupancy, eagle density and territory density

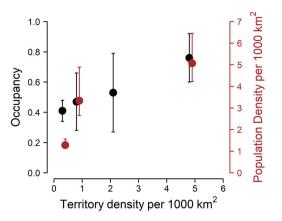
Territory density was lowest for Finnmark (0.3 territories per 1000 km<sup>2</sup>), slightly higher for Børgefjell (0.8 per 1000 km<sup>2</sup>), higher again for Sylan-Forollhogna (2.1 per 1000 km<sup>2</sup>) and highest for

**TABLE 2** Detection coefficient estimates (logit-scale) for bait (bait = 1), previous day presence (prev.pres = 1) and year (with 2005 being the reference level) for golden eagles associated with estimates of golden eagle occupancy at camera sites in Sylan-Forollhogna, Finnmark, Børgefjell and Dovrefjell

Area	ρ	Estimate	$\pm SE$
Sylan Forollhogna	Intercept	-14.60	64.00
	Bait	12.00	64.00
Dovrefjell	Intercept	-6.54	1.01
	Bait	4.55	1.01
	Prev. pres	1.47	0.28
Bjørgefjell	Intercept	-6.76	1.02
	Bait	4.08	1.02
	Prev. pres	2.39	0.44
Finnmark	Intercept	-5.17	0.40
	Bait	2.63	0.32
	Prev. pres	2.18	0.14
	2006	0.06	0.34
	2007	0.58	0.32
	2008	0.33	0.38
	2009	0.84	0.33
	2010	0.54	0.35
	2011	0.96	0.34
	2012	0.73	0.39
	2013	0.80	0.33
	2014	0.07	0.36
	2015	0.45	0.33

Dovrefjell (4.8 per 1000 km<sup>2</sup>, all estimates based on 0 km buffer zone; Table S1). The rank of the areas with respect to territory density was independent of the width of the buffer zone used around the camera traps when calculating territory densities (Table S1). The estimates of the population density of eagles, based on population size estimates using mark-recapture models, showed the same pattern across areas with 1.3, 3.3 and 5.1 individuals per 1000 km<sup>2</sup> for Finnmark, Børgefjell and Dovrefjell, respectively (r = 0.89; Figure 3 and Table S1). The average golden eagle occupancy in the four study areas were also strongly correlated to their territory density (r = 0.99; Figure 3).

As one territory contains one eagle pair, population densities, estimated from population size could be expected to be at least twice the territory density. While the relationship between territory density and population density was positive, the ratio of population density to territory density decreased with increasing territory density and was close to 1 for Dovrefjell (Figure 3). If assuming reasonable territory sizes of 100 km<sup>2</sup> - 300 km<sup>2</sup> when estimating territory densities (Table S1) population density was only about two thirds the territory density for Børgefjell and around half the estimated territory density in Dovrefjell (Table S1).



**FIGURE 3** Relationship between estimated density of golden eagle territories (per 1000 km<sup>2</sup> and 0 km buffer), estimated golden eagle occupancy (black points) and estimated golden eagle population densities (per 1000 km<sup>2</sup>, brown points). Estimates are plotted with 95% Cl. The data points represent areas of increasing territory densities from Finnmark with lowest density, then Børgefjell and Sylan-Forollhogna and Dovrefjell with the highest density

## 5 DISCUSSION

The data from baited camera traps resulted in population size estimates based on individual feather patterns that had relatively high precision. This suggests that such study designs could be useful in monitoring variation in golden eagle abundance on an annual scale. We also found that average density estimates for the study areas, based on our population size estimates, showed high correlation with estimates of average territory density and occupancy. This suggests that all of these estimates are spatially consistent. Population size estimates based on individual identification of feather patterns therefore seems like the most promising approach for monitoring golden eagle abundance in monitoring programs utilizing baited camera traps. A challenge is, however, the large amount of work involved in distinguishing individual feather patterns, and also that many images do not allow individual identification. Lack of suitable images was largely due to a lack of relevant body shots of the eagles. The use of video instead of pictures could improve the chances of individual identification, as birds can be quite active, presenting different body angles and postures whilst feeding. Vukovich et al. (2015) have suggested an alternative approach by identifying individuals based on unique adult tail patterns. However, we found very few pictures that were suitable for tail-based identification, and far fewer than using left and right-hand side body images.

The camera-trap data resulted in annual estimates for occupancy with very low precision. This suggests that the study designs used in the two existing monitoring programs for research on arctic fox is not suitable for documenting between year variation in golden eagle occupancy. The model we used (MacKenzie et al., 2002) is designed to account for incomplete detection in rare species, however, low precision is a common problem in these situations (e.g. Sileshi et al., 2009; Steenweg et al., 2018). Hamel et al. (2013) found that estimation of occupancy stabilized, and precision was maximized when data from 20 to 30 consecutive days of problem free camera functioning was available for species with intermediate presence, including golden eagles. Furthermore, frequent renewals of the bait would help to maintain its attractiveness. We had more than 30 sampling days for most camera traps, except for Sylan-Forollhogna, where only one of four survey years had more than 30 sampling days. Still, occupancy analysis appears to have limited use for the monitoring of between year variation in the abundance of golden eagles.

Area-level average estimates of occupancy that were pooled over multiple years had higher precision, suggesting that this measure resulted in useful information with respect to large scale spatial variability in abundance. Accordingly, both estimates of occupancy and population size showed a positive relationship to abundance estimated by territory density. For all the measures of golden eagle abundance, the estimates of abundance decreased with latitude. The lowest estimates of abundance were from the northernmost tundra in Finnmark (territory density 1 pair per c.1000-3000 km<sup>2</sup>; Figure 3). Golden eagle abundance estimates were lower in the mountain region of Børgefjell (1 pair per c.400-1200 km<sup>2</sup>), and the highest estimates were for the most southern regions of Sylan-Forollhogna (1 pair per 300-500 km<sup>2</sup>) and Dovrefjell (1 pair per 200 km<sup>2</sup>; Figure 1 and Table S1). The estimates of territory densities in Finnmark were similar to estimates obtained at high latitudes in North America (1 pair per 961 km<sup>2</sup> in Hudson Bay; Katzner et al., 2020). Territory sizes consistent with the territory densities in the study areas further south in Norway have been reported for breeding birds in Finland (150-320 km<sup>2</sup>; Tikkanen et al., 2018) while smaller territories have been reported from Sweden (30-70 km<sup>2</sup>; Singh et al., 2016). Territory size is expected to be negatively related to the local food availability (Watson, 2010).

Our study provides proof of the concept that monitoring programs using baited camera traps can deliver suitable data for the monitoring of the abundance of golden eagle. Camera-trap data have wide reaching applicability, including quantification of demographic processes (e.g. Abadi et al., 2010; Arnold et al., 2018; Fasce et al., 2011), the role of carcass consumers in ecosystem functioning and wildlife conflicts (e.g. Blazquez et al., 2009; Moleon et al., 2014; Tveraa et al., 2014), regional variation in movement patterns (Katzner et al., 2020), intraspecies and interspecies interactions at baits (Halley & Gjershaug, 1998) and improved understanding of individual variation in moult (e.g. Orrhult, 2017). Camera-trap monitoring programs are expensive to run, e.g. field and image processing costs in the monitoring program for mid-Norway are c.40 000 EUR per year. Therefore, using the data generated from monitoring multiple target species can be a cost-effective strategy. Costs of utilizing image data from camera traps are likely to be cut further with the continual development of automatic taxonomic and individual identification of species (e.g. Delplanque et al., 2021; Ferreira et al., 2020). Estimation of population size is widely applicable for any species where identification of individuals from visual body patterns is possible from camera-trap images and utilizing existing data series is especially useful considering the importance and need for long-time data series for knowledge-based management of biodiversity and ecosystems (Legge et al., 2018; O'Donnell et al., 2021; Rushing et al., 2016).

A logical next step will be to expand the network of camera traps to include a wider range of areas with known golden eagle territory densities. This will facilitate independent evaluation of the relationship between territory densities and abundance estimates based on camera traps. In addition, camera placement and an increase in the number of cameras at each bait should be trialled to provide optimal angle and distance to collect image data that increase the chance of individual identification of naturally marked and/or ringed individuals. Indeed, improved registration of individual rings could aid the identification of individuals younger than 4th winter which was not possible in the current study due to lack of variation in plumage patterns, as juvenile eagles are annually ringed in the nest in Norway (pers. comm. Husebø). Such data could improve current survival estimates, for both golden eagles and white-tailed eagles (Haliaeetus albicilla), and also improve age specific survival estimates, thereby providing valuable additional knowledge for eagle conservation management.

### ACKNOWLEDGEMENTS

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### AUTHOR CONTRIBUTIONS

Audun Stien, Torkild Tveraa and Jennifer Stien conceived and designed the study. Jennifer Stien led the analysis, interpretation and writing with contributions from Audun Stien and Torkild Tveraa. Siw Killengreen, Nina Eide and Lars Rød Eriksen provided the data and discussed its use in the analysis. All authors critically reviewed the article and gave final approval for the publication.

#### CONFLICT OF INTEREST

There is no conflict of interest.

#### DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10. 5061/dryad.fxpnvx0v7 (Stien et al., 2022).

#### PEER REVIEW

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### REFERENCES

Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R., & Schaub, M. (2010). Estimation of immigration rate using integrated population models. *Journal*  of Applied Ecology, 47, 393–400. https://doi.org/10.1111/j.1365-2664. 2010.01789.x

- Arnold, T. W., Clark, R. G., Koons, D. N., & Schaub, M. (2018). Integrated population models facilitate ecological understanding and improved management decisions. *Journal of Wildlife Management*, 82, 266–274. https://doi.org/10.1002/jwmg.21404
- Bailey, L. L., MacKenzie, D. I., & Nichols, J. D. (2014). Advances and applications of occupancy models. *Methods in Ecology and Evolution*, *5*, 1269–1279.
- Blazquez, M., Sanchez-Zapata, J. A., Botella, F., Carrete, M., & Eguia, S. (2009). Spatio-temporal segregation of facultative avian scavengers at ungulate carcasses. Acta Oecologica-International Journal of Ecology, 35, 645–650. https://doi.org/10.1016/j.actao.2009.06.002
- Brown, J. L., Bedrosian, B., Bell, D. A., Braham, M. A., Cooper, J., Crandall, R. H., DiDonato, J., Domenech, R., Duerr, A. E., & Katzner, T. E. (2017).
  Patterns of spatial distribution of Golden Eagles across North America: How do they fit into existing landscape-scale mapping systems? *Journal* of *Raptor Research*, 51, 197–215.
- Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. (2015). Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, 52, 675–685. https://doi.org/10.1111/1365-2664. 12432
- Caravaggi, A., Banks, P. B., Burton, A. C., Finlay, C. M. V., Haswell, P. M., Hayward, M. W., Rowcliffe, M. J., & Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, 3, 109–122. https://doi.org/10.1002/rse2.48
- COAT. (2021). Fjellrev. https://www.coat.no/Fjellrev/Varanger. Last accessed 23.03.2022
- Dahl, E. L., Nilsen, E. B., Brøseth, H., & Tovmo, M. (2015). Estimering av antall hekkende par kongeørn basert på kjent forekomst i Norge for perioden, 2010– 2014.
- Delplanque, A., Foucher, S., Lejeune, P., Linchant, J., & Theau, J. (2021). Multispecies detection and identification of African mammals in aerial imagery using convolutional neural networks. *Remote Sensing in Ecology* and Conservation. https://doi.org/10.1002/rse2.234
- Denes, F. V., Silveira, L. F., & Beissinger, S. R. (2015). Estimating abundance of unmarked animal populations: Accounting for imperfect detection and other sources of zero inflation. *Methods in Ecology and Evolution*, 6, 543– 556. https://doi.org/10.1111/2041-210x.12333
- Derlink, M., Wernham, C., Bertoncelj, I., Kovacs, A., Saurola, P., Duke, G., Movalli, P., & Vrezec, A. (2018). A review of raptor and owl monitoring activity across Europe: Its implications for capacity building towards pan-European monitoring. *Bird Study*, 65, S4–S20. https://doi.org/10. 1080/00063657.2018.1447546
- Ellis, D. H. (1979). Development of behavior in the Golden Eagle. Wildlife Monographs, 3–94.
- Fasce, P., Fasce, L., Villers, A., Bergese, F., & Bretagnolle, V. (2011). Long-term breeding demography and density dependence in an increasing population of Golden Eagles Aquila chrysaetos. *Ibis*, 153, 581–591. https://doi. org/10.1111/j.1474-919X.2011.01125.x
- Ferreira, A. C., Silva, L. R., Renna, F., Brandl, H. B., Renoult, J. P., Farine, D. R., Covas, R., & Doutrelant, C. (2020). Deep learning-based methods for individual recognition in small birds. *Methods in Ecology and Evolution*, 11, 1072–1085. https://doi.org/10.1111/2041-210x.13436
- Fiske, I. J., & Chandler, R. B. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of* statistical software, 43, 1–23.
- Gjershaug, J. O., Broseth, H., Kleven, O., Kalas, J. A., Mattisson, J., & Tovmo, M. (2018). Monitoring methods for the Golden Eagle Aquila chrysaetos in Norway. *Bird Study*, 65, S43–S51. https://doi.org/10.1080/00063657. 2018.1478389
- Halley, D., & Gjershaug, J. (1998). Inter-and intra-specific dominance relationships and feeding behaviour of golden eagles Aquila chrysaetos and sea eagles Haliatetus albicilla at carcasses. *Ibis*, 140, 295–301.

- Hamel, S., Killengreen, S. T., Henden, J. A., Eide, N. E., Roed-Eriksen, L., Ims, R. A., & Yoccoz, N. G. (2013). Towards good practice guidance in using camera-traps in ecology: Influence of sampling design on validity of ecological inferences. *Methods in Ecology and Evolution*, *4*, 105–113. https://doi.org/10.1111/j.2041-210x.2012.00262.x
- Haworth, P. F., McGrady, M. J., Whitfield, D. P., Fielding, A. H., & McLeod, D. R. A. (2006). Ranging distance of resident Golden Eagles Aquila chrysaetos in western Scotland according to season and breeding status. *Bird Study*, 53, 265–273. https://doi.org/10.1080/00063650609461442
- Henden, J. A., Stien, A., Bardsen, B. J., Yoccoz, N. G., & Ims, R. A. (2014). Community-wide mesocarnivore response to partial ungulate migration. *Journal of Applied Ecology*, 51, 1525–1533. https://doi.org/10.1111/ 1365-2664.12328
- Hostetter, N. J., Gardner, B., Sillett, T. S., Pollock, K. H., & Simons, T. R. (2019). An integrated model decomposing the components of detection probability and abundance in unmarked populations. *Ecosphere*, 10, e02586.
- Jachowski, D. S., Katzner, T., Rodrigue, J. L., & Ford, W. M. (2015). Monitoring landscape-level distribution and migration phenology of raptors using a volunteer camera-trap network. *Wildlife Society Bulletin*, 39, 553–563. https://doi.org/10.1002/wsb.571
- Johansson, O., Samelius, G., Wikberg, E., Chapron, G., Mishra, C., & Low, M. (2020). Scientific Reports 2020, Vol., 10(Issue1), Pages 6393. https://doi. org/10.1038/s41598-020-63367-z
- Karanth, K. U., Chundawat, R. S., Nichol, J. D., & Kumar, N. S. (2004). Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture-recapture sampling. *Animal Conservation*, 7, 285–290. https://doi.org/10.1017/S1367943004001477
- Katzner, T. E., Kochert, M. N., Steenhof, K., McIntyre, C. L., Craig, E. H., & Miller, T. A. (2020). *Golden Eagle (Aquila chrysaetos).*, Ithaca, NY,USA: Cornell Lab of Ornithology.
- Killengreen, S. T., Ims, R. A., Yoccoz, N. G., Brathen, K. A., Henden, J. A., & Schott, T. (2007). Structural characteristics of a low Arctic tundra ecosystem and the retreat of the Arctic fox. *Biological Conservation*, 135, 459–472. https://doi.org/10.1016/j.biocon.2006.10.039
- Killengreen, S. T., Stromseng, E., Yoccoz, N. G., & Ims, R. A. (2012). How ecological neighbourhoods influence the structure of the scavenger guild in low arctic tundra. *Diversity and Distributions*, 18, 563–574. https://doi. org/10.1111/j.1472-4642.2011.00861.x
- Lanzone, M. J., Miller, T. A., Turk, P., Brandes, D., Halverson, C., Maisonneuve, C., Tremblay, J., Cooper, J., O'Malley, K., Brooks, R. P., & Katzner, T. (2012).
  Flight responses by a migratory soaring raptor to changing meteorological conditions. *Biology Letters*, *8*, 710–713. https://doi.org/10.1098/rsbl. 2012.0359
- Legge, S., Robinson, N., Lindenmayer, D., Scheele, B., Southwell, D., & Wintle, B. (2018). Monitoring threatened species and ecological communities. CSIRO publishing.
- Leksands Fågelklubb. (2021). https://www.leksandsfagelklubb.se/projekt/ orn/golden-aging.html Last accessed 23.03.2022
- Mabille, G., Stien, A., Tveraa, T., Mysterud, A., Brøseth, H., & Linnell, J. D. (2015). Sheep farming and large carnivores: What are the factors influencing claimed losses? *Ecosphere*, 6, 1–17.
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248–2255. https://doi.org/ 10.1890/0012-9658(2002)0832248:ESorwd2.0.Co;2
- MacKenzie, D. I. (2006). Modeling the probability of resource use: The effect of, and dealing with, detecting a species imperfectly. *Journal of Wildlife Management*, 70, 367–374. https://doi.org/10.2193/0022-541x(2006) 70367:MTporu2.0.Co;2
- MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L., & Hines, J. E. (2017). Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Elsevier.
- Mattisson, J., Jacobsen, K.-O., & Kjørstad, M. (2017). Kungsörn, havsörn och tamren. En kunskapssammanställning.

- McClintock, B. T. (2015). multimark: An R package for analysis of capturerecapture data consisting of multiple "noninvasive" marks. *Ecol Evol*, 5, 4920–4931. https://doi.org/10.1002/ece3.1676
- McIntyre, C. L., Douglas, D. C., & Collopy, M. W. (2008). Movements of Golden Eagles (Aquila chrysaetos) from interior Alaska during their first year of independence. Auk, 125, 214–224. https://doi.org/10.1525/auk. 2008.125.1.214
- McClintock, B. T., Conn, P. B., Alonso, R. S., & Crooks, K. R. (2013). Ecology 2013, Vol., 94(7), Pages 1464–1471. https://doi.org/10.1890/12-1613.1
- Méndez, D., Marsden, S., & Lloyd, H. (2019). Assessing population size and structure for Andean Condor Vultur gryphus in Bolivia using a photographic 'capture-recapture'method. *Ibis*, 161, 867–877.
- Moleon, M., Sanchez-Zapata, J. A., Selva, N., Donazar, J. A., & Owen-Smith, N. (2014). Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biological Reviews of the Cambridge Philosophical Society*, 89, 1042–1054. https://doi.org/10.1111/brv. 12097
- Moss, E. H. R., Hipkiss, T., Ecke, F., Dettki, H., Sandstrom, P., Bloom, P. H., Kidd, J. W., Thomas, S. E., & Hornfeldt, B. (2014). Home-range size and examples of post-nesting movements for adult Golden Eagles (Aquila Chrysaetos) in Boreal Sweden. *Journal of Raptor Research*, 48, 93–105. https://doi.org/10.3356/Jrr-13-00044.1
- Murray, D. L., & Sandercock, B. K. (2020). *Population ecology in practice*. John Wiley & Sons.
- Nichols, J. D. (2014). The role of abundance estimates in conservation decision-making. pp. 117–131. Applied Ecology and Human Dimensions in Biological Conservation. Springer.
- Nilsen, E. B., Mattisson, J., Nygård, T., & Hamre, Ø. (2015). Kongeørn: Bestands-og habitatmodellering. NINA minirapport, 570.
- Nygård, T., Jacobsen, K.-O., Johnsen, T. V., & Systad, G. H. (2016). Dispersal and survival of juvenile golden eagles (Aquila chrysaetos) from Finnmark, Northern Norway. *Journal of Raptor Research*, 50, 144–160.
- O'Donnell, M. S., Edmunds, D. R., Aldridge, C. L., Heinrichs, J. A., Monroe, A. P., Coates, P. S., Prochazka, B. G., Hanser, S. E., Wiechman, L. A., Christiansen, T. J., Cook, A. A., Espinosa, S. P., Foster, L. J., Griffin, K. A., Kolar, J. L., Miller, K. S., Moser, A. M., Remington, T. E., Runia, T. J., & Wightman, C. S. (2021). Synthesizing and analyzing long-term monitoring data: A greater sage-grouse case study. *Ecological Informatics*, *63*, 101327. ARTN 10132. https://doi.org/10.1016/s.ecoinf.2021. 101327
- Orrhult. (2017). http://www.orrhult.eu/index.htm. Last accessed 22.03.2022
- Poessel, S. A., Bloom, P. H., Braham, M. A., & Katzner, T. E. (2016). Age- and season-specific variation in local and long-distance movement behavior of golden eagles. *European Journal of Wildlife Research*, 62, 377–393. https://doi.org/10.1007/s10344-016-1010-4
- R Core Team. (2020). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.Rproject.org/
- Rich, L. N., Davis, C. L., Farris, Z. J., Miller, D. A. W., Tucker, J. M., Hamel, S., Farhadinia, M. S., Steenweg, R., Di Bitetti, M. S., Thapa, K., Kane, M. D., Sunarto, S., Robinson, N. P., Paviolo, A., Cruz, P., Martins, Q., Gholikhani, N., Taktehrani, A., Whittington, J., & Kelly, M. J. (2017). Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. *Global Ecology and Biogeography*, *26*, 918–929. https://doi.org/10.1111/geb.12600
- Royle, J. A., & Dorazio, R. M. (2008). Hierarchical modeling and inference in ecology: The analysis of data from populations, metapopulations and communities. Elsevier.
- Rushing, C. S., Ryder, T. B., Scarpignato, A. L., Saracco, J. F., & Marra, P. P. (2016). Using demographic attributes from long-term monitoring data to delineate natural population structure. *Journal of Applied Ecology*, 53, 491–500. https://doi.org/10.1111/1365-2664.12579
- Rød-Eriksen, L. (2020). Drivers of change in meso-carnivore distributions in a northern ecosystem. PhD. NTNU.

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- Sánchez-Zapata, J. A., Calvo, J. F., Carrete, M., & Martínez, J. E. (2000). Age and breeding success of a Golden Eagle Aquila chrysaetos population in southeastern Spain. *Bird Study*, 47, 235–237.
- Sileshi, G., Hailu, G., & Nyadzi, G. I. (2009). Traditional occupancy-abundance models are inadequate for zero-inflated ecological count data. *Ecological Modelling*, 220, 1764–1775. https://doi.org/10.1016/j.ecolmodel.2009. 03.024
- Singh, N. J., Moss, E., Hipkiss, T., Ecke, F., Dettki, H., Sandstrom, P., Bloom, P., Kidd, J., Thomas, S., & Hornfeldt, B. (2016). Habitat selection by adult Golden Eagles Aquila chrysaetos during the breeding season and implications for wind farm establishment. *Bird Study*, *63*, 233–240. https://doi.org/10.1080/00063657.2016.1183110
- Steenhof, K., Kochert, M., & Doremus, J. (1983). Nesting of subadult Golden Eagles in southwestern Idaho. *The Auk*, 743–747.
- Steenhof, K., Kochert, M. N., McIntyre, C. L., & Brown, J. L. (2017). Coming to terms about describing Golden Eagle reproduction. *Journal of Raptor Research*, 51, 378–390. https://doi.org/10.3356/Jrr-16-46.1
- Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J. T., Burton, C., Townsend, S. E., Carbone, C., Rowcliffe, J. M., Whittington, J., Brodie, J., Royle, J. A., Switalski, A., Clevenger, A. P., Heim, N., & Rich, L. N. (2017). Scaling-up camera traps: Monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and the Environment*, 15, 26–34. https://doi.org/10.1002/fee.1448
- Steenweg, R., Hebblewhite, M., Whittington, J., Lukacs, P., & McKelvey, K. (2018). Sampling scales define occupancy and underlying occupancyabundance relationships in animals. *Ecology*, 99, 172–183. https://doi. org/10.1002/ecy.2054
- Stien, J., Stien, A., Tveraa, T., Rød-Eriksen, L., Eide, N. E., & Killengreen, S. (2022). Dryad Digital Repository. https://doi.org/10.5061/dryad. fxpnvx0v7
- Tikkanen, H., Rytkonen, S., Karlin, O. P., Ollila, T., Pakanen, V. M., Tuohimaa, H., & Orell, M. (2018). Modelling golden eagle habitat selection and flight activity in their home ranges for safer wind farm planning. *Environmental Impact Assessment Review*, 71, 120–131. https://doi.org/10.1016/j.eiar. 2018.04.006
- Tjernberg, M. (1977). Individuell igenkänning av kungsörnar Aquila chrysaetos i fält samt resultat av vinterinventeringar i sydvästra Uppland.[Individual recognition of Golden Eagles Aquila chrysaetos in the field, and results of winter censuses in southwest Uppland, central Sweden.]. Vår Fågelvärld, 36, 21–32.
- Tovmo, M., Mattisson, J., & Kleven, O. (2020). Overvåking av kongeørn i Noreg 2020. Resultat frå 12 intensivt overvaka område, NINA Rapport 1927. Norsk institutt for naturforskning.

- Tveraa, T., Stien, A., Broseth, H., & Yoccoz, N. G. (2014). The role of predation and food limitation on claims for compensation, reindeer demography and population dynamics. *Journal of Applied Ecology*, *51*, 1264–1272. https://doi.org/10.1111/1365-2664.12322
- Vukovich, M., Turner, K. L., Grazia, T. E., Mims, T., Beasley, J. C., & Kilgo, J. C. (2015). Wintering Golden Eagles on the coastal plain of South Carolina. *Journal of Field Ornithology*, 86, 337–344. https://doi.org/10.1111/ jofo.12127
- Vukovich, M., Garabedian, J. E., Zarnoch, S. J., & Kilgo, J. C. (2021). Do remote camera arrangements and image capture settings improve individual identification of Golden Eagles? Wildlife Society Bulletin.
- Watson, J. (2010). The golden eagle (2nd edn.). Bloomsbury Publishing.
- Weingarth, K., Zeppenfeld, T., Heibl, C., Heurich, M., Bufka, L., Daniszova, K., & Muller, J. (2015). Hide and seek: Extended camera-trap session lengths and autumn provide best parameters for estimating lynx densities in mountainous areas. *Biodiversity and Conservation*, 24, 2935–2952. https://doi.org/10.1007/s10531-015-0986-5
- Whitfield, D. P., Mcleod, D. R. A., Fielding, A. H., Broad, R. A., Evans, R. J., & Haworth, P. F. (2001). The effects of forestry on golden eagles on the island of Mull, western Scotland. *Journal of Applied Ecology*, 38, 1208–1220. https://doi.org/10.1046/j.0021-8901.2001. 00675.x
- Yoccoz, N. G., Nichols, J. D., & Boulinier, T. (2001). Monitoring of biological diversity in space and time. Trends in ecology & evolution, 16, 446–453. https://doi.org/10.1016/S0169-5347(01)02205-4

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