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RESEARCH ARTICLE

Estimating red deer population size using vantage point counts at baited sites

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Abstract

Accurate estimates of population size are central to the management and conservation of wild ungulates. Counting animals from vantage points of baited sites is a method that is traditionally used in Europe to obtain abundance estimates of wild ungulates, but its reliability in forested landscapes is contested. We assessed the accuracy of vantage point counts (VPCs) for estimating population size in red deer (*Cervus elaphus*) at De Hoge Veluwe National Park, a fenced, partially forested game reserve in the Netherlands. We compared estimates from duplicated VPCs for 1977–2010 with population sizes reconstructed from cohort analyses of age-specific mortality records, including and excluding supplementation with vehicular direct counts (VDCs) and field knowledge on herd composition and herd size from game wardens. Estimates from VPCs supplemented with VDCs matched the reconstructed population size well for 2001–2010. In addition, estimates based on ≥1 VPC site/11 km^2 provided representative estimates of the reconstructed population size in that period. Simultaneous VPCs at multiple baited sites can yield precise population estimates for red deer in forests.

KEYWORDS

abundance, baiting, *Cervus elaphus*, cohort analysis, hunting bag, population reconstruction, red deer, vantage point counts

Accurate estimates of population size are central to the management and conservation of wild ungulates. They allow managers to assess the status of populations and decide whether conservation measures are warranted, to assess whether populations exceed a desired level, to decide whether interventions are needed, and to assess stocks of game to decide how much can be sustainably harvested (Putman et al. 2011). Estimation of population size of ungulates is especially challenging in forests, where animals tend to be poorly visible (Putman et al. 2011). Moreover, many ungulates cannot be individually recognized and the application of marks is often undesirable or not feasible, which prohibits the use of mark-recapture methods.

A variety of methods have been developed to count unmarked forest wildlife (Morellet et al. 2010, Grignolio et al. 2020, Forsyth et al. 2022), including nocturnal spotlight counts (Corlatti et al. 2016, Donini et al. 2021), thermal infrared counts (Wiggers and Beckerman 1993), distance sampling on line transects (Thomas et al. 2010, Anderson et al. 2013), and modeling of motion-sensitive camera data (Rowcliffe et al. 2008, Howe et al. 2017). A traditional and simple method for estimating population size of forest ungulates that is used in many European countries (Morellet et al. 2010) employs simultaneous vantage point counts (VPCs) at sites that are baited to attract the animals (Meriggi et al. 2009, Morellet et al. 2010, van Wieren and Groot Bruinderink 2010, Putman et al. 2011, Zaccaroni et al. 2018). These VPCs are often conducted by game wardens, hunters, or volunteers, and typically include a classification of the observed animals by sex and age (Downing et al. 1977, Putman et al. 2011). To estimate the absolute population size, it is assumed that all individuals are predictably lured to one of the baited sites such that they are visible to the observers; hence, the study area is sufficiently covered with bait sites to directly count the entire population (Morellet et al. 2010).

The reliability of VPCs at baited sites for estimating the absolute population size of ungulates in woodlands remains contested (Putman et al. 2011). Vantage point counts are considered suitable for open areas, where animals can be observed over large distances (Mayle and Staines 1998, Dekker and Drever 2018). In forests, however, VPCs, even at baited sites, are likely to provide an underestimation of the true population size because not all individuals of a species are active at the same time of day on the same location, or not all animals may simultaneously be lured to baited sites (e.g., owing to weather; Morellet et al. 2010, Putman et al. 2011). To date, few studies have examined the accuracy of VPCs with baiting (Ratcliffe 1984, Staines and Ratcliffe 1987, Meriggi et al. 2009, Putman et al. 2011).

To understand how well VPCs match the actual population size, the latter needs to be determined first. One way to determine the actual population size is retrospective deterministic cohort analysis (Fryxell et al. 1988, Ueno et al. 2009), a population-reconstruction method that finds its roots in fisheries (Morellet et al. 2010). A cohort is defined as a group of individuals of the same age (Donini et al. 2021). Deterministic cohort analyses require that the population is closed and all deaths, either of natural causes or through hunting, are documented by age and sex. The age at death can then be used to determine in what years the individual was alive. The number of individuals alive at a given point in time then equals the reconstructed total population size at that time (Ueno et al. 2009). If all assumptions are met, cohort analyses provide the exact size of all past populations that have been fully culled, and the sex and age structure. In practice, such detailed data are rarely available on mammals (Imperio et al. 2010). One exception is Lowe (1969), who successfully used cohort-based population reconstruction to examine the accuracy of direct counts.

We assessed the accuracy of simultaneous VPCs at multiple baited sites for estimating population size in red deer (*Cervus elaphus*) by comparing them with population estimates acquired through cohort analysis. We predicted that the VPCs can track the variation in, and provide a reliable, albeit underestimated, indication of, the actual population size.

STUDY AREA

We conducted the study in De Hoge Veluwe National Park (the Park; 52.1°N, 5.8°E), a 54-km^2 fenced protected area in the center of the Netherlands (Figure 1), over a period of 45 years (1977–2021). The climate was temperate maritime, with strong seasonality (winter, spring, summer, and autumn) and a mean yearly

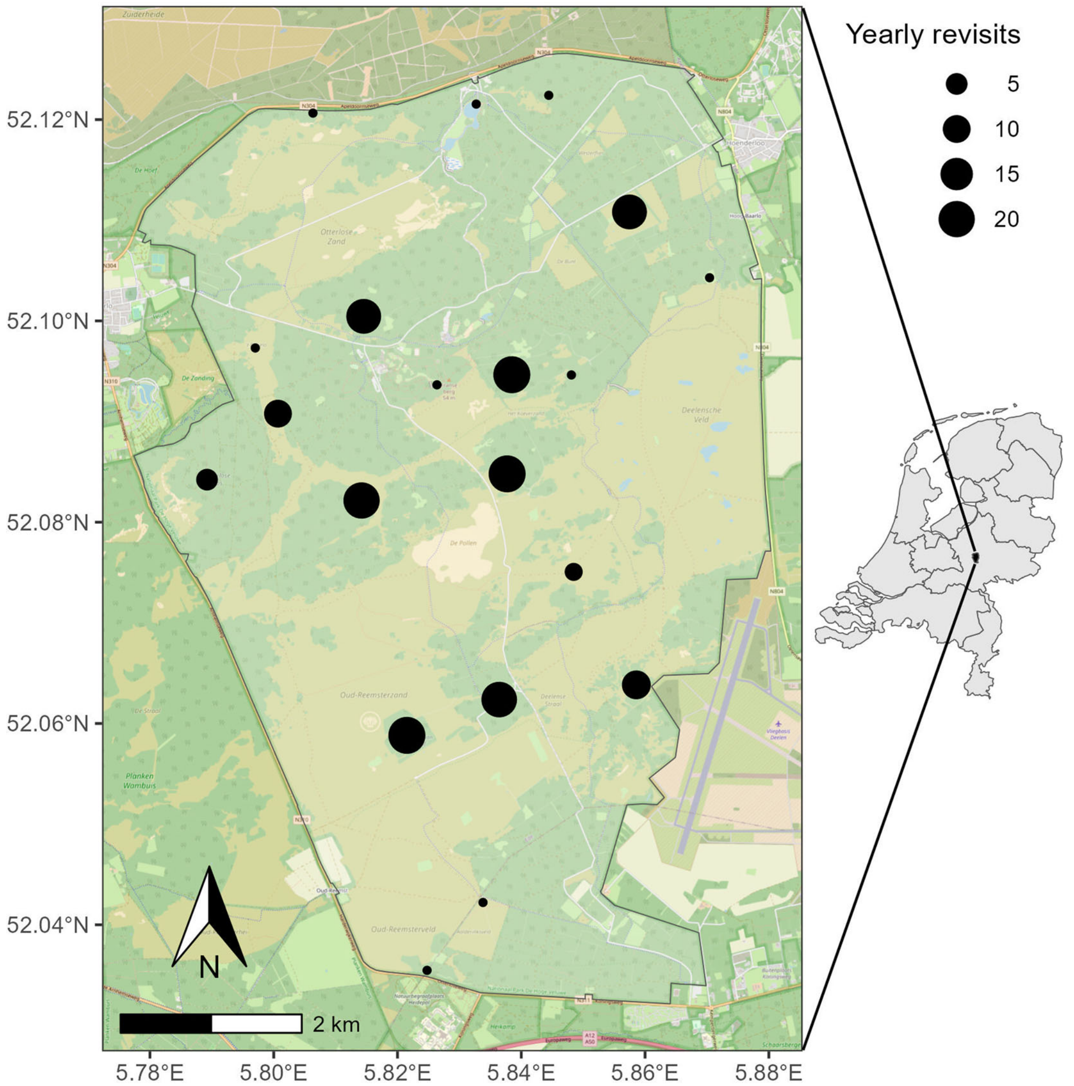

FIGURE 1 Baited sites where teams conducted vantage point counts of red deer in De Hoge Veluwe National Park, the Netherlands, 1977–2021. Dot size indicates the frequency of use. Green hue is forest area, yellow is open area.

precipitation of 850 mm. The mean temperature ranged from 3°C in winter to 17°C in summer. The Park is located on a plateau with course sandy soils, deposited during the latest glacial period, with a maximum elevation of approximately 60 m above sea level. It includes 6 main land cover types with discrete boundaries: early successional consolidated drift sand, wet heathland, dry heathland, Scots pine (*Pinus sylvestris*) forest, forest culture (various species, consisting mainly of pedunculate oak [*Quercus robur*], beech [*Fagus sylvatica*], red oak [*Quercus rubra*], Douglas-fir [*Pseudotsuga menziesii*], and Japanese larch [*Larix kaempferi*]), and fertilized game pastures. Forests were partly managed for wood production, while other land cover types were managed for nature purposes only. The 4 ungulate species present in the Park (i.e., red deer, wild boar [*Sus scrofa*], mouflon [*Ovis aries musimon*], and roe deer [*Capreolus capreolus*]) have been managed by culling throughout the Park's 120-year history.

Red deer were the largest (average adult mass = 130 kg), and most abundant, ungulate species in the Park. They are highly adaptive intermediate feeders whose diet at the Park consists mostly of grasses such as wavy hair-grass (*Avenella flexuosa*), dwarf shrubs such as European blueberry (*Vaccinium myrtillus*), and leaves and twigs of broadleaved shrub and tree species (Groot Bruinderink and Hazebroek 1995). In the Park, red deer reached a maximum age of 16 years, but normally animals were culled before they reached 12 years of age.

The Park management has been controlling the abundance of red deer through culling, with a target population size and with a cull bias towards younger individuals (<2 yr). Culling targets were based on the counted population size plus an expected percentage of newborns in the following spring, a desired population structure (following the expansive population pyramid, with approximately 50% of the population younger than 2 years old and approximately 5% older than 10 years old), and the target spring population size, which varied throughout the years. The culling season ran from 1 July to 1 February and culling was done either from hunting stands or through stalking. Few natural deaths occurred during our study period. Those that occurred were mostly due to fights between males or traffic collisions.

METHODS

Vantage point counts

The ungulate populations in the Park were monitored on a yearly basis through VPCs at baited sites, supplemented with vehicular direct counts (VDCs; Putman 2010, van Wieren and Groot Bruinderink 2010, Forsyth et al. 2022) and field knowledge of the game wardens on the composition and whereabouts of the herds. Multiple observers conducted VPCs simultaneously from hunting stands or blinds at multiple sites that were baited with pellets every late afternoon, starting approximately 3 weeks preceding the count and lasting until the last counting day. Observers conducted VPCs on 2 evenings between 1 March and 15 March (i.e., after the hunting season and before calving, typically separated by 1 day) and starting 1.5 hours before sunset and ending after sunset. An average of 9 ± 3 (SD) VPC sites were used each year (Figure 1). At least 2 people per site conducted the counts, including game wardens, hunters, and volunteers. Observers recorded the time, sex, and age class of all observed red deer and recorded group composition, compass directions, and times of entry and departure to allow for detecting double counts afterwards. Two to 4 teams of observers conducted VDCs at the same time as the VPCs to count any deer in areas without vantage points and those not attracted to the bait sites. The combination of VPCs and VDCs is referred to by the Park as spring counts (i.e., counts).

Raw data from individual counts of red deer were available for 2000–2022, except for 2002 and 2004. For these years, we imputed the count values as the sum of the largest day counts for each sex and age class, corrected for double counts and missed herds. For 1977–1999, 2002, and 2004, only estimates of total population size were available, not the underlying raw count data. For these years, we could not reproduce the total count.

Population reconstruction

We used deterministic cohort analysis (Fryxell et al. 1988, Ueno et al. 2009) to reconstruct the historical size and composition of the red deer population from mortality data. We had detailed sex- and age-specific records of mortality events available for 1977–2021, except 1996, 1997, and 1999, of which <1% were not caused by hunting. In the latter 3 years, we only knew the age and sex of calves (<1 yr old) and yearlings (1 yr old), but for older animals (≥2 yr old), we had only totals for each sex class. We assumed that the group of older animals in these culls had the average age structure of the 5 adjacent years (1994, 1995, 1998, 2000, 2001).

Following common practice, game wardens estimated ages of culled red deer based on tooth eruption and tooth wear (Lowe 1967, Veiberg et al. 2020, Donini et al. 2021). In the field these estimates were supplemented with antler development for individually recognized males (Azorit et al. 2002, Bartoš et al. 2009). To estimate the precision of the age estimation, we had the game wardens independently assess the age of 30 lower jaws of a representative sample of the age distribution of culls of the deer population in the Park, which had a mean deviation of 0.7 and a standard deviation of 0.7 years.

We reconstructed the population size by calculating the year of birth from the cull data (Ueno et al. 2009), assuming that all births happened on 1 May. Then, we summed the yearly number of deer alive in each birth cohort to obtain the number alive over time. Using this approach, we obtained a complete population reconstruction for 1977 to 2010. Within this range, we defined 2 periods based on change in head managers: 1977–2000 and 2001–2010. For 2010–2022, we could not obtain a complete reconstruction because the cohorts born in these years had not yet been culled completely by 2022. In addition, a possible influx of deer from neighboring protected areas may have occurred via migration corridors, which opened in 2013. Monitoring of animal activity at these corridors indicated that there had been no net migration of deer up to 2016 (van der Grift et al. 2017); however, after culling was reinstated in the adjacent Deelerwoud protected area in fall 2016, game wardens observed immigrant herds (J.R.K. Leidekker, De Hoge Veluwe National Park, personal communication). In 2019, the corridors were closed again.

Statistical analysis

We used R version 4.2.1 with the stats package (R Core Team 2022) for our statistical analyses. We examined the consistency of the consecutive count days with a Pearson's correlation test because it is possible that not all animals are always attracted to the sampling sites. To understand the influence of variation in daily weather conditions on the differences in VPCs held on consecutive days, we tested for relationships with weather variables using linear models. We obtained daily weather variables (mean daily temperature, mean wind speed, mean cloud cover, and the sum of daily precipitation) from the Royal Netherlands Meteorological Institute (2023).

To determine how well VPC-based estimates predicted the reconstructed population size, we used generalized linear models with predictors period (factorial) and field count (continuous), with the reconstructed population size as response, and that varied with a fixed and free intercept. To assess how the fit depended on the number of VPC sites and the inclusion of VDCs, we also evaluated the predictive power for different subsets of the data. Subsets were the total count, only totals from VPCs, and the 4–7 most used VPC sites (Table 1; Table S1, available in

TABLE 1 Modeling results of count, and count and period, as predictors for the reconstructed population size of red deer in De Hoge Veluwe National Park, the Netherlands, including coefficient (β) values (and SE in parentheses) from generalized linear models. Period 1 refers to 1997–2000 and period 2 refers to 2001–2010. Model 1 includes data from both periods and model 2 only uses counts from period 2. For model 2, we modeled subsets of data based on the number of vantage point count (VPC) sites and compared models with Akaike's Information Criterion (AIC). All coefficients were significant at $P < 0.001$.

	Model 1	Model 2				
Variables	All counts	All VPC sites	7 VPC sites	6 VPC sites	5 VPC sites	4 VPC sites
Count	1.019 (0.024)	1.153 (0.029)	1.194 (0.021)	1.276 (0.023)	1.413 (0.018)	1.559 (0.026)
Count × period 1	−0.1657 (0.028)					
AIC	267.02	69.96	47.41	47.70	43.74	63.92
df	29	7	5	5	5	7
Number of years	31	8	6	6	6	8

Supporting Information). In the VPC site selection, we used the most continuous set of VPC sites, to limit spatial variation over the years. We selected the best fitting regression function parameters with an analysis of variance (ANOVA) using the lowest residual sum of squares (RSS), after which we compared model performance using Akaike's Information Criterion (AIC) as a measure of good fit. We used this model to predict the population size for 2010 onwards.

RESULTS

Yearly count totals were available for 43 years and averaged 234 ± 37.6 individuals/day, with a maximum of 308 and a minimum of 160 individuals. For 2001–2010, counts of the first and second day were moderately correlated (Pearson's $r = 0.51$; Figure 2A). Difference between counts of the first and the second day were not explained by differences in mean daily temperature, mean daily wind speed, the sum of sun hours, or the sum of daily rainfall (linear model, $P > 0.05$, with and without interactions; Table S2, available in Supporting Information).

Data on mortality events from the Park comprised 4,632 red deer over 45 years, with a mean of 103 ± 49.3 deaths/year and a maximum of 246. Of the culled animals, 38.3% were calves (<1 yr old) and 4.6% were >10 years old (Table S1). The mean documented age at death was 2.2 ± 3.15 years, and the maximum was 16 years. We could infer red deer population densities, ranging from 2.5 deer/km^2 to 4.6 deer/km^2, with a mean density of 3.8 ± 0.3 deer/km^2. The hunting bag was male-biased, with a male:female sex ratio of 1.2:1 and a sex ratio of 1:1 in calves. Average yearly sex ratio of the hunting bag was 1.3:1. We reconstructed population size for 1977–2010 (Figure 3A).

To assess how precise the counts were in predicting the reconstructed population size, we regressed the reconstructed population size on counts, using generalized linear models. We found no difference in performance

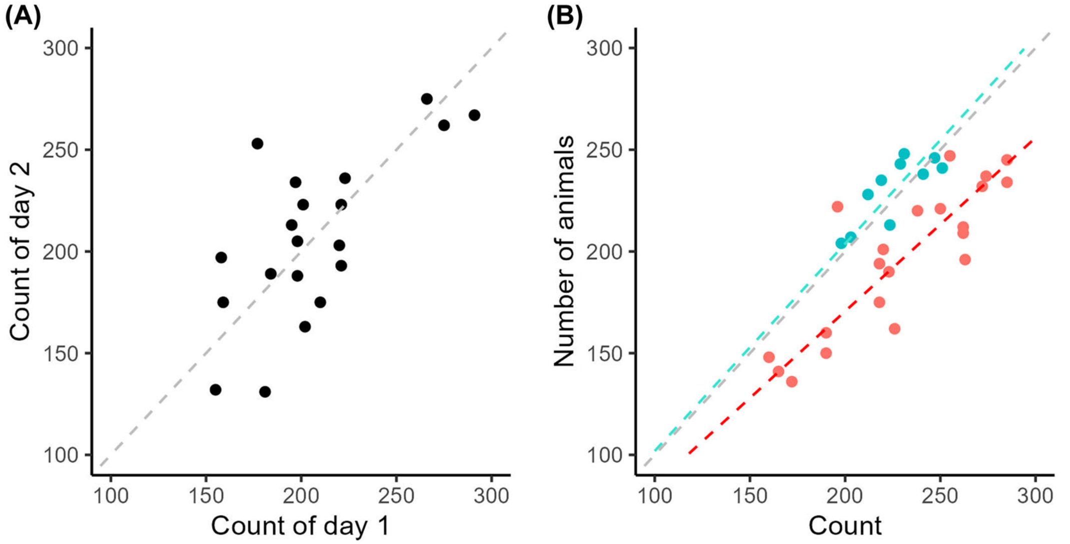

FIGURE 2 Relationships in De Hoge Veluwe National Park, the Netherlands, A) between the number of red deer counted during the first and second count day for years 2000–2022, and B) between count totals and reconstructed number of red deer. Lines are model fits for 2 periods with different sampling methods and personnel, where 2001–2010 (period 2; blue) proved more accurate than 1977–2000 (period 1; red). The grey dotted line in A and B indicates a 1:1 ratio.

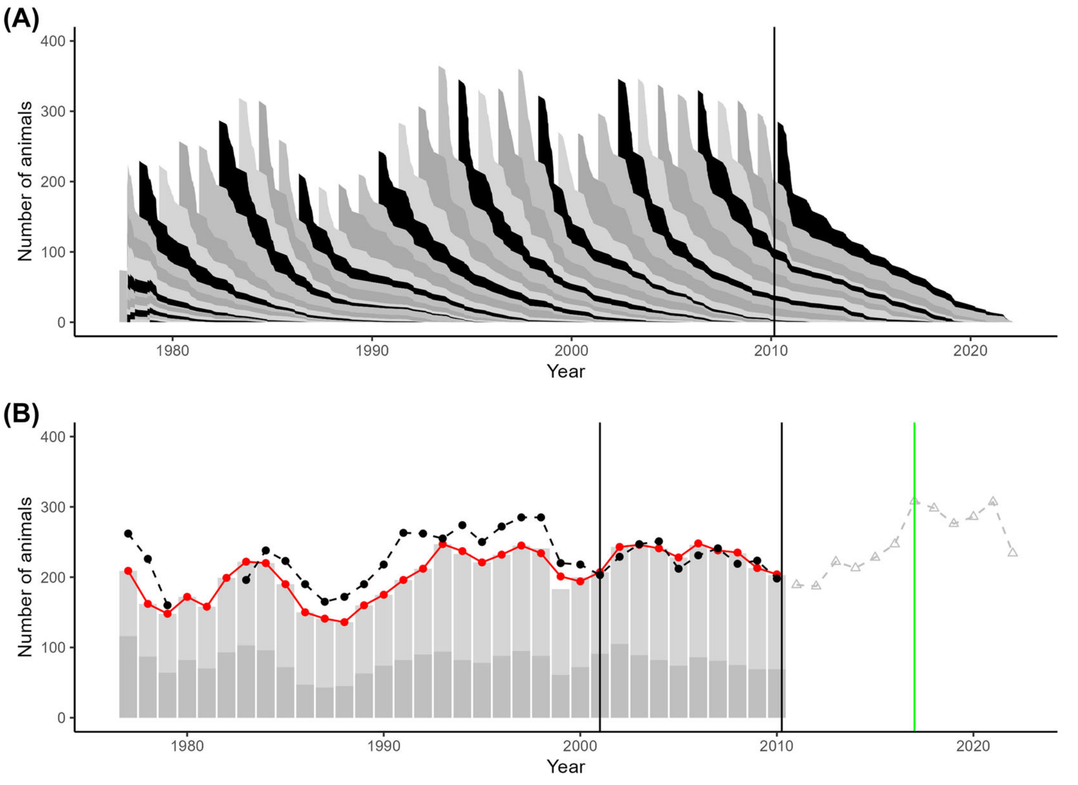

FIGURE 3 Size and composition of the red deer population in De Hoge Veluwe National Park, the Netherlands, between 1977–2021. A) Population size reconstructed from the age and sex distribution of mortality events, with cohorts color-coded and stacked. The black vertical line marks the year (2010) beyond which reconstruction was not possible; B) Population size in March over 1977–2010 reconstructed for males (light grey bars) and females (grey bars), total reconstructed number from the cohort analysis (red dotted line), and estimated number using all counts (black dotted line). Vertical black lines delimit the 2 periods for comparison with counts. The right side shows the spring population size estimated from the total count for 2010–2021 (triangles on dashed line). The green vertical line marks the onset of deer immigration from a neighboring area.

between models with a free intercept and models with a zero intercept (ANOVA, $P > 0.05$); hence, we progressed with the latter.

Count predicted the reconstructed population size well for period 2 ($\beta = 1.019$, $t = 42.27$, $P \le 0.001$) and overestimated the population for period 1 ($\beta = 0.853$; slope difference: $t = -5.84$, $P \le 0.001$; Table 1, Figure 2B). Thus, estimates from counts until 2000 overestimated the reconstructed population size by approximately 18%, whereas estimates from counts during 2001–2010 underestimated the reconstructed population size by 2% (Figure 2B).

To understand how the number of VPC sites affected the accuracy and precision of the reconstructed population size, we excluded VDCs and stepwise reduced the number of VPC sites in our analysis (Table 1). The fraction of the population missed increased with a reduced number of VPC sites. A minimum of 5 VPC sites, or 1 site/11 km^2, were required to predict the reconstructed population size well ($\Delta AIC < 5$; Figure 4; Table 1).

Using the model function parameterized for 2001–2010, we estimated the population size for 2011–2022 from count data with the formula: $N = 1.02 \times count$ (Figure 3B). This population projection suggests that the population of red deer increased after 2016, which coincides with the observations of the game wardens and the influx from the adjacent protected area.

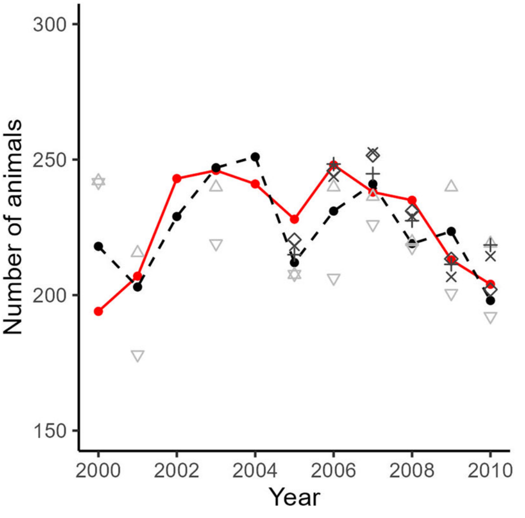

FIGURE 4 Modeled red deer population size from vantage point counts (VPC) and all counts in De Hoge Veluwe National Park, the Netherlands, for 2000–2010, with the total reconstructed number from the cohort analysis (red line), and total counted population (dashed black line). Icons show the estimated number of red deer through modeling, using: $N = 0 + \beta 1 \times$ count at sites, where ● = all counts, △ = all VPC sites, + = 7 VPC sites, × = 6 VPC sites, ◇ = 5 VPC sites, and ▽ = 4 VPC sites.

DISCUSSION

Vantage point counts at pre-baited sites are used to obtain total counts of ungulates in reserves and parks in many European countries, including the Netherlands, Belgium, Hungary, Italy, Portugal, Scotland, and Slovakia (Apollonio et al. 2010, Morellet et al. 2010, Zaccaroni et al. 2018), but the accuracy and precision of this method to estimate population size has been contested. We used cohort analyses on a 45-year data set of mortality data to obtain reconstruction of the size and age structure of a closed population of red deer in De Hoge Veluwe National Park and assessed how well simultaneous VPCs at multiple baited sites, supplemented with VDCs, predicted the reconstructed population size. They performed well.

Vantage point counts with pre-baiting supplemented with VDCs as applied by the Park, can yield precise estimates of the population size reconstructed with mortality data, with an underestimation of <5%. The detailed mortality data records of the Park allowed us to use the cohort method (Ueno et al. 2009) to reconstruct the population size and composition of red deer for 33 out of 45 consecutive years. This represents one of the longest population reconstructions reported for red deer (Coulson et al. 2004, Imperio et al. 2010, Donini et al. 2021).

Of the few other studies that compared cohort reconstruction to population estimation through counts, our findings agree with Lowe (1969), who used a similar approach to determine the accuracy of VPCs of red deer on the Isle of Rhum and reported a deviation of the counts of only 2.1 ± 1.6%, and with Donini et al. (2021), who successfully used incomplete cohort analysis to predict deer population trends. Among other researchers that studied count accuracy in predicting true population size, Le Moullec et al. (2017) reported that estimating absolute abundance of reindeer (*Rangifer tarandus platyrhynchus*) using total counts in a population with high site fidelity, can provide accurate results.

In addition to the total counts, we found that VPCs with pre-baiting can be used to sample a representative subset of the population size of red deer, that can then be corrected for using a fraction of increase. Reducing the density of pre-baited VPC sites from 1 site/8 km^2 to 1 site/11 km^2 strongly affected the beta-coefficient, increasing β with decreasing VPC site density; however, it minimally affected the modeled population size. Hence, the number of counted deer proportionally increases with additional sampling sites. Using a ΔAIC < 5 model selection criterion, we identified 1 VPC site/11 km^2, or 1 VPC site/50 red deer, as the minimum sampling density to obtain accurate estimates of population size. In our study, this corresponded with 60% of the total population counted. A lower VPC site density decreased model fit and resulted in higher uncertainty of the estimate.

Both analyses showed that it is possible to obtain a good prediction of the population size in forests, even though this approach has been criticized for such usage (Putman et al. 2011, Zaccaroni et al. 2018). This is an important finding in wildlife management studies because it adds to the list of methods in Forsyth et al. (2022) and Grignolio et al. (2020), and may therefore contribute substantially to the use and interpretation of wildlife monitoring methods. Furthermore, baiting results in predictable deer behavior and site fidelity, which increases the visibility of the animals under survey and the capture probability.

We concluded that the method performed well despite variation in the number of animals observed between consecutive VPC days. We suspect that this variation was influenced by disturbance and weather. First, red deer in the Park tend to respond strongly to encounters with visitors at unexpected times and locations (game wardens, De Hoge Veluwe National Park, personal communication); a single visitor straying from the path might therefore cause deer to postpone or even abandon routine movement patterns. How these disturbance effects change temporal distribution needs to be investigated. Second, visibility of red deer appears to be higher during windless weather and clear skies, in particular shortly after drizzly rain (game wardens, De Hoge Veluwe National Park, personal communication). We learned of these field observations through discussions with the game wardens of the Park, meaning that our findings that daily weather does not show a relationship with the counts, may be a type II error. The variation in counts between days, however, appears to be properly accounted for by the summing of the maximum day count by sex and age class. Supplementing VPCs with VDCs, as done by the Park, can be used as a method to improve the understanding of spatial distribution of red deer during counts and may be used as a method to improve distribution of VPC sites and to correct total counts from vantage points in retrospect.

Key in the application of cohort analyses is precise and accurate estimation of age. The Park estimates the age of dead individuals primarily by visual inspection of tooth eruption and dental wear. This method is widely studied and used and may provide a good estimation of the true age of ungulates; however, it becomes increasingly uncertain with age of the animal (Lowe 1967, Veiberg et al. 2020). Our results suggest that the game wardens were precise in their age estimation with a mean deviation of ±1 year between individuals, which is in accordance with literature (Veiberg et al. 2020). Therefore, we are confident to say that our reconstruction of historical population size and structure using cohort analysis was sufficiently accurate.

We furthermore aimed to predict the population size after 2010. In particular, after 2016, we observed an increase in the predicted population size from the VPC-based estimates, while the method of sampling did not change. This corresponds with the reinstatement of culling in Deelerwoud, a neighboring protected area, that may have resulted in an influx of red deer via fauna overpasses, and consequently a strong population increase and culling effort in response. If this inference is correct, then the estimations based on VPCs captured this pulse from 2017 onwards as a sharp increase. Additionally, the culling data suggests an increased effort (Figure S1, available in Supporting Information), which is a logical response of the Park management to reach the target population. This also suggests a large influx of young-adult individuals (<6 yr old). Consequentially, the Park did not have a closed population of red deer since this influx. Because the cohort method backtracks the population based on estimated age, we likely see an overestimation of the true population size after 2012 and we would violate the assumption of closed population.

The high accuracy of the VPCs in our study area may be explained by the high density of baited sites and the use of sites with high deer activity. Furthermore, red deer in this study showed site fidelity, with male and female herds maintaining rather stable home ranges throughout the year (game wardens, De Hoge Veluwe National Park, personal communication). Direct counts on ungulates exhibiting high site fidelity provide accurate estimates of population size (Le Moullec et al. 2017). At an even finer scale, deer activity was directed towards small game pastures that are mown and fertilized, which are also targeted as VPC sites. Red deer in the Park have a strong crepuscular activity pattern (Vazquez et al. 2019), with a large fraction of the population entering open areas, mostly pastures, around sunset. This results in highly predictable temporal behavior. The high accuracy of counts, such as shown in this research, may therefore only apply to wildlife populations with a similar context of predictability.

Our research had a few limitations. First, detailed data on the counts from the period 1977–2000 were missing. Consequentially, we cannot infer why the counts were not accurate. The tipping point between the 2 periods coincides with different managers and illustrates how the interpretation of wildlife counts may depend on individual interpreters (Putman et al. 2011). Second, our reconstruction of population size based on cohort analyses was inherently imperfect because some natural mortality may have gone undetected. This bias was negligible given the low natural mortality (Table S1) and the daily frequency at which the study area is patrolled. Lastly, count discrepancies between days show that not all animals are attracted to the baited sites at all times. This inconsistency seems to be properly solved by using the maximum per sex-age class over the count days. Supplementation with VDCs and field knowledge to detect missing herds appears to be a good addition to VPC sampling, but VPCs also provided reasonable population estimates without added VDCs.

In conclusion, long-term data sets of counts and mortality events of the red deer population in the Park enabled assessment of the accuracy of the commonly applied method of VPCs to estimate deer population size at densities ranging from 2.5 to 4.6 deer/km^2. At the Park, these counts were characterized by a high density of VPC sites (up to 1 site/4 km^2), pre-baiting of count sites with pellets, repeated counts, and supplementary VDCs to detect any herds not attracted to the bait sites. Vantage point counts using baits, supplemented with VDCs and field knowledge, estimated the reconstructed population size well. In a wider context, red deer population size was underestimated when using a standardized fraction of the VPC total and could be extrapolated to match the reconstructed population size with simple linear models until a minimum of 1 VPC site/11 km^2.

MANAGEMENT IMPLICATIONS

In the Park, and perhaps also in other reserves, a minimum of 1 vantage point site/11 km^2 provides consistent underestimation of population size of red deer. Red deer population size can thus be estimated using a standardized correction factor on the count. Given the daily variation we observed, which may be due to human disturbance, site fidelity, and competition between herds, we recommend the use of repeated sampling of VPC sites over 2 (or more) days. Extra care may be taken in selecting days with low recreation pressure for the VPCs, so that the risk of disturbance is reduced. Supplementing baited VPCs with VDCs and year-round counts to understand the spatial distribution of deer herds may be used to understand how much of the population VPC sites miss.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

This study made use of already available data on mortality of animals and animal counts. All mortality data were collected from dead animals and no animal experiments were conducted for this study.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from Hoge Veluwe National Park. Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the authors with the permission of Hoge Veluwe National Park.

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