



Estimating red deer (*Cervus elaphus*) population size in the Southern Black Forest: the role of hunting in population control

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Abstract

Numerous studies have addressed the question of whether hunting is capable of limiting the abundance of ungulates in the northern hemisphere. We investigated whether the hunting of red deer (*Cervus elaphus*) has reduced their abundance in the Southern Black Forest (area 17,500 ha), Southern Germany, since 2006. Red deer abundance was estimated using data obtained from visual counts at winter feeding sites, track counts, and bag records. An age- and sex-structured population model to estimate the winter population size was also constructed using bag records. The estimated red deer population size was evaluated according to a non-invasive genetic mark-recapture approach. The results showed that the hunting of red deer can reduce their population size if the hunting regime is part of a holistic management concept that takes into account the uncertainty of population size estimates and is implemented at scales appropriate to the management of this species.

Keywords Red deer management · Density estimates · Non-invasive genetic mark-recapture · Structured population model

Introduction

The case has been made that the exploitation of natural resources, including hunting should be based on clear goals (Morellet et al. 2007) which, in practice, frequently include the satisfaction of human needs (Holling and Meffert 1996). Thus, the question of whether hunting quotas should be increased or decreased is usually answered by decision-makers (Warren 2011), who must also consider economic and ecological constraints. Over the last few decades, the number of hunted roe deer (*Capreolus capreolus*) (Apollonio et al. 2010b; Hagen et al. 2014a) and red deer (*Cervus elaphus*)

(Milner et al. 2006) has increased throughout Europe. In this context, management objectives changed from species protection to population control (Milner et al. 2007). The current attitude towards abundant large cervids might be summarized as seeking to minimize both the economic damage they cause to forestry and the collisions of these animals with vehicles, while maximizing the economic benefits related to ecosystem services and hunting (Seiler 2004; Mysterud et al. 2006; Morellet et al. 2007). Management actions therefore frequently involve the hunting of cervid populations to reduce their population size (Milner et al. 2006; Heinze et al. 2011; Kuijper 2011). However, although it is obvious that annual variations in the number of cervids shot can lead to variations in population size (Fryxell 1991; Byrom et al. 2000), hunting is not able to modulate fluctuations at large spatial scales (Milner et al. 2006; Simard et al. 2013; Hagen et al. 2014a). Additive effects have been documented for small geographical ranges and highly managed hunting systems (Fryxell 1991; Giles and Findlay 2004). Accordingly, if the management goal is to reduce the size of the cervid population, then the question is whether hunting-related cervid mortality is additive or compensatory (Kokko 2001; Sandercock et al. 2011). To reduce cervid population size, wildlife managers often manipulate the length of the hunting season, the overall bag limits, or the age and sex composition of hunting quotas (Milner et al. 2007, 2011; Ueno et al. 2010). For polygamous species, a female-

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biased hunting is assumed to be more effective in reducing population size (Ueno et al. 2010), even though hunting traditions, economic considerations (Milner et al. 2006), and ethical considerations might conflict with this strategy. In addition to female-biased selective hunting, Simard and co-authors (Simard et al. 2013) concluded that the bag records of ungulates have to be at least 30–50% of the total population size to become additive which further depends on the sex ratio in bag records and the age and sex structure of the hunted population. Thus, estimates of the population size of ungulates are frequently the principal component not only to inform management decisions (Williams and Johnson 2017), but also in evaluating the success of management actions (Hauser et al. 2006). Unfortunately, evidence of problems of bias and imprecision in estimating the abundance of ungulates has accumulated over the last decade (Morellet et al. 2007; Hagen et al. 2014b). Those findings highlight the necessity of comparing multiple abundance indices (Uno and Kaji 2006; Morellet et al. 2007), which allows not only the quantification of methodological errors arising from each single method but also the detection of reliable trends in species abundance (Hagen et al. 2014b). Techniques for estimating population size of large mammals include capture-mark-recapture, distance sampling, ecological indices, and for hunted species population reconstruction (Buckland et al. 2000). To satisfy population control objectives in terms of a predefined population size interval, Hagen and co-authors suggested the implementation of long-term monitoring and pair-wise comparisons of different abundance estimates as part of an adaptive management framework (Hagen et al. 2014b). Simard and co-authors pointed out the need for control sites to differentiate between the roles of hunting and extrinsic factors in inducing variations in population size (Simard et al. 2013).

In this study, we present estimates of the red deer population size in the Southern Black Forest (area of 17,500 ha) from 2006 to 2015 and examine whether hunting was successful in reducing red deer abundance. The latter topic currently constitutes one of the major subjects of discussion in the management of large and abundant ungulates in North America, Europe, and Asia (Apollonio et al. 2010a; Ueno et al. 2010; Simard et al. 2013).

Our investigation of potential changes in red deer abundance in the Southern Black Forest since 2006 relied on (i) visual counts at feeding stations, (ii) bag records (including not only the number of red deer shot but also carcasses found by hunters and/or foresters in the management area), (iii) deer movements during the winter season to assess the number of animals leaving or entering the red deer management area, and (iv) the results of an age- and sex-structured population model (2006–2015). If red deer management practices in the Southern Black Forest were successful in reducing red deer abundance, then all indicators of red deer abundance should point to a decrease in population size since 2006. To increase

confidence in the calculations based on bag records, we used a non-invasive capture-mark-recapture (CMR) approach based on fecal samples collected in April 2016. In addition, we compared bag records of the Southern Black Forest to bag records of other red deer management areas in Baden-Württemberg (control sites). We expect a decrease in bag records in the Southern Black Forest owing to a decrease in red deer numbers and an increase in red deer bag records in the other management areas since 2006.

Data and methods

Red deer management in Baden-Württemberg

The federal state of Baden-Württemberg has five red deer management areas Odenwald (19,000 ha), Nordschwarzwald (Northern Black Forest, 105,000 ha), Südschwarzwald (Southern Black Forest, 17,500 ha), Schönbuch (4,000 ha), and Adelegg (4,000 ha). The mean Euclidean distance of the Southern Black Forest where this study was conducted, to the other red deer management areas is 115 km (edge to edge, a minimum of ~ 50 km from the Southern Black Forest to the Northern Black Forest and a maximum of ~ 180 km from the Southern Black Forest to the Odenwald). Elevations in the red deer management area of the Southern Black Forest are between 690 and 1410 m above sea level. The spatial isolation of the red deer management areas in Baden-Württemberg and the fact that each red deer individual outside the management areas that is seen by a hunter has to be shot (exception: vital male red deer with valuable antlers) have resulted in each red deer management area resembling an island. A telemetry study of 15 red deer individuals [five males and ten females roughly comprising three age classes: 1–3 years (11), 3–5 years (2), and > 5 years (2)] in the Southern Black Forest between 2007 and 2009 (Coppes et al. 2017) revealed that none left the red deer management area. However, no juveniles were collared, which are the most likely cohort to permanently disperse from natal to adult home ranges.

Red deer management in the Southern Black Forest

Most (77%) of the area of the red deer management area in the Southern Black Forest consists of managed forest (timber production) dominated by Norway spruce (*Picea abies*), European silver fir (*Abies alba*), and beech (*Fagus sylvatica*) (Coppes et al. 2017). About half of the forest area is governmental property which centers at the core region of the management area. For the Southern Black Forest, the annual bag record has been documented by governmental authorities since 1968. In 1994, governmental institutions developed a zonation scheme, subsequently implemented in 2008 by a management group consisting of hunters, scientists, foresters,

nature conservationists, and landowners (Coppes et al. 2017). The group has met regularly (two to three times a year) since 2004 and developed a management concept that includes a spatial zonation, a feeding program, and regulations for hunting and recreational activities (Coppes et al. 2017). The aims of winter feeding include minimizing forest damage (Arnold et al. 2018) and minimizing seasonal migration, with the latter reducing the number of deer-vehicle collisions. In accordance with different management objectives, the management group suggested a reduction in the red deer winter population size to a target level of 400 individuals. However, an increase in bag records between 1999 and 2006 raised the question of whether a high bag record can be sustained by solitary hunts without drastic increases in both the disturbance of the deer by hunters and the total effort expended by hunters (the estimated mean time per red deer shot in the Southern Black Forest was 26 h, the shortest time of all red deer management areas in Baden-Württemberg; unpublished results Schmieder 2008). Annual hunting quotas were set by the management group at the first annual meeting and took into consideration the amount of food consumed at the feeding locations, the duration of the feeding period, the number of red deer counted at those feeding locations, and the results of track surveys at the border between the core and outer zones. Further, hunting quotas were compared annually to bag records (see Fig. S3, Online Resource 1) which included not only the number of individuals shot but also the number of individuals found dead (i.e., mortality owing to deer-vehicle collisions or to any other reason, known or unknown).

To limit human disturbance resulting from hunting activities, hunting has been regulated according to a spatial scheme and modified stepwise since 2006 (Coppes et al. 2017). First, driven hunts (red deer were driven out by trained dogs; hunting was conducted from hunting stands) were implemented in 2006, and information on the sex and age of the red deer shot was used to set future hunting quotas. Between 2006 and 2016, the proportion of deer shot during driven hunts increased up to 40% of the total amount of red deer shot (Hagen 2017). Second, in 2008, a zonation scheme consisting of an outer zone, a border zone, and a core zone containing the refuge areas was implemented (Coppes et al. 2017), and the length of the red deer hunting season was limited (August–November in the core zone; August–December and, additionally, May 1–June 15 for individuals age 1–2 years in other red deer management areas). Third, although between 2006 and 2010 the sex ratio in the bag records was already female-biased, for 2011 scientists recommended a higher quota of females shot in order to reduce red deer abundance. For bag records since 2006, we determined that the data were complete and accurate (Fig. S1A Online Resource 1). Red deer bag records in the management area between 2006 and 2015 (252, 315, 283, 237, 234, 236, 255, 238, 180, 165) included the number of red deer shot (red deer shot outside of the

management area were not included) and the number of red deer found dead by the foresters (18, 7, 12, 10, 7, 7, 4, 1, 3, 5) whereas large predators such as lynx (*Lynx lynx*) or gray wolf (*Canis lupus*) were absent (Coppes et al. 2017).

In addition, the number of deer using the feeding location between 2006 and 2016 and the number of red deer leaving or entering the red deer management area during winter were documented. The number of deer approaching/leaving a feeding location was counted once a week (2–4 times in January if the snow height was > 1 m) by foresters from special observation points that afforded good visibility to count the deer sequentially (red deer had to jump over a runlet to approach the feeding location). Thereafter, the foresters roughly estimated the mean number of individuals that used a feeding location. Red deer tracks in snow were recorded until the end of February (only in years where snow conditions were adequate). Tracks were searched by one person from a car, on foot or using skis/snowshoes. If tracks were found, the direction and number of deer were recorded. The number of deer counted each year at two of the four feeding sites between 2006 and 2016 was 210, 170, 170, 170, 160, 140, 155, 145, 135, 125, and 129, respectively. The number of red deer leaving/entering the border zone, as determined by counting deer tracks outside that zone, was 301 (2005); 40 (2006); 48 (2009); 44 (2010), 72 (2012), 65 (2013); 17 (2015), and 57 (2016). The Spearman rank correlation coefficient (ρ) between bag records and all other red deer abundance indicators was also calculated.

Structured population model

The population size of red deer in the Southern Black Forest was estimated using an age- and sex-structured population model that included both the total bag record and the sex and age-class of each individual. In 2006, the size of the red deer winter population estimated by local foresters ranged between 696 and 736 individuals. This estimate included the count data from the foresters at the feeding locations and the deer track data from the border between the core and outer zones. According to visual counts conducted in 2006 at the feeding locations, the estimated sex ratio (females \geq 1 year:males \geq 1 year) was 1.2:1. Based on the ratio of adult females older than 1 year:1-year-old females in the bag record of 2005/06, the initial proportion of 1-year-old living females was set to 0.2.

The sex ratio at birth was set according to the sex ratio of shot juveniles, as we assumed that year to year changes in the sex ratio of juveniles shot reflected year to year changes in the sex ratio at birth (i.e., hunters did not select for a specific sex of juveniles). The age- and sex-structured population model considered five classes: female adult (age \geq 2 years, FA); female subadult (age 1–2 years, FSA); female juveniles, male juveniles (age < 1 year, FJ and MJ), and male adult red deer

(all individuals > 1 year, MA). The number of individuals in each class was calculated for each year as follows:

$$\begin{aligned} FA_{i+1} &= FA_i - \text{BaR}_{FA_i} + \text{FSA}_i - \text{BaR}_{\text{FSA}_i} \\ \text{FSA}_{i+1} &= \text{FJ}_i - \text{BaR}_{\text{FJ}_i} \\ \text{FJ}_{i+1} &= FA_i \times r \times \text{PF}_i \\ \text{MJ}_{i+1} &= FA_i \times r \times (1 - \text{PF}_i) \\ \text{MA}_{i+1} &= \text{MA}_i - \text{BaR}_{\text{MA}_i} + \text{MJ}_i - \text{BaR}_{\text{MJ}_i} \end{aligned} \quad (1)$$

with i being 2006, 2007, ..., 2015; BaR the bag record including red deer found dead by foresters (death owing to deer-vehicle collisions, starvation or any other reason), PF the proportion of female juveniles at birth, and r the recruitment rate of > 1-year-old female red deer. The recruitment rate r (Eq. 1) was set to 0.75 (Briedermann 1982), which is smaller than the expected conception rate in red deer (i.e., 50–60% of 1-year-old and 80–100% of older females conceive, cf. Langvatn et al. 1996; Langvatn et al. 2004). To evaluate changes in red deer population size, we calculated the annual population growth rate lambda as follows:

$$\text{lambda}_{i+1} = N_{i+1}/N_i \quad (2)$$

with i being 2006, 2007, ..., 2015 and N the estimated population size (see Eq. 1).

Non-invasive genetic mark-recapture

The non-invasive genetic CMR approach was designed according to Ebert and co-authors (Ebert et al. 2012). Red deer feces were collected within 78 plots of 1 km × 1 km located in the central part of the red deer management area. Each plot was sampled by one person on 1 day, and only fresh feces were collected. In case of fecal pellet group, only one pellet was taken. In 2016, sampling took place from April 12 to April 15. The daily track and the locations where feces were collected were recorded using a GPS device (GARMIN etrex 30). A total of 1549 feces samples were collected. The track length within plots varied between 5.5 and 13.94 km, with an average length of 9.11 km. Samples were stored frozen (−30 °C) until their analysis. DNA was extracted from 1000 of these samples, selected according to the location (at least one sample per square) and using the freshest samples. DNA extraction was conducted by Seq-It GmbH & Co. KG (Kaiserslautern, Germany). For the genotyping of individuals, seven markers and for sex determination one marker were used (Ebert et al. 2012). The software GENECAP (Wilberg and Dreher 2004) was used to determine matching genotypes, capture frequency, and the probability of identifying siblings (PI sib).

This CMR approach is widely applied in non-invasive genetic investigations to estimate the population size of the species of interest (Miller et al. 2005; Ebert et al. 2012). Population size estimates were obtained using the urn models

implemented by Miller and co-authors (Miller et al. 2005) assuming a closed red deer population and the R package Capwire (Pennell and Miller 2015).

More specifically, we calculated the even capture probability model (ECM), which assumes that every individual is equally likely to be captured, and the two innate rate model (TIRM) (Miller et al. 2005), which assumes that the monitored population consists of two groups of individuals that differ according to their capture probability. For both models, confidence intervals were calculated using a parametric bootstrap with 1000 iterations (function bootstrapCapwire; Pennell and Miller 2015). To select between the ECM and TIRM, we used the function lrtCapwire (Pennell and Miller 2015), which provides an estimate of population size under the ECM and then simulates the capture data. After the data were compared to both the ECM and the TIRM, a likelihood ratio test was conducted to select between ECM and TIRM. Significance was assessed by comparing the observed likelihood ratio to the distribution of the likelihood ratio obtained by simulation.

Results

Between 2007 and 2016, red deer bag records of the Southern Black Forest decreased by 150, such that the bag records in 2007 were almost twice as large as those in 2016 (Fig. 1a). Mortality due to hunting ranged between 31.2 and 45.3% of the estimated population size (Fig. 1b). Based on the ratio between bag records and estimated population size (structured population model), hunting was more likely to lead to a decrease in red deer population size (i.e., lambda < 1) when the mortality due to hunting exceeded 38% of the estimated population size (Fig. 1b). The bag records correlated significantly with the visual counts (positive association - $\rho = 0.79$; $N = 10$; $p < 0.01$) but were not significantly related to the track counts (positive association - $\rho = 0.66$; $N = 7$; $p = 0.18$) (cf. Fig. 2). In 2016, the structured population model (Fig. 1a) predicted a population size between 360 and 712 ($N_{\text{mean}} = 536$). Although this interval overlapped with the initial interval of the population size estimates for 2006 (696–736), the calculated mean population size (N_{mean}) correlated significantly with the bag records of 2006–2015 (positive association - $\rho = 0.7$; $N = 10$; $p = 0.03$) indicating a decline in population size. A microsatellite analysis was used to evaluate the model estimates according to the non-invasive CMR approach, resulting in the assignment of 636 useable consensus genotypes to 306 individuals (females = 157, males = 149): 157 individuals (84 females, 73 males) were sampled once, 61 (35, 26) twice, 38 (15, 23) three times, 24 (11, 13) four times, 16 (6, 10) five times, and 8 (5, 3) six times; 1 (1, 0) was sampled seven times, 2 (1, 1) were sampled eight times, and 1 individual (1, 0) was sampled ten times. The probability of two samples having the

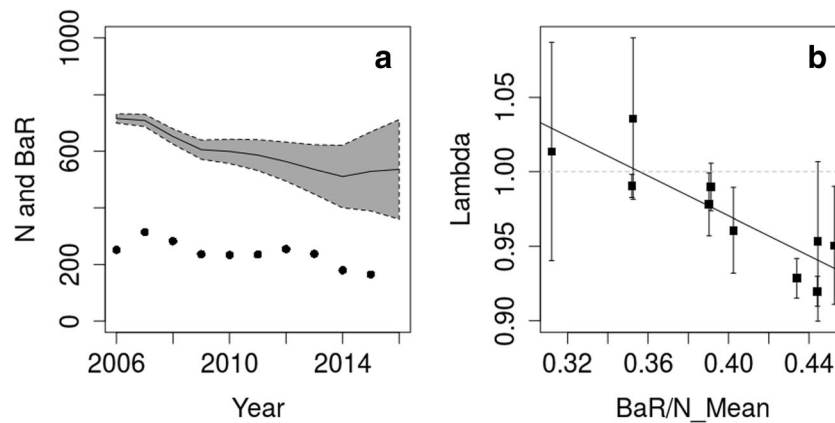


Fig. 1 **a** Estimated abundance of red deer in the Southern Black Forest, represented by the gray polygon (N), using the age- and sex-structured population model. Annual bag records (BaRs) are shown as filled circles. The black line within the polygon indicates the estimated mean number (in 2006: 710) while the polygon indicates the standard deviation. **b** The

relationship between the ratio of the bag records and the estimated population size (BaR/N_Mean) and population growth rate (lambda). The bars indicate the standard deviation of lambda for the initial population size in 2006 (range 696–736), with lambda > 1 (horizontal dashed gray line at lambda = 1) indicating an estimated increase in population size

same genotype and thus representing closely related individuals (PI sib) was smaller than 0.001.

Estimates for red deer population size were calculated as 373 (CI95 = 339–405) in the ECM and 500 (CI95 = 486–651) in the TIRM. The estimated sex ratio (f:m) according to the two models was 1.12 (ECM) and 1.14 (TIRM). The likelihood ratio was 157.75 and the estimated *p* value < 0.001 pointing to the fact that there is no within-population heterogeneity in the probability of capture. Consequently, the TIRM value was selected. To account for the unknown number of red deer in the outer zone that might not have been sampled in the core area during the sampling period, we added the recorded number of individuals (57) that in 2016 used the border area between the outer zone and core zone. Whether these individuals

had been sampled during the sampling period was unknown, as was the exact number of red deer living in the outer zone of the red deer management area during the winter period. However, the sum of the TIRM value (500) and the track counts (57) yielded a first estimate of the total winter red deer population size. Further, the estimate of 557 individuals in 2016 increases confidence that the number of red deer decreased since 2006. A comparison of bag records between the red deer management areas of the Southern Black Forest, Northern Black Forest, and Odenwald revealed that the decrease in bag records in the Southern Black Forest since 2007 did not reflect a general pattern in red deer bag records in Baden-Württemberg. While red deer bag records increased in all three management areas between 1999 and 2005, the increase was particularly noteworthy for the Northern Black Forest and Odenwald between 2006 and 2016 (Fig. 3).

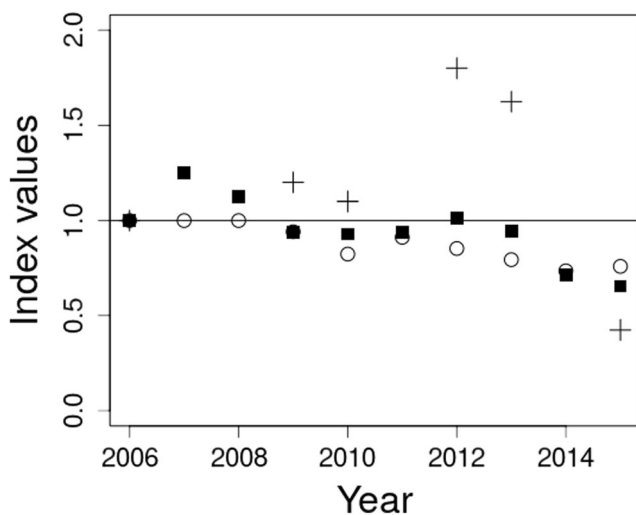


Fig. 2 Index values of red deer abundance in the Southern Black Forest. Filled squares represent red deer bag records, open circles the red deer number determined at the feeding locations, and crosses the results from deer tracked at the border between the outer and core zones. To facilitate visual comparisons, all time series were normalized by the value for 2006

Discussion

All indicators of red deer abundance (bag records, visual counts, track surveys) were assessed over a period of 10 years and pointed to a decrease in the Southern Black Forest since 2007. The modeled population density (Eq. 1) for the period between 2006 and 2016 correlated positively with red deer bag records. However, the reliability of structured population models depends on knowledge of the initial conditions as well as correct assumptions regarding the population dynamics. The structured population model predicted a mean population size in 2016 of 534 individuals (range 360–712). Estimates of the population size based on the genetic CMR method (TIRM: 500 individuals) supported the predictions of red deer population size in 2016 obtained by the structured population model. In addition, application of the CMR method provided an

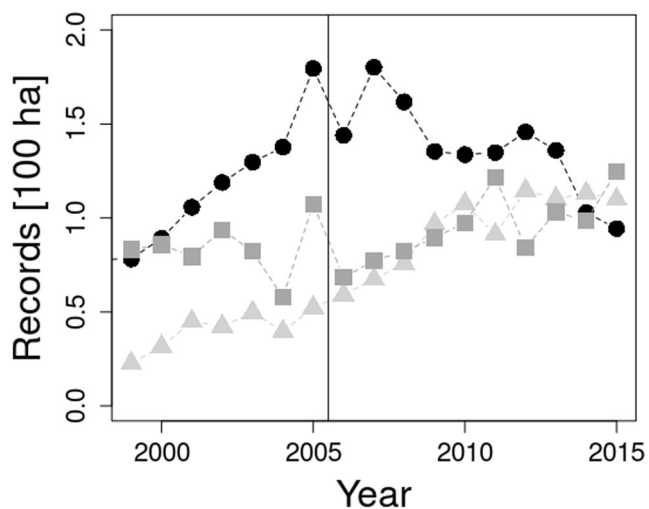


Fig. 3 Annual bag records in the Southern Black Forest (black circles), Northern Black Forest (light gray triangles) and Odenwald (gray squares) for the years 1999–2015. The vertical line separates the time with (2006–2015) and without (1999–2005) an adaptive management approach in the Southern Black Forest

independent evaluation of the estimated population size obtained by the structured population model, thus increasing confidence in the accuracy of the calculations based on bag records. These results are in line with the conclusion reached by Norton and co-authors (Norton et al. 2013), that a structured population model approach drawing on detailed information from bag records may be appropriate to predict trends in both population size and population structure. For red deer in the Southern Black Forest, mortality due to hunting ranged between 31.2–45.3% of the estimated population size, with a mortality > 38% increasing the likelihood of a decline in the population size. These findings are in line with those of Simard and co-authors, who stated that a harvest mortality of 30–50% of the total population size is necessary (Simard et al. 2013). Although the female-biased bag records (Figs. S1A and S1B of Online Resource 1) affected the sex ratio of the population, the female bias (estimated female:male ratio of 1.14) of the population in 2016 was unexpected. Ueno and co-authors demonstrated that female-biased hunting did not lead to a balanced sex ratio for sika deer in Japan (Ueno et al. 2010).

However, as red deer population size and population structure are affected not only by hunting, trends in bag records might reflect systematic variations in the environmental conditions. Winter conditions, for instance, are well known to impact both the population density and the bag records of large herbivores (Kruuk et al. 1999; Hagen et al. 2017). During the course of our investigation (2006–2016), the winter conditions in the Southern Black Forest were milder than the mean winter conditions of 1961–1990 (Fig. S2 Online Resource 1). Even though the decrease in bag records in 2006 can be attributed to the severe winter conditions in

2005/2006 (Fig. S2 Online Resource 1), the continuous decrease in bag records cannot. Moreover, if large-scale changes in the environmental conditions were the main driver of the decrease in red deer bag records, then a similar pattern should have been found in other red deer management areas in Baden-Württemberg, which was not the case (Fig. 3).

Although management practices were successful in reducing red deer abundance during the last decade, the successful control of a winter population of 500 individuals or a further reduction in red deer population size (400 individuals) may be challenging. First, adaptive behavioral responses by the deer to hunting can be expected, such as their use of dense cover during hunting (Lone et al. 2015). Second, the sex ratio of shot juveniles in 2015 suggests a current shift towards female juveniles (Fig. S1A Online Resource 1). A similar sex ratio in juveniles shot was documented in 2006 (Fig. S1A), after the severe winter of 2005/2006 (Fig. S2 Online Resource 1). A drastic shift in the sex ratio of shot juveniles towards females likely reflects a stress situation in the managed population (for instance caused by a drastic decrease in red deer numbers or severe winter conditions). In the study of Kruuk and co-authors (Kruuk et al. 1999), the proportion of males born declined with (nutritional) stress during pregnancy. Third, it can be assumed that, at a low red deer density, females will have a higher probability of conceiving (Albon et al. 1983; Langvatn et al. 1996). In red deer, body weight positively affects the fertility of females (Albon et al. 1983) but is negatively related to abundance (Langvatn et al. 1996).

The success in reducing red deer abundance in the Southern Black Forest can largely be attributed to the participative decision-making process of the management group, which chose to conduct research and management simultaneously as part of an adaptive resource management strategy (Lancia et al. 1996; McCarthy and Possingham 2007).

Conclusion

The results of this case study highlight that a successful reduction of cervid populations can be achieved by: (1) the long-term monitoring of species abundance by wildlife management authorities as the basis for implementing changes in hunting practices and setting annual hunting quotas (Fig. S3 Online Resource 1) and (2) the coordination of management actions over areas of appropriate size (Meisingset et al. 2017) (in this study, a red deer management area of 17,500 ha). Given the increasing bag records of ungulates, including roe deer and wild boar [*Sus scrofa*] in Europe (Apollonio et al. 2010b; Vetter et al. 2015), white-tailed deer [*Odocoileus virginianus*] in North America (Simard et al. 2013), and sika deer [*Cervus nippon*] in Asia (Ueno et al. 2010), and a decline in public acceptance of hunting activities (Lexer et al. 2005),

our results will contribute to an understanding of the role of hunting in adaptive management.

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References

- Albon SD, Mitchell B, Staines BW (1983) Fertility and body weight in female red deer: a density-dependent relationship. *J Anim Ecol* 52: 969–980
- Apollonio M, Andersen R, Putman R (2010a) Introduction. In: Apollonio M, Andersen R, Putman R (eds) *European ungulates and their management in the 21st century*, Cambridge, pp 1–13
- Apollonio M, Andersen R, Putman R (2010b) Present status and future challenges for European ungulate management. In: Apollonio M, Andersen R, Putman R (eds) *European ungulates and their management in the 21st century*, Cambridge, pp 578–604
- Arnold JM, Gerhardt P, Steyaert SMJG, Hochbichler E, Hackländer K (2018) Diversionary feeding can reduce red deer habitat selection pressure on vulnerable forest stands, but is not a panacea for red deer damage. *For Ecol Manag* 407:166–173. <https://doi.org/10.1016/j.foreco.2017.10.050>
- Briedermann (1982) *Der Wildbestand die große Unbekannte*. Deutscher Landwirtschaftsverlag, Berlin
- Buckland ST, Goudie IJ, Borchers DL (2000) Wildlife population assessment: past developments and future directions. *Biometrics* 56: 1–12
- Byrom AE, Karels TJ, Krebs CJ, Boonstra R (2000) Experimental manipulation of predation and food supply of arctic ground squirrels in the boreal forest. *Can J Zool* 78:1309–1319. <https://doi.org/10.1139/z00-055>
- Coppes J, Burghardt F, Hagen R, Suchant R, Braunisch V (2017) Human recreation affects spatio-temporal habitat use patterns in red deer (*Cervus elaphus*). *PLoS One* 12:1–19. <https://doi.org/10.1371/journal.pone.0175134>
- Ebert C, Sandrini J, Spielberger B et al (2012) Non-invasive genetic approaches for estimation of ungulate population size: a study on roe deer (*Capreolus capreolus*) based on faeces. *Anim Biodivers Conserv* 35:267–275
- Fryxell JM (1991) Forage quality and aggregation by large herbivores. *Am Nat* 138:478–498. <https://doi.org/10.2307/2678832>
- Giles BG, Findlay CS (2004) Effectiveness of a selective harvest system in regulating deer populations in Ontario. *J Wildl Manag* 68:266–277. [https://doi.org/10.2193/0022-541X\(2004\)068\[0266:EOASHS\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2004)068[0266:EOASHS]2.0.CO;2)
- Hagen R (2017) *Rotwildstrecke im Südschwarzwald*. Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg
- Hagen R, Heurich M, Kröschel M, Herdtfelder M (2014a) Synchrony in hunting bags: reaction on climatic and human induced changes? *Sci Total Environ* 468–469:140–146. <https://doi.org/10.1016/j.scitotenv.2013.08.022>
- Hagen R, Kramer-Schadt S, Fahse L, Heurich M (2014b) Population control based on abundance estimates: frequency does not compensate for uncertainty. *Ecol Complex* 20:43–50. <https://doi.org/10.1016/j.ecocom.2014.07.006>
- Hagen R, Heurich M, Storch I, Hanewinkel M, Kramer-Schadt S (2017) Linking annual variations of roe deer bag records to large-scale winter conditions: spatio-temporal development in Europe between 1961 and 2013. *Eur J Wildl Res* 63:97. <https://doi.org/10.1007/s10344-017-1155-9>
- Hauser CE, Pople AR, Possingham HP (2006) Should managed populations be monitored every year? *Ecol Appl* 16:807–819
- Heinze E, Boch S, Fischer M, Hessenmöller D, Klenk B, Müller J, Prati D, Schulze ED, Seele C, Socher S, Halle S (2011) Habitat use of large ungulates in northeastern Germany in relation to forest management. *For Ecol Manag* 261:288–296. <https://doi.org/10.1016/j.foreco.2010.10.022>
- Holling CS, Meffe GK, (1996) Command and control and the pathology of natural resource management. *Conserv Biol* 10(2):328–337
- Kokko H (2001) Optimal and suboptimal use of compensatory responses to harvesting: timing of hunting as an example. *Wildl Biol* 7:159–168
- Kruuk LEB, Clutton-Brock TH, Albon SD, Pemberton JM, Guinness FE (1999) Population density affects sex ratio variation in red deer. *Nature* 399:459–461. <https://doi.org/10.1038/20917>
- Kuijper DPJ (2011) Lack of natural control mechanisms increases wildlife–forestry conflict in managed temperate European forest systems. *Eur J For Res* 130:895–909. <https://doi.org/10.1007/s10342-011-0523-3>
- Lancia RA, Braun CE, Collopy MW et al (1996) ARM! For the future: adaptive resource management in the wildlife profession. *Wildl Soc Bull* 24:436–442
- Langvatn R, Albon SD, Burkeley T, Clutton-Brocks TH (1996) Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *J Anim Ecol* 65:653–670
- Langvatn R, Myrseter A, Stenseth NC, Yoccoz NG (2004) Timing and synchrony of ovulation in red deer constrained by short northern summers. *Am Nat* 163:763–772. <https://doi.org/10.1086/383594>
- Lexer W, Reimoser F, Hackl J, Heckl F, Forstner M (2005) Criteria and indicators of sustainable hunting—the Austrian assessment approach. *Wildl Biol Pract* 1:163–183. <https://doi.org/10.2461/wbp.2005.1.20>
- Lone K, Loe LE, Meisingset EL, Stamnes I, Myrseter A (2015) An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Anim Behav* 102: 127–138
- McCarthy MA, Possingham HP (2007) Active adaptive management for conservation. *Conserv Biol* 21:956–963. <https://doi.org/10.1111/j.1523-1739.2007.00677.x>
- Meisingset EL, Loe LE, Brekkum Ø, Bischof R, Rivrud IM, Lande US, Zimmermann B, Veiberg V, Myrseter A (2017) Spatial mismatch between management units and movement ecology of a partially migratory ungulate. *J Appl Ecol* 55:1–9. <https://doi.org/10.1111/1365-2664.13003>
- Miller CR, Joyce P, Waits LP (2005) A new method for estimating the size of small populations from genetic mark-recapture data. *Mol Ecol* 14:1991–2005. <https://doi.org/10.1111/j.1365-294X.2005.02577.x>
- Milner JM, Bonenfant C, Myrseter A et al (2006) Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *J Appl Ecol* 43:721–734. <https://doi.org/10.1111/j.1365-2664.2006.01183.x>
- Milner JMM, Nilsen EB, Andreassen HP (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conserv Biol* 21:36–47
- Milner JM, Bonenfant C, Myrseter A (2011) Hunting Bambi—evaluating the basis for selective harvesting of juveniles. *Eur J Wildl Res* 57: 565–574
- Morellet N, Gaillard JM, Hewison AJM et al (2007) Indicators of ecological change: new tools for managing populations of large herbivores. *J Appl Ecol* 44:634–643. <https://doi.org/10.1111/j.1365-2664.2007.01307.x>
- Myrseter A, Tryjanowski P, Panek M (2006) Selectivity of harvesting differs between local and foreign roe deer hunters: trophy stalkers

- have the first shot at the right place. *Biol Lett* 2:632–635. <https://doi.org/10.1098/rsbl.2006.0533>
- Norton AS, Diefenbach DR, Rosenberry CS, Wallingford BD (2013) Incorporating harvest rates into the sex-age-kill model for white-tailed deer. *J Wildl Manag* 77:606–615. <https://doi.org/10.1002/jwmg.486>
- Pennell MW, Miller CR (2015) Package ‘capwire’. 29
- Sandercocock BK, Nilsen EB, Brøseth H, Pedersen HC (2011) Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. *J Anim Ecol* 80:244–258. <https://doi.org/10.1111/j.1365-2656.2010.01769.x>
- Schmieder M (2008) Auswertungen, Zahlen und Karten zum Abschlussbericht Rotwildprojekt. Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg, pp 1–102
- Seiler A (2004) Trends and spatial patterns in ungulate-vehicle collisions in Sweden. *Wildl Biol* 10:301–313
- Simard MA, Dussault C, Huot J, Côté SD (2013) Is hunting an effective tool to control overabundant deer? A test using an experimental approach. *J Wildl Manag* 77:254–269. <https://doi.org/10.1002/jwmg.477>
- Ueno M, Kaji K, Saitoh T (2010) Culling versus density effects in management of a deer population. *J Wildl Manag* 74:1472–1483. <https://doi.org/10.2193/2009-339>
- Uno H, Kaji K (2006) Survival and cause specific mortality rates of female sika deer in eastern Hokkaido, Japan. *Ecol Res* 21:215–220. <https://doi.org/10.3106/mammalstudy.25.49>
- Vetter SG, Ruf T, Bieber C, Arnold W (2015) What is a mild winter? Regional differences in within-species responses to climate change. *PLoS One* 10:e0132178. <https://doi.org/10.1371/journal.pone.0132178>
- Warren RJ (2011) Deer overabundance in the USA: recent advances in population control. *Anim Prod Sci* 51(4):259–266
- Wilberg MJ, Dreher BP (2004) GENECAP: a program for analysis of multilocus genotype data for non-invasive sampling and capture-recapture population estimation. *Mol Ecol Notes* 4:783–785. <https://doi.org/10.1111/j.1471-8286.2004.00797.x>
- Williams BK, Johnson FA (2017) Frequencies of decision making and monitoring in adaptive resource management. *PLoS One* 12:1–18. <https://doi.org/10.1371/journal.pone.0182934>