Precision and reliability of indirect population assessments for the Caspian red deer Cervus elaphus maral

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The elusive Caspian red deer *Cervus elaphus maral* lives at low densities in rugged forest habitats of the Caucasus and the south Caspian region, and its declining population requires urgent attention. We here address the precision and reliability of dung counts (fecal standing crop approach FSC) and camera trapping (random encounter model REM) for estimating its population size. We surveyed 36 km of strip transects arranged in systematic random design and applied 1585 camera trap nights of effort in the mountainous forest habitats of Golestan National Park, Iran. We also conducted a dung decay analysis of 80 samples. Dung decay rates were not habitat-specific and the mean time to decay was 141.8 ± 15.1 days, i.e. only ca 52% of the most reliable estimate available for red deer dung. Estimated deer population size and density from dung counts was lower (194 ± 46 individuals, 0.46 ± 0.11 individuals km^{-2}, 2012–2013) than from REM (257 ± 84 individuals, 0.61 ± 0.20 individuals km^{-2}, 2011), but this difference was insignificant. Both these estimates confirm a sharp decline of the population from an estimated 2096 animals in the 1970s. Density estimates reached a stable level and were most precise at a sampling effort of 15 transects (FSC) and 1345 camera trap-days (REM). Our results confirm that FSC and REM can both be reliable for assessing populations of Cervidae.

Knowledge of population size is crucial for the development of effective wildlife management strategies (Laing et al. 2003). In many cases, traditional total counts of large ungulates do not provide reliable and precise density estimates because of logistical constraints, unrealistic assumptions or poor theoretical background (Buckland et al. 2001). Several techniques of population estimation are well developed, but the selection of monitoring methods is often an intricate process depending on available logistics and time, species biology, budget, purposes and habitat physiognomies (Campbell et al. 2004, Waltert et al. 2008, Alves et al. 2013). In case of cryptic species living in mosaics of open and closed vegetation such as deer *Cervus* spp., specific survey approaches are required (Buckland et al. 2001).

Direct counts such as distance sampling are among the most popular techniques for density estimation of large herbivores (Buckland et al. 2001). For deer, these counts are applicable in open areas where animals are most visible (Smart et al. 2004). However, in closed habitats such as forests and dense scrublands direct counts are difficult to apply and in most cases this method fails to produce reliable results (Marques et al. 2001). Counts become even more problematic in small populations and/or naturally cryptic species, in which detection probabilities are low (Zero et al. 2013). Under these circumstances, indirect monitoring techniques such as dung counts and camera trapping can provide valuable alternatives (Burton et al. 2015).

In contrast to direct counts, indirect dung counts estimate an average abundance over several months and not only for the day of the survey, thus leading to higher accuracy (Marques et al. 2001, Tsaparis et al. 2009). As a disadvantage, they cannot account for the sex/age structure of the population (Buckland et al. 2001). Furthermore, dung counts on strip transects may underestimate density because of litter and grass cover affecting detection probability and encounter rate (Hemami and Dolman 2005).

Dung count techniques are well described and are among the most preferable survey methods for deer monitoring (Buckland et al. 2001, Tsaparis et al. 2009). Two

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approaches to dung counts have been developed: 1) fecal standing crop (FSC) estimation of animal density as a function of the number of recorded dung samples, decay rate as the probability of dung presence/absence and the defecation rate and 2) the fecal accumulation rate (FAR) method, which is based on counts of pellet groups in previously cleared sampling units and substituting time to disappearance by the period of time between two visits (Hemami and Dolman 2005). The latter has a substantial advantage over FSC by not requiring an estimate of decay rate. Thus, abundance can be estimated relatively quickly, without the need to monitor dung samples over a lengthy period of time (Alves et al. 2013). However, FAR also has several limitations, such as highly variable decay rates which demand for quite short periods between visits (counts of pellet groups) during which dung samples do not decay and can be sampled (Laing et al. 2003). Laing et al. (2003) suggested that at least six pellets per dung sample should persist during subsequent visits, otherwise the sample is considered as decayed. FSC has recently been shown to be more precise than FAR (Alves et al. 2013) and it can be conducted using both line and strip transects. Like FAR, FSC depends on the knowledge of defecation rates, which can be estimated in controlled (semi)captive conditions (Hemami and Dolman 2005, Buckland et al. 2001). Overall, the most cost-efficient and effective method for estimating deer number via dung counts is FSC, particularly in small populations (Laing et al. 2003, Alves et al. 2013).

Camera trapping is another important technique to estimate animal population size and density (Burton et al. 2015). The use of camera traps is especially encouraging in studies of activity patterns and behavior of elusive species in forests (Cusack et al. 2015b). The most common analytical approach for capture–recapture data relies on individual recognition of camera-trapped animals, but this is difficult to do in most ungulates, which do not have natural markings (Foster and Harmsen 2012, Anile et al. 2014). To overcome this limitation, Rowcliffe et al. (2008) have suggested an alternative approach, the random encounter model (hereafter, REM), which is based on the ideal gas model. This model, developed originally in physics to describe the collision between gas molecules, was adapted by ecologists to characterize encounters between animals and observers (Hutchinson and Waser 2007). Thereafter, Rowcliffe et al. (2008) modified that theory in REM, which similarly describes contact rates between camera traps and animals. The REM technique has already been successfully applied to rare ungulate species (Rovero and Marshall 2009, Zero et al. 2013). As REM is a relatively new technique, its application is still uncommon and not tested in many regions, including the Middle East.

In this study, we estimate abundance and density of the Caspian red deer *Cervus elaphus maral* in montane forests of Iran by analyzing data from FSC and REM and discuss the precision and reliability of these two techniques for population estimation. The main threats to Caspian red deer are poaching, competition with livestock, and habitat loss. While livestock encroachment to natural habitats is certainly on the rise, poaching for meat and trophy antlers appears to be the most important cause of the rapid decline of this large herbivore (Kiabi et al. 2004).

Materials and methods

Study area

We conducted this research in Golestan National Park (GNP) located in northeastern Iran (Fig. 1). GNP is the first Iranian protected area, which was designated as a national park in 1957 and became a UNESCO biosphere reserve in 1977 (Zehzad et al. 2002). The park is located in the mountainous terrain and represents a transitional zone between humid Caspian deciduous forest and dry steppe, with mean annual precipitation of 142 and 866 mm in the east and west, respectively. The GNP comprises a total area of 874 km² with an elevation range of 450 to 2411 m a.s.l. The forested part, where this study was conducted, covers approximately 422 km² in the western part of GNP (Fig. 1, Akhani 2005). GNP has been considered as one of the last refuges for large mammals in Iran (Ghoddousi et al. 2016a, b). The red deer shares its habitat with the Persian leopard *Panthera pardus saxicolor*, urial *Ovis vignei*, bezoar goat *Capra aegagrus*, wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, brown bear *Ursus arctos*, gray wolf *Canis lupus*, jungle cat *Felis chaus* and wild cat *Felis silvestris* (Kiabi et al. 2004).

In the past decades, maral distribution in the Caspian forest was significantly reduced and many populations were locally extirpated, mainly due to poaching; now, several surviving populations are restricted to protected areas (Kiabi et al. 2004). In GNP, red deer suffers from intensive poaching and ineffective law enforcement (Kiabi et al. 2004, Ghoddousi et al. 2016a). The red deer is officially protected in Iran (Kiabi et al. 2004).

Dung decay surveys

One of the key components in the sampling design is to ensure adequate and spatially standardized sampling to cover the study area (Sutherland 2006). The red deer range in GNP was stratified into closed forest (CF, 58% of the range), closed scrubland (CS, 24%) and open scrubland (OS, 18%) using ArcGIS 9.1 (ESRI Inc.) and Google Earth 7.1.5 (Fig. 1, Supplementary material Appendix 1 Table A1). Mean time to decay was estimated by monitoring the status of fresh dung samples (n = 80) recorded from deer resting places between December 2011 and November 2012, roughly once every four weeks. Each dung sample represented a group of pellets produced in a single act of defecation. Samples were identified as being fresh based on their size, moisture content, texture, shiny and wet surface, smell and lack of decomposition signs (Laing et al. 2003). Any dung samples, which could be confused with co-existing roe deer, were excluded. Thus, all dung samples used in this study were assumed to be fresh and 0–2 days old. For better visibility during subsequent visits, each recorded sample was marked by staining trees nearby. Dung samples that were covered by leaves, scattered as a result of animal trampling, washed away by precipitation or removed by invertebrates were all considered as decayed or disappeared (Laing et al. 2003, Tsaparis et al. 2009). Decay was recorded if ≤ 6 pellets were re-found in a dung sample during subsequent visits (Laing et al. 2003).

Twelve visits were undertaken across three habitats in order to record fresh dung samples for the decay experiment
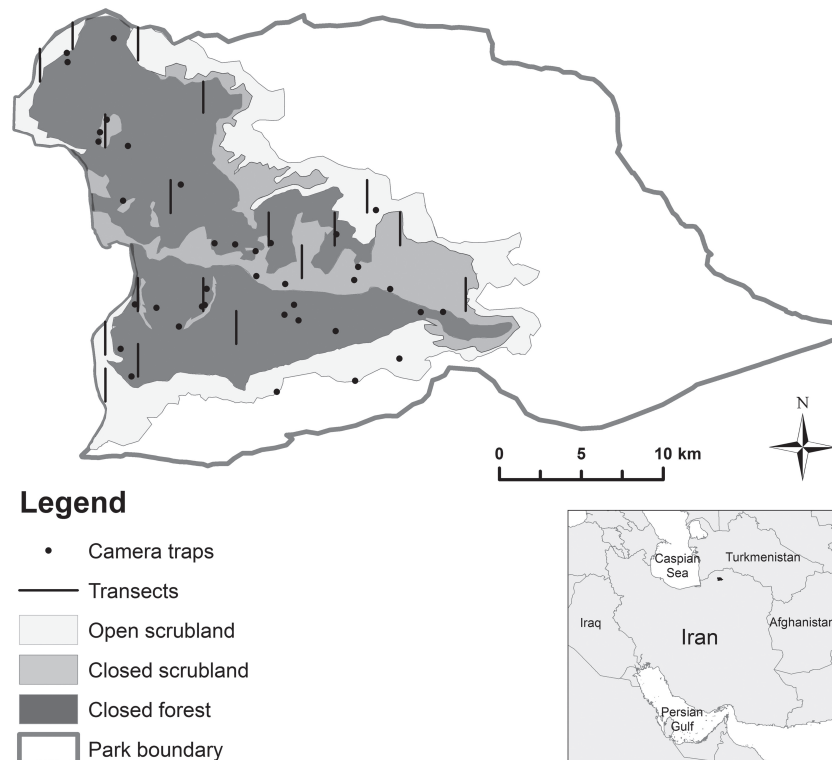
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Figure 1. The study area, habitats and location of transects and camera-trap stations in Golestan National Park, Iran.

(Tsaparis et al. 2009). During each visit, at least two samples per habitat were recorded due to very low deer population density and detection probability of fresh deer dung.

Estimation of defecation rate

Defecation rate was estimated in December 2015 in a 2-ha enclosure with 20 deer individuals located in Ghorogh, 125 km away from GNP. The area is covered by native *Quercus castaneifolia*, *Zelcova carpinifolia*, *Parrotia persica*, *Carpinus betulus* and *Celtis caucasia*. We cleared the area carefully of any dung and chose an 8-days period for estimation of defecation rate, considering that the decay rate in GNP is more than two weeks. We fed red deer with plants collected from GNP: *Poa mazandaranica*, *Vicia variabilis*, *Heracleum gorganicum*, *Hypericum perfratum*, *Phlomis cancellata*, *Asperula gorganica*, *Saponaria bodeana*, *Centaurea golestanica*, *Poa bulbosa*, *Physocaulis nodosus*, *Arabidopsis thaliana* and *Hordeum bulbosum*. Overall, 1676 dung samples were counted by four observers moving 1 m apart at the end of the 8-day period.

Dung count surveys

Originally, 26 strip transects were randomly selected using a 2 × 2 km grid (systematic random sampling) in ArcGIS 9.1 (ESRI Inc.) and Hawth's Tools (Beyer 2004), of which eight transects were inaccessible. Of the 18 remaining transects, eight were located randomly in CF, four in CS and six in OS. For logistical reasons, we used strip transect sampling, which is accurate and comparable with the line transect method (Alves et al. 2013). The survey was conducted in

January–February 2013. All transects were oriented in the south-north direction as it complies with the general density gradient from the core of the park to the boundaries (Buckland et al. 2001, Fig. 1). Each strip transect of 2-km length and 2-m width was surveyed by two observers, one on either side of the strip to minimize the chance of double counts (Buckland et al. 2001). We assumed detection probability of deer dung to equal 1 (Alves et al. 2013) as transects in our study area were narrow and 2 m of transect width minimized the probability of non-detections. These observers were sufficiently skilled to recognize red deer dung based on size and general appearance. Any dung samples of doubtful origin were discarded from the study. To investigate the optimum number of transects and dung samples, we used the standard error (SE) of dung samples as a measure of precision (Alves et al. 2013).

Camera trapping

We used the camera trapping database of the Persian leopard population assessment project in GNP, which was conducted during May–December 2011 (Hamidi et al. 2014). We mounted 53 passive 35-mm film camera traps (Deercam TM, Park Falls WI, USA) in the forested area at a height of ~40 cm for 42.83 ± SE 0.02 consecutive camera days in each station along the trails and ridge tops, whenever leopard signs were present (Hamidi et al. 2014, Ghoddousi et al. 2016a). The minimum distance between camera traps was 2 km (Ghoddousi et al. 2016b). Since 16 camera traps were stolen during the study period (Hamidi et al. 2014, Fig. 1), we used data from 37 camera traps. Although camera traps were set up for leopard captures, we assume that they were

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placed randomly in relation to red deer movements (Rowcliffe et al. 2013, Ghoddousi et al. 2016b). Camera traps were programmed to take pictures at 1 min delay, operate 24 h day^{-1} and stamp date and time on pictures.

Data analysis

Decay rate

To estimate dung decay, each ith marked dung sample ($i = 1$, …, 80) was assigned 1 if present during subsequent visits or 0 if absent (decayed). The period between the time of defecation and the time of the visit was denoted as age (t, days) and the habitat was denoted as H. Binary logistic regression was used to analyze the effect of t and H on dung presence or absence during re-visits (Laing et al. 2003, Tsaparis et al. 2009, Amos et al. 2014). We tested four candidate models (Table 1): model f_0 was the null model without covariates, model f_1 incorporated dung age (t), f_2 described the additive effect of the covariates habitat (H) and age (t) and f_3 addressed the interaction between H and t (Laing et al. 2003, Tsaparis et al. 2009). The Akaike information criterion corrected for small sample size (AIC$_c$), AIC$_c$ weights (w_i) and delta Δ_i (difference between a given model's AIC$_c$ and the best model's minimum AIC$_c$) were used for model selection. The best models were defined as those with $\Delta_i < 2$ (Burnham and Anderson 2002). The mean time to decay (T_{decay}) was computed from dung age t using Eq. 1 (Laing et al. 2003):

$$T_{decay} = \int_0^\infty \frac{-\beta_1 t[1 + \exp(-\beta_0)] \exp[-(\beta_0 + \beta_1 t)]}{[1 + \exp(-(\beta_0 + \beta_1 t))]^2} dt \qquad (1)$$

where the intercept β_0 and the slope β_1 of age t were obtained from logistic regression (Laing et al. 2003). The SE and the 95% confidence interval (95% CI) of T_{decay} were estimated by means of bias-corrected and accelerated bootstrapping with 10 000 iterations (Efron and Tibshirani 1993). The predictive power of the logistic model was tested with the area under the curve (AUC) of receiver operating characteristic (ROC). The score AUC = 0.5 means that the model has no discriminatory ability and AUC = 1 means that models are perfectly discriminated (Stephanie et al. 2001). χ^2-square test was performed to test for difference of density estimates between habitats.

Defecation rate

We estimated defecation rate as 10.48 dung samples per individual and day using Eq. 2 from Buckland et al. (2001):

$$P = \frac{N_{dung}}{N_{deer} \times N_{days}} \qquad (2)$$

where N_{dung} is the number of dung samples counted, N_{deer} is the number of deer in the enclosure and N_{days} is the number

of days during which dung had been accumulated. It was not possible to estimate the SE because defecation rates of individual deer were unknown. The precision of N_{dung} was expressed as the coefficient of variation CV% = (SE/mean) × 100 (Plumptre 2000).

Density estimation: FSC

Deer density (individuals km^{-2}) in GNP was calculated as in Eq. 3 (Laing et al. 2003):

$$D_{FSC} = \frac{N_{dung}}{T_{decay} \times P} \times A \qquad (3)$$

where D_{FSC} is the estimated deer density (individuals km^{-2}), N_{dung} is the estimated dung density (dung samples km^{-2}), T_{decay} is the estimated mean time to decay (days), P is the estimated defecation rate (dung samples/individual and day) and A is the study area (km^2). The precision of FSC was measured by the delta method of Eq. 4 proposed by Laing et al. (2003):

$$[CV_{total}(D_{FSC})]^2 \approx [cv(N_{dung})]^2 + [cv(T_{decay})]^2 + [(P)]^2 \qquad (4)$$

where CV_{total} is the total coefficient of variation.

Density estimation: REM

REM was used to estimate deer density from photo-captures as in Eq. 5 (Rowcliffe et al. 2008):

$$D_{REM} = \frac{y}{t} \frac{\pi}{vr(2 + \theta)} \times g \qquad (5)$$

where D_{REM} is the estimated deer density (individuals km^{-2}), y is the number of independent photo-captures per camera station, t is the sampling effort (camera days) per camera station, v is the animal daily distance walked (km day^{-1}), r is the camera trap detection distance (m), θ is the camera trap angle (radians), π is the constant (3.14), and g is the average animal group size (individuals group^{-1}) (Rowcliffe et al. 2008). The mean group size was estimated as 2.78 ± SE 0.26 individuals group^{-1} from 57 group observations by GNP rangers. These observations came from daily patrolling records, which covered the camera trapping period across the red deer habitats in 2012 (Table 2). The values of θ (0.175 radians) and r (0.012 km) were taken from Rowcliffe et al. (2008) who used the same model of camera traps as we did. We extracted the range of daily distances walked v from the literature on red deer radio-telemetry: 3.85, 2.78 and 3.2 km day^{-1} in France (Pepin et al. 2004, 2008, 2009) and 3.62 km day^{-1} in Portugal (Carranza et al. 1991). From these estimates, we calculated the average daily distance walked as 3.36 ± SE 0.23 km day^{-1}. This average estimate was used in REM density calculations using Eq. 5, whereas the extreme estimates were taken for fixing the simulation and sensitivity analysis. The overall CV of the REM density was computed using the delta method (Rowcliffe et al. 2008). A threshold value of 10 photo-captures which is a minimum number of captures to achieve from expected trap rates was used to estimate the deer density as indicated by Rowcliffe et al. (2008). The 95% CI of REM density was calculated as the mean ± 1.96 × SE (Zero et al. 2013).

Sensitivity analysis

To evaluate the sensitivity of our population estimates to potential violations of the underlying methodical

Table 1. The logistic models of red deer dung decay rates in Golestan National Park, Iran. AIC$_c$ = Akaike information criterion corrected for small sample size, DF = degree of freedom, H = habitat, t = dung age (days), w_i = AIC weight, and Δ_i = delta of the model.

Model	Covariates	Residual deviance	DF	AIC$_c$	Δ_i	w_i
f_1	t	59.46	78	63.62	0.00	0.77
f_2	$H + t$	58.17	76	66.70	3.09	0.16
f_3	$H \times t$	55.40	74	68.56	4.94	0.07
f_0	Null	85.30	79	87.36	23.74	0.00

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Table 2. The parameters required for estimating red deer density from camera-trapping rates using the random encounter model. CV% = coefficient of variation, SE = standard error.

Parameters	Mean $\pm$ SE	CV%	Reference
Photo-captures/camera station (y)	0.27 ± 0.09	33.34	Hamidi et al. (2014)
Camera days/camera station (t)	42.83 ± 0.02	0.04	Hamidi et al. (2014)
Daily distance walked (v, km day^{-1})	3.36 ± 0.23	6.84	Pepin et al. (2004, 2008, 2009), Carranza et al. (1991)
Detection distance (r, km)	0.012		Rowcliffe et al. (2008)
Detection angle (θ, radians)	0.175		Rowcliffe et al. (2008)
Group size (g, individuals group^{-1})	2.78 ± 0.26	9.35	Golestan National Park, unpubl. data (2011–2012)
Total		35.30	

assumptions, we conducted two types of sensitivity analyses. First, we simulated dung encounter rates and camera trapping data to account for non-random distribution of deer and non-random placement of camera traps based on Rowcliffe et al. (2008). Random dung and trapping data was simulated for each transect and camera trap, respectively, using a negative binominal distribution. The mean was calculated as the expected number of samples (dung or photos) per sampling unit (transect or camera) from field-collected samples and the variance was calculated as the observed variance of encounter rate (Rowcliffe et al. 2008). We then recalculated population estimates based on the methods described above (Eq. 3 and 5, respectively), resampling for 10 000 times each. We extracted the 95% CI as the mean $\pm$ 1.96 $\times$ SE of population estimates. Second, we used the extreme ranges of the model parameters to account for their variability. For FSC, we used the lower and upper 95% CI of decay rate

(114.57 and 173.65) and recalculated population size. For REM, we used the lowest and highest observed mean group sizes per season (2.42 and 3.58 individuals group^{-1}) and the most extreme daily movement estimates (2.78 and 3.85 km day^{-1}) and recalculated population size based on all four combinations. For both methods, we reported the full range of the population estimates.

Finally, we performed the Z-test in order to evaluate the difference of population estimates between FSC and REM (Buckland et al. 2001). All statistical analyses were done in R statistical software ver. 3.2.3 (<www.r-project.org>).

Results

Using FSC, we estimated deer population size as 194 $\pm$ SE 46 individuals (overall CV% = 28.44) and density as
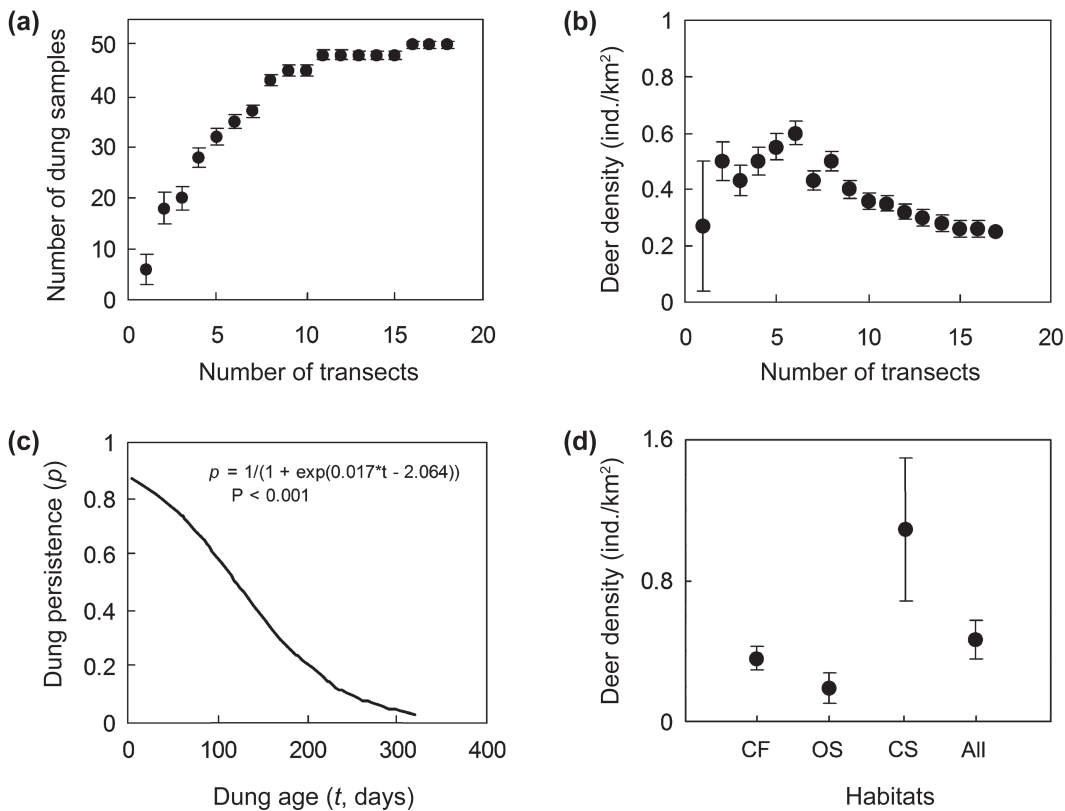

Figure 2. The number of dung samples (a) and red deer *Cervus elaphus maral* density estimates (b) in relation to the number of transects, the logistic regression curve of the probability of dung persistence over time (c) and the distribution of FSC deer density estimates across the closed forest CF, open scrubland OS and closed scrubland CS (d). The standard errors are displayed by bars.

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0.46 ± SE 0.11 individuals km^{-2}. With the increasing numbers of dung samples (N_{dung} = 50) and transects surveyed, precision increased (Fig. 2a–b) and leveled off at approximately 15 transects (Fig. 2b). Although we monitored dung samples only once every four weeks, pooling dung records from all three habitats provided a smooth dung decay curve (Fig. 2c). Deer density was higher in closed scrubland than in other habitat types (Fig. 2d, Supplementary material Appendix 1 Table A2), but this difference was non-significant (χ^2 = 0.875, p = 0.831). For estimating the mean time to dung decay, we sampled 80 fresh dung samples, of which 28 were in CF, 26 in CS and 26 in OS. Of the logistic models of dung decay rates, the age-based model f_1 was the best with $\Delta_i < 2$ (Fig. 2, Table 1). The habitat-based models received less support and the null model was not supported (Table 1). The fitted logistic regression curve of the model f_1 (Fig. 2) had high predictive power (AUC = 0.87 ± SE 0.04, $p_{AUC} < 0.001$, % correct classification = 81.3%). The mean T_{decay} was estimated as 141.81 ± SE 15.07 days (95% CI = 114.57–173.65).

A total of 1585 camera days was accumulated over 37 camera trap stations and 10 photo-captures of red deer were obtained.

Using REM, we estimated the population size as 257 ± SE 84 individuals (overall CV% = 35.30) and density as 0.61 ± SE 0.20 individuals km^{-2}. REM precision leveled off at 31 camera traps and 1345 camera days.

The difference between the estimates of the population size and density obtained by FSC and REM was insignificant (Table 3). The 95% CIs of sensitivity analysis were similar to those of original FSC and REM estimates. The FSC simulation yielded a 95% CI of 135–257 individuals compared to the original FSC 95% CI of 102–285 individuals. The REM simulation analysis estimated a 95% CI of 77–440 individuals compared to the original REM 95% CI of 91–423 individuals. Also, the sensitivity analyses using the extreme values of each parameter resulted in similar population estimates. They ranged from 237 to 486 individuals for REM (compared to the original estimate of 257 individuals) and from 163 to 248 individuals for FSC (compared to the original estimate of 194 individuals).

Discussion

Monitoring red deer is challenging throughout its global range (Marques et al. 2001). This research is the first attempt to fill a gap in empirical knowledge on red deer population size and density by applying two independent count techniques in a montane forest ecosystem. Although direct observation methods are methodologically well developed,

they are difficult to apply in places where this species is rare or less habituated to human presence (Tsaparis et al. 2009), and in hardly accessible rugged landscapes (Singh and Milner-Gulland 2011).

Dung counts are often applied as an alternative method to count deer species (Alves et al. 2013, Amos et al. 2014). In this study, we successfully estimated population size and density of red deer in Golestan from dung counts (Table 3). In contrast to the study by Tsaparis et al. (2009), we did not find variation in decay rates between habitats. However, the mean time to decay was 52% shorter than elsewhere (141.81 ± SE 15.07 versus 275 ± SE 42 days; Laing et al. 2003). The high rate of dung decay in our study area could result from high diversity of dung beetles and intensive wildlife movements, which potentially accelerate dung decomposition (Bahrami et al. 2011). An accurate density estimate via pellet counts relies mainly on accurate estimation of dung encounter and decay rates (Alves et al. 2013). Although we attempted to minimize variation of dung counts by obtaining local estimates of dung decay and defecation rates, still many transects contained no dung, which reduced the overall precision of FSC estimates of deer number and density. Further progress in counting deer in Golestan could be reached with the application of a stratified random survey design and species distribution modeling, for which independent historical data on population trends could serve as a reliable baseline (Kiabi et al. 2004, Hemami et al. 2007, Tsaparis et al. 2009, Alves et al. 2013).

Our results also suggest that red deer numbers and density can be reliably estimated by REM from camera-trap records without the need for individual recognition of animals (Rowcliffe et al. 2008). An allometric diagram of species densities and distances walked provided by Rowcliffe et al. (2008) shows that at least 1000 camera-days are required to obtain 10 photographs of rare ungulates. We reached this threshold at a similar camera trapping effort of 1345 camera days. As camera trapping rates are intuitively linked with animal abundance, encounter rates between individuals and camera traps are expected to increase with population density (Rowcliffe et al. 2008, Rovero and Marshall 2009). This relationship between camera trapping rates and population density is strong and can be linear, as in forest ungulates of Tanzania (Rovero and Marshall 2009). According to Rowcliffe et al. (2008), the number of camera trap stations and the amount of effort in our study were adequate and could not affect deer capture rates. Therefore, low capture rates of red deer in Golestan are most likely caused by low densities of this ungulate.

Nevertheless, there are some limitations involved in study design and methodology, which might have influenced our results. Our camera trapping data comes from a study focused on leopards and this could have affected red deer capture rates. Although the predator–prey relationship between leopard and red deer may have affected the capture rates, we assume that the movement pattern of red deer is independent from leopard movements and therefore is spatially unbiased. Moreover, a recent study (Cusack et al. 2015a) revealed that herbivore capture rates are insensitive to placement of camera traps. Additional biases may arise from the application of non-local daily distance estimates

Table 3. Comparison of red deer density estimates from fecal standing crop (FSC) and random encounter model (REM) methods. CI = confidence interval, SE = standard error.

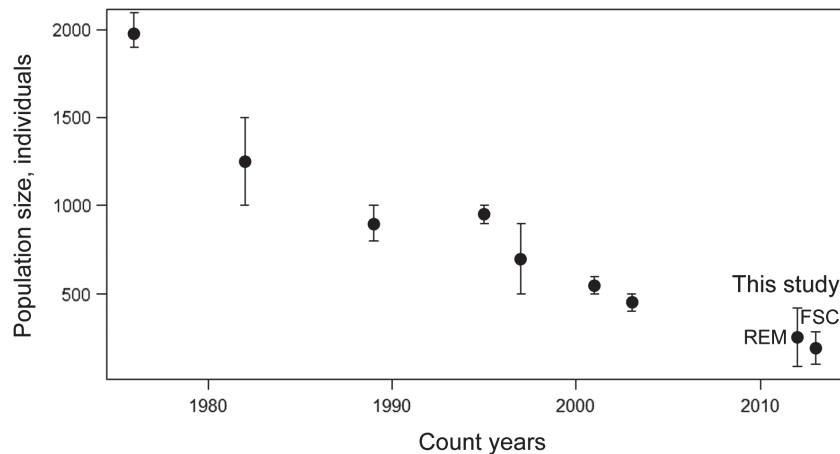| Estimated parameters	FSC	REM
Density, individuals km^{-2} ± SE	0.46 ± 0.11	0.61 ± 0.20
95% CI of density	0.25–0.67	0.22–1.08
Population size, individuals	194.12 ± 46.57	257.42 ± 84.55
95% CI of population size	102–285	91–423

Figure 3. The estimates of red deer population size in Golestan National Park according to dung counts in 1976–1977 and total counts during the rutting season in 1978–2003 (Kiabi et al. 2004). Our REM (2011) and FSC (2012–2013) estimates are given for a comparison. The error bars show the limits of total counts (1976–2003) and 95% confidence intervals (present study).

and seasonal variation of group size, but the sensitivity analysis showed that our results are sufficiently reliable. As daily distances moved by red deer were unavailable for our study area, we had to borrow them from the Mediterranean region in France and Portugal (Carranza et al. 1991, Pepin et al. 2004, 2008, 2009). We strongly encourage researchers who apply REM to use local data, in particular on the most influential population parameters such as group size and animal movements. Another source of uncertainty is that the defecation rate may differ between captive and free-living animals and also depend on seasons, forage intake, sex and age (Buckland et al. 2001). We attempted to minimize such potential bias by feeding animals with natural vegetation. Other studies also found that defecation rates are less variable than other parameters used in density estimation from dung counts (Neff 1968, Buckland et al. 2001, Marques et al. 2001). We also acknowledge that our camera trapping and dung count data were collected in distinct years (2011 and 2013), which also might affect the results. However, we have no ground to surmise that the population of red deer experienced any significant changes during this short period. Finally, our results could be affected by theft of 16 out of 53 camera traps by poachers, which reduced sample size and habitat coverage (Rovero and Marshall 2009).

Both FSC and REM have clearly shown the rarity of red deer in Golestan. A comparison of our estimates with historical records suggests that the local deer population may have dropped by ~90% from ca 2096 (dung count, 1976–1977), 1897 (transects, 1976–1978), 900–1500 (rutting counts, 1982–1995) and 400–900 (rutting counts, 1995–2003) individuals to only 194–257 individuals now (Fig. 3, Table 3; Kiabi et al. 2004). The other indicators of population decline are smaller group size (2.8 versus 4.6 individuals group^{-1} in Kiabi et al. 2004) and heavy impact of poaching pressure on large mammals in Golestan in general (Ghoddousi et al. 2016a).

Most of red deer poaching occurs during the rutting season (September–October) when stags are easily attracted by call imitation. In order to control poaching, the Iranian Dept of Environment (DoE) implements constant patrolling throughout the red deer habitat in Golestan. Despite this, the scales of deer poaching are alarming. According to Kiabi et al. (2004), the main threat to red deer in Golestan is a combination of poaching and habitat degradation. This is indirectly confirmed by our study as deer were detected mainly in safe core zones rather than in ecotones along the forest edge. Thus, in line with Kiabi et al. (2004) we also emphasize the necessity to protect areas close to reserve borders similar to those within the core zone of the park. Moreover, getting more knowledge on poachers' incentives may help in reversing the population decline of red deer in Golestan (Kiabi et al. 2004).

Overall, we concluded that FSC and REM could serve as the practical techniques to count and monitor red deer populations living at low densities in montane forests. We strongly recommend to carefully consider opportunities and limitations of these methods and to use locally obtained variables of population size and density. We further confirm the plight of the red deer population in Golestan and appeal for urgent, targeted and practical evidence-based conservation actions. It is advised to conduct socio-economically oriented studies to unveil the potential reasons for poaching and decrease their incentives.

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Supplementary material (available online as Appendix wlb-00230 at <www.wildlifebiology.org/appendix/wlb-00230>). Appendix 1.