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Evaluating the effectiveness of two distance-sampling techniques for monitoring roe deer (*Capreolus capreolus*) densities

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Monitoring wild cervid populations have become a priority for management. However, accurate and reliable estimates of densities are difficult to achieve since they may be affected by environmental variation, species behaviour or observational issues. Therefore, to obtain unbiased estimates of densities it is necessary to adopt sampling methods that quantify the probability to detect the target species. In this study, we compare the results of roe deer sampling based on distance detection performed by two techniques: surveys on foot in the evening and nocturnal surveys by car. Estimates of roe deer population densities were conducted in Sierra de Guadarrama (Madrid, Spain). Distance sampling was conducted along tracks in 10 pine forests in October. Observations from the surveys done on foot were better fitted with detection functions, although this technique required more days and more observers for its realization, hence increasing field effort. Nocturnal surveys by car were also a proper technique and decreased distance sampling costs, since only three people were needed for 6 days to carry them out. However, observations obtained with this technique showed an imbalance in the detection function in the first few metres. This model was limited by the small number of roe deer observed in or near the line of progression. This is a handicap because functions used by the Distance software assume that the highest probability of detecting specimens is in the line of progression, causing an imbalance in the detection function at zero distance. To compensate for this, data were left-truncated at 20 m. Therefore, when it is necessary to estimate absolute densities of roe deer populations, nocturnal distance sampling by car seems to be the most appropriate method due to its low cost, yet the influence of the vehicle on the distribution of roe deer and, therefore, on the estimated density, must be taken into account when carrying out such studies.

Introduction

Throughout the 20th century, deer populations significantly increased their distribution in both North America and Europe (Gill 1990), probably due to the recovery of habitats and management of the species (Gill *et al*. 1996, Cederlund *et al*. 1998). During the final decades of the 20th century, European roe deer (*Capreolus capreolus*) experienced an expansion in most of its range (Danilkin & Hewison 1996). In Spain, its population has benefited from a decline in ranching, abandonment of agriculture in foothill areas, and a significant increase in forest areas (Acevedo *et al*. 2005). Furthermore, roe deer hunting management has been improved considerably in recent decades, with shorter hunting seasons, limited quotas, supplementary feeding, improved habitat quality and increased reintroductions (Meriggi *et al*. 2008).

Social interest in the management of this species, both in Spain and the rest of Europe, has increased substantially (Staines & Ratcliffe 1987, Cederlund *et al*. 1998, Radeloff *et al*. 1999). On one hand, increasing distribution areas and densities have substantially benefited hunting, also increasing nature tourism in many places. Furthermore, species like the wolf (*Canis lupus*) have benefited from the increased abundance of roe deer, which is the basis of its diet in many areas of northern Spain which in turn minimizes conflicts with cattle (Mattioli *et al*. 2004, Gazzola *et al*. 2005, Barja 2009). However, an increase in the abundance of roe deer has also caused an increase in damage to forests and agriculture (Boh *et al*. 1998, Acevedo *et al*. 2005). For these reasons, studies on the effectiveness of distance sampling of cervids have gained importance as a critical tool in making management decisions in situations of animal excess or shortage.

A number of factors are important in the distance sampling of wildlife, including environmental changes (weather, habitat and season), species behaviour (flight distance and mimicry) and observation skills (Verner 1985, Bibby & Buckland 1987, Verner & Milne 1989, Diefenbach *et al*. 2003, Norvell *et al*. 2003). Therefore, to estimate density objectively, it is necessary to adopt distance sampling methods capable of quantifying the probability of detecting the species under study, taking into account the above-mentioned factors (White 2005).

Sampling based on detection distance (Thomas *et al*. 2002, Buckland *et al*. 2004) is widely used because of its ease of use and the availability of free software for estimating population densities through models based on detection probability. These methods are based on the distance at which animals are detected on both sides of a line along which the observer moves. Thus, the three basic premises on which these techniques are based are the following (Buckland *et al*. 2001): (1) animals located in the line of progression are identified with probability 1, (2) animals are detected in their initial location, prior to any movement in response to the observer, and (3) distances from the line of progression to animals are measured accurately. The first and last of these assumptions are dependent on the distance-sampling design, equipment and the rigour of the viewer and, therefore, can be controlled by the observer. However, the second assumption depends on the response of the animal to the observer. The observer's ability to avoid detection could also affect the second assumption, so having skilled people is important.

Sampling based on detection distance has proven to be a reliable technique for density estimates, although it is necessary to take other factors into account, such as animal activity rhythms and habitat type (Buckland *et al*. 2001). Since these techniques offer suitable solutions for population surveys, they are often chosen by researchers to study such a large and varied group of animals like ungulates (Focardi *et al*. 2002, Ward *et al*. 2004, Liu *et al*. 2008, Wegge & Storaas 2009, Schmidt *et al*. 2012).

The following factors affect the ability to detect individuals: limitations of the observer (fatigue, vision, ability to move quietly), habitat variables (vegetation cover, relief), the observer's moving speed, weather conditions (wind, rain), the type of soil on which he/she walks (stony, with dry leaves), and variables related to the species (sex, size, behaviour) (Burnham & Anderson 1984, Anderson *et al*. 2001). The observer's experience significantly increases detection rates of animals. Therefore, visual and

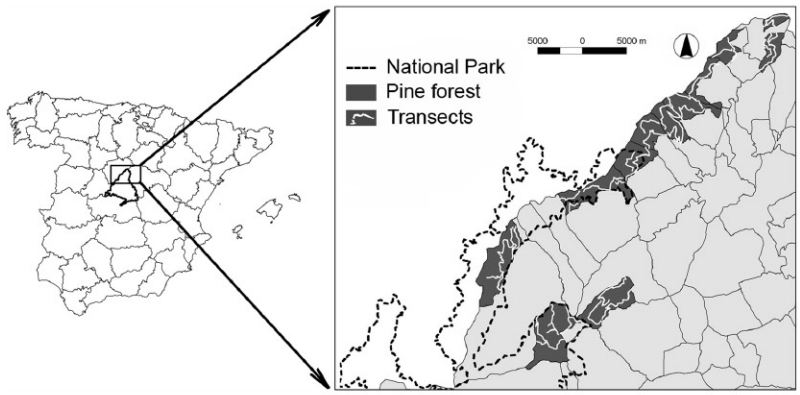

Fig. 1. Location of the study area in the Iberian Peninsula showing pine forests and the transects sampled by car and on foot in Sierra de Guadarrama (Madrid, Spain).

auditory skills are often necessary to distinguish species. Furthermore, training level and experience will determine the degree of these skills (Gregori *et al*. 2002). Vegetation structure also affects the detection of animals. Thus, Gill *et al*. (1997) indicated that the lack of vegetation and greater visibility provided more accurate density estimates of a species. Factors related to animals, including size, colour or mobility, can also lead to increased detection. Furthermore, sex differences (size of the animal, differences in behaviour, mobility, flight distance, habitat segregation and group size) may affect detectability (Focardi *et al*. 2002).

Reliable distance-sampling techniques to estimate wild mammal densities, particularly game species such as ungulates, are very useful to managers and conservationists because they provide key data for conservation programme decisions. Therefore, the aim of this study was to compare the effectiveness of two distance sampling techniques in monitoring roe deer: surveys on foot in the evening and nocturnal surveys by car with spotlights. Differences between both techniques are likely based on changes in roe deer behaviour in response to the observer. Our aims are to verify compliance with the second premise of these distance sampling techniques (animals are detected at their initial location prior to any movement in response to the observer), and to analyse the influence of both distance sampling techniques on density estimation. We predict that nocturnal surveys by car compared with surveys on foot provide advantages in terms of costs and in avoiding detection of the observer. However, since car noise could affect roe deer behaviour, we expect a decrease in the number of individuals observed in or near the line of progression.

Material and methods

Study area and species studied

The roe deer population in Sierra de Guadarrama, in the centre of the Iberian Peninsula, was sampled in October 2007 in 10 Scots pine (*Pinus sylvestris*) reforestations, which ranged in size from 292.6 to 2513.8 ha (mean ± SD = 1410.0 ± 692.3 ha) (Fig. 1). These pine forests represent the main vegetation type of the Guadarrama oro-mediterranean floor (Rivas-Martínez 1987). Pine forests were located in public use areas of the Community of Madrid, five of which are within the territory of the National Park of Sierra de Guadarrama (declared on 25 June 2013) (Fig. 1). However, it should be noted that this study was conducted for one year only and there was limited site replication.

The mountainous landscape of the study area consists of forests, shrublands and grasslands. Pine forests are located between 1200 and 1900 m a.s.l. with understory species such as mountain broom (*Cytisus oromediterraneus*), common juniper (*Juniperus communis*) or Guadarrama broom (*Adenocarpus hispanicus*), enriched with holly (*Ilex aquifolium*) and isolated oaks (*Quercus pyrenaica*) (Rivas-Martínez 1987).

The abundance of roe deer in the study area is directly related to forest size (Sáez-Royuela & Tellería 1991). Namely, similar densities of

roe deer were detected in oak and pine forests, decreasing significantly in shrublands or valley bottoms (Horcajada 2007). Seasonal variation in the gregarious structure of roe deer is consistent with trends observed in other populations (Delibes 1996), showing maximum isolation in spring and summer and regrouping during the autumn and winter.

Distance sampling on foot and by car

To estimate the roe deer density in the study area, on tracks and forest roads we established transects to be surveyed on foot and by car (Fig. 1) in the evening and at night. Data collection was in line with the nocturnal and crepuscular activity (Ellenberg 1978, Chapman *et al*. 1993) and a circadian activity pattern polyphase of the roe deer (Delibes 1996, Mateos-Quesada 2002). Transects were separated by 250 to 500 m. A track width did not exceed 4 m and there was tree cover on both sides of the transects.

The transects were surveyed by car during 6 nights (16 transects, 179 km in total). A transect length varied from 2.8 to 39.3 km (mean ± SD = 11.2 ± 8.8 km). Transects covered the entire study area, including all tracks and roads accessible by car. Distance sampling was conducted once per transect, between the hours of 21:00 and 05:00. Data were not collected during nights with rain or fog. The census team consisted of a driver and two observers placed in the back seat of the car. The driver was also an observer. The sport utility vehicle (SUV) was driven at 10–15 km h^{-1}. Observers watched through open windows to both sides of the road, each using a spotlight (Interface, brightness: 1 000 000 candlepower, power: 100 W). In most cases, the animals observed were identified by all three observers.

The same transects were surveyed on foot during 21 days. Since some transects surveyed by car were too long to cover by walking during one evening, they were divided into several sections, with resulted in a total of 64 transects. A transect length in this case varied from 2.1 to 3.6 km (mean ± SD = 2.7 ± 0.4 km) and surveys were carried out once along tracks and forest roads during sunset, between the hours of 19:30 and 21:00. Wind direction was taken into account during the surveys on foot and surveys were not carried out when observers could be detected by animals. A single observer walked quietly at a speed of approximately 2 km h^{-1}. A total of 6 observers, all experienced in this type of studies, participated in the survey on foot, including the three people who surveyed the transects by car.

Observers were equipped with binoculars with rangefinders (Leica Geovid 8 × 42) to facilitate identification of animals and to measure distance to the detected animals. For each detection event, we recorded the number of roe deer in the group, their behaviour during the observation (moving or motionless) and the direction of escape. During nocturnal surveys by car, when a roe deer was located, the driver stopped the car and recorded the perpendicular distance to the animal(s). When an animal was detected on foot, we recorded its initial location before recording the perpendicular distance. In addition, contact coordinates were recorded with the GPS (Thales Mobile Mapper).

Data analysis

According to Buckland *et al*. (2001), very little efficiency is lost by grouping sighting data. Thus, to achieve a better fitting of the function model, sightings were grouped into perpendicular distance intervals.

For density estimates, only those contacts between 0 and 150 m (n = 125) were included. Sightings at > 150 m were excluded from the analysis due to the difficulty in accurately estimating the distance. Buckland *et al*. (2001) recommend the truncation of data to eliminate outliers and improve model fitting. Furthermore, if detection of animals in or near the transect line is consistently reduced (< 1), but there is perfect parallel detection (Quang & Lanctot 1991), then by left-truncating the data the maximum detection can be estimated (Pollock & Kendall 1987).

The estimated density was achieved after detection functions had been modelled based on the perpendicular distances. The detection function, $g(y)$, is the probability of detecting an animal at a given distance. The proportion of

animals detected can be assessed by calculating the difference between the expected number of roe deer detected and the number of individuals observed (Buckland *et al*. 1993, Thomas *et al*. 2002). For an adequate density estimation, a relatively large number of detections is required, at least 60–80 according to Buckland *et al*. (2001) although it is also possible with 40 individuals (Burnham *et al*. 1980).

The data were analysed using the Distance software ver. 6.0 (Thomas *et al*. 2010) and the multiple covariates distance sampling (MCDS) engine. We followed the analysis guidelines of Buckland *et al*. (2001), which include exploratory analysis, model selection, and final analysis and inference. The Distance programme allows for several key functions and series expansion terms to model the detection function. For each sampling technique (by car/on foot), we tested the following models (and series expansion terms): half-normal (cosine or hermite polynomial), hazard-rate models (cosine or simple polynomial), exponential negative (cosine) and uniform (cosine). MCDS analyses were conducted to test for effects of the covariate distance sampling techniques (by car/on foot) with a single model implementing the post-stratification (Buckland *et al*. 2001). This method of the data analysis is recommended for stratified sampling based on non-geographical data (Marques & Buckland 2003). Model fit and ranking were assessed using Akaike's Information Criterion with correction for small samples sizes (AIC) (Buckland *et al*. 2001), and the goodness of fit test (χ^2).

Results

General distance sampling using post-stratification

During the study, 127 roe deer were observed in 108 different groups (Fig. 2). The mean ± SD roe deer group size was 1.18 ± 0.42 individuals: 71.6% of the roe deer were seen alone and 23.6% were observed in groups of two animals. Only 4.7% of the roe deer were observed in groups of more than 2 individuals. The hazard-rate function model best fitted all encounters with animals

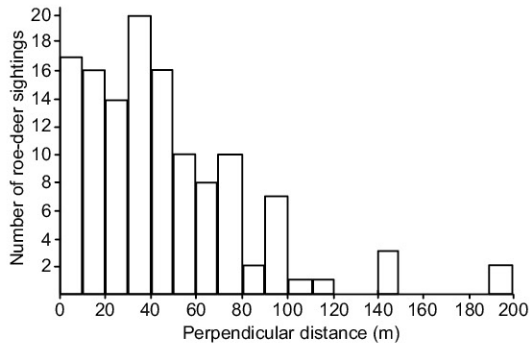

Fig. 2. Histogram and distance of detection for surveys of roe deer in pine forests of the Sierra de Guadarrama (Iberian Peninsula). n = 127.

along the transects (AIC = 287) (Table 1). The mean density (roe deer/100 ha) obtained with the current method was 1.91 (95%CI = 1.42–2.56, CV = 14.84%) (Table 1 and Fig. 3A).

Nocturnal surveys by car

During the nocturnal surveys by car, 77 roe deer were observed in 58 different groups. Mean ± SD group size was 1.33 ± 0.54 individuals: 53.2% of the roe deer were seen alone and 38.9% were observed in groups of two animals. Only 7.7% of the roe deer were observed in groups of more than two individuals. Data analysis revealed that the model was limited by the low number of roe deer observed along or near the line of progression (Fig. 3B), so we decided to truncate the data to the left, avoiding the first 20 m (Fig. 3C). The density estimation was 18.1% higher with left-truncated data than with non-truncated data (Table 1). The mean density of roe deer for left-truncated data was 3.13 indiv./100 ha (95%CI = 2.26–4.34, CV = 16.4%) (Table 1 and Fig. 3C), whereas without truncation, density estimation was 2.65 (95%CI = 2.01–3.48, CV = 13.7%) (Table 1 and Fig. 3B).

During detection, 76.0% of the roe deer remained still and 82.0% did not change their behaviour in the presence of the car. Of the roe deer observed at a distance of 0–20 m (n = 9) from the car, three individuals run away, three continued walking, one crouched and two remained still. All roe deer observed at 0 m ran away during observation (n = 3).

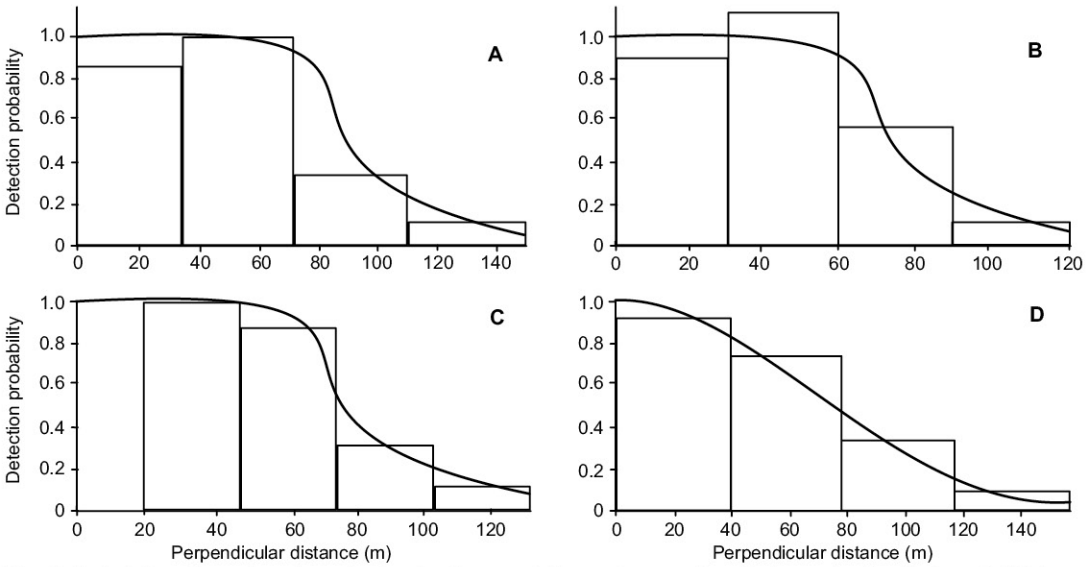

Fig. 3. Probability of roe deer detection in pine forests of the study area. Bars indicate the distribution of sightings. The curves represent the detection function best fitting model for each type of distance sampling. (**A**) General line surveys using "post-stratification", (**B**) nocturnal surveys by car, (**C**) nocturnal surveys by car left-truncated at 20 m, and (**D**) surveys on foot. For techniques **A**, **B** and **C**, the cosine-adjusted hazard function was used in the models and for **D**, we used Fourier series of cosine-adjusted uniform function.

Surveys on foot

During surveys on foot, 50 roe deer were individually detected. The mean density of roe deer was 1.43 indiv./100 ha (95%CI = 1.03–1.99, CV = 16.40%) (Table 1 and Fig. 3D); 78% moved while detected, and all animals changed their behaviour during observation.

Comparison of the two distance-sampling techniques

The estimated roe deer density obtained from the nocturnal surveys by car, using left-truncated data, was 18.1% higher than that from the non-truncated data, and 118.0% higher than that from the data from the surveys on foot. During the

Table 1. Roe deer densities in the study area estimated with different distance-sampling techniques. In all cases the best fit (in boldface) was obtained with the cosine-adjusted hazard function, except for surveys on foot in which Fourier series with the cosine-adjusted uniform function were used. The table also shows 95% confidence intervals (95%CI), AIC values, standard errors (SE), coefficient of variation (CV) and probability from the goodness of fit test (*p*).

Distance sampling techniques	Function model	Deer density (indiv. km^{-2})	95%CI	AIC	CV	SE	*p*
General line surveys using "post-stratification"	**Hazard/cosine**	1.91	1.42–2.56	287	0.14	0.28	–
	Half-normal/cosine	2.21	1.64–2.97	290	0.15	0.33	–
Nocturnal surveys by car	**Hazard/cosine**	2.65	2.01–3.48	191	0.13	0.36	0.48
	Half-normal/cosine	3.15	2.33–4.25	193	0.15	0.47	0.13
	Uniform/cosine	2.78	1.85–4.18	192	0.21	0.58	0.14
Nocturnal surveys by car left-truncated	**Hazard/cosine**	3.13	2.26–4.34	155	0.16	0.51	0.98
	Half-normal/cosine	4.56	3.20–6.50	156	0.18	0.82	0.27
	Exp.neg/cosine	4.82	0.38–61.03	157	2.01	9.69	0.16
Surveys on foot	**Uniform/cosine**	1.43	1.03–1.99	117	0.16	0.23	0.99
	Hazard/cosine	1.35	0.87–2.07	119	0.22	0.29	0.75
	Half-normal/cosine	1.48	1.01–2.14	117	0.19	0.28	0.98

surveys by car and on foot, 0.43 and 0.24 roe deer per km were observed, respectively. As per roe deer behaviour during detection, 76% of roe deer in the surveys by car were motionless while only 22% were not moving during the surveys carried out on foot. In the surveys by car, only 53.2% of roe deer were seen alone while in the surveys on foot all individuals were detected alone.

Discussion

Similarly to the rest of Europe (Danilkin & Hewison 1996), the roe deer population in the centre of the Iberian Peninsula increased in range during the last decades (Acevedo *et al*. 2005). For this reason, interest in the management of this species has increased significantly (Cederlund *et al*. 1998, Radeloff *et al*. 1999). The use of reliable methods to estimate vertebrate population densities is the basis for sound management (Barea-Azcón *et al*. 2007). However, there is a disagreement regarding the estimation accuracy of different methods, especially those based on distance sampling techniques (Álvarez 1988, Gill *et al*. 1997), although the goodness of fit of this method has been highlighted by some authors. The effectiveness of distance sampling in the study of roe deer abundance in forest areas has been evaluated by several authors (Gaillard *et al*. 1993, Ward *et al*. 2004, Focardi *et al*. 2005). Furthermore, Smart *et al*. (2004) indicated that this method provided estimates equally good or better than other techniques, being frequently used for ungulates by several authors (Marques *et al*. 2001, Walter & Hone 2003). In the present study, the obtained mean densities were within the minimum values given by other authors for roe deer populations both in Spain and the rest of Europe (Costa 1992, Aragon 1993, Mateos-Quesada 2005). There are also references reporting low densities in coniferous forests both in Spain (Mateos-Quesada 2005) and in Europe (Cederlund 1981). Pine forests in the study area have low vegetation diversity and a reduced shrub layer mainly due to management to combat forest fires (Bailón *et al*. 2008), and are being avoided by roe deer compared with deciduous forests with a good shrub layer (Pedroli *et al*. 1981, Prior 1995, Mateos-Quesada 2005). This, together with competition with livestock, seems to be the main causes of a low roe deer density, as observed by other authors for roe deer and other wild ungulate species (Fuller 1990, San José *et al*. 1997).

Using different distance-sampling methods (e.g. surveys on foot *vs*. by car) occasionally involves considerable differences regarding efficiency. Thus, ecological parameters such as density or behaviour can be affected but also the costs, which are key for any wildlife management. Although a better fit was obtained in the detection function with the surveys on foot, showing a uniform distribution on both sides of the line of progression, the nocturnal surveys by car better met the assumption regarding the animal's response to the observer (Buckland *et al*. 2001): most roe deer were motionless when detected and almost none changed their behaviour during observation. In contrast, this did not occur in the surveys on foot: most roe deer were moving after they were detected. A relevant consideration when using these methods is that the behaviour of individuals within the first few metres from zero distance can influence distance-sampling results by violating one of the key premises (Ward *et al*. 2004). During the surveys by car, roe deer were more tolerant to the observer than in the surveys on foot, although animals avoided the first few metres on both sides of the road where the vehicle was travelling, causing an imbalance in the detection function within these first few metres. This has also been observed in other studies (Heydon *et al*. 2000, Sadlier *et al*. 2004). Gill *et al*. (1997) also showed that roe deer avoided roads during night in response to the presence of vehicles from which poachers usually hunt at night. Since in our study area there is no evidence of poaching by car, it is possible that roe deer moved out of the way simply to avoid direct contact with the vehicle. Therefore, due to the small number of roe deer observed along or near the line of progression, we chose to manipulate our data by truncating the first 20 m (Buckland *et al*. 1993). The effect of the manipulation is impossible to judge when the actual density is not known, as is the case in this study. However, two scenarios are likely: first, left-truncation could result in underestimation since it is probable that

not all animals in the first 20 m were detected, especially when forests are dense. Second, if an area of higher density was effectively used as zero distance, this could lead to overestimation, especially if roe deer positively selected this margin between roads and forests as described by Ward *et al*. (2004) in their study. Even though we did not observe exaggerated peaks in frequencies within the first distance interval (20–45 m), thus showing a homogeneous roe deer distribution, the estimated roe deer density with left-truncated data was higher than that obtained from the non-truncated data, therefore, possibly leading to overestimation.

Even so, in the surveys by car, observer-dependent factors such as fatigue, stealth to avoid detection, visual acumen to detect animals and the odour emitted by the observer, described by some authors as causes of imprecision and loss of contacts in the estimates on foot (Burnham & Anderson 1984, Anderson *et al*. 2001), were minimized. Observer fatigue as well as human detection and body odour is reduced when travelling by car. Furthermore, using spotlights enhances the observer's visual capacity by easing the observation of the eye-shine caused by the "*tapetum lucidum*". Thus, since in ungulates it is blue reflected (Martin 1990), this clearly facilitates the detection of individuals behind vegetation or bedridden. This avoids any confusion between roe deer and other mammals such as carnivores.

Furthermore, regarding environmental factors (downwind, speed of progression along the route, vegetation cover and season) (Burnham & Anderson 1984, Anderson *et al*. 2001), nocturnal surveys by car solve some problems present in surveys on foot. For instance, the vehicle prevents the detection of the observer due to his/her location downwind; moreover, it is easier to maintain a constant speed during the survey (15 km h^{-1}). Regarding variables related to this species, such as animal behaviour when detecting the observer, this study has shown that most roe deer located from the car did not alter their behaviour when detected. All above-mentioned factors could lead to an underestimate of population density in surveys on foot, because a large number of animals could flee before being seen by the observer.

Since during the nocturnal surveys by car most roe deer maintained their behaviour during observation, this supports the second basic premise on which these techniques are based; animals are detected in their initial location prior to any movement in response to the observer (Buckland *et al*. 2001).

In terms of time spent and cost-effectiveness, the nocturnal surveys by car were more economical than those made on foot, since only three observers were needed. This difference is primarily based on the number of kilometres per work day. Since light is not a limited factor for surveys by car, distance sampling can be done between sunset and sunrise. In addition, thanks to vehicle speed, sampling can be carried out for longer (21:00 and 05:00), so the number of days required to complete sampling is significantly reduced.

Finally, based on the differences between the two distance-sampling techniques used here, we conclude that sampling by car with spotlights favours the detection of animals but this also involves an imbalance in the first meters of the detection function. Therefore, the advantages and limitations of each distance-sampling technique should be taken into account when calculating reliable population estimates for this species.

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References

Acevedo, P., Delibes-Mateos, M., Escudero, M. A., Vicente, J., Marco, J. & Gortazar, C. 2005: Environmental constraints in the colonization sequence of roe deer (*Capreolus capreolus* L., 1758) across the Iberian mountains, Spain. — *Journal of Biogeography* 32: 1671–1680.

Álvarez, G. 1988: Problemas asociados a la aplicación del transecto lineal para el censo de las poblaciones de cérvidos en un biotopo mediterráneo (Quintos de Mora,

Montes de Toledo). — *Ecología* 2: 233–249.

Anderson, D. R., Burnham, K. P. Lubow, B. C., Thomas, L. E. N., Corn, P. S., Medica, P. A. & Marlow, R. W. 2001: Field trials of line transect methods applied to estimation of desert tortoise abundance. — *Journal of Wildlife Management* 65: 583–597.

Aragón, S. 1993: El corzo (*Capreolus capreolus*) en Cádiz. Caracterización y encuadre de sus poblaciones en el conjunto de la especie. — Ph.D. thesis, Universidad de Sevilla, Spain.

Bailón, L. J., García, F. M. & Tenerio, M. C. 2008: Estudio comparado de la diversidad florística en masas de origen natural y repoblado de *Pinus sylvestris* L. en la Sierra de Guadarrama (Sistema Central). — *Forest Systems* 15: 111–123.

Barea-Azcón, J. M., Virgos, E., Ballesteros-Duperon, E., Monleón, M. & Chirosa, M. 2007: Surveying carnivores at large spatial scales: a comparison of four broad-applied methods. — *Biodiversity and Conservation* 16: 1213–1230.

Barja, I. 2009: Prey and prey-age preference by Iberian wolf (*Canis lupus signatus*) in a multiple-prey ecosystem. — *Wildlife Biology* 15: 147–154.

Bibby, C. J. & Buckland, S. T. 1987: Bias of bird census results due to detectability varying with habitat. — *Acta Oecologica* 8: 103–112.

Boh, B., Kosir, I., Kukovic, M., Skerlavaj, V. & Skvarc, A. 1998: Experimental microencapulation and testing of the repellent daphne for prolonged protection of plants against roe deer (*Capreolus capreolus* L.). — *Sodobno Kmetijstvo* 31: 553–558.

Buckland, S. T., Anderson, D. R., Burnham, K. P. & Laake, J. L. 1993: *Distance sampling: estimating abundance of biological populations*. — Chapman and Hall, London.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. 2004: *Advanced distance sampling: estimating abundance of biological populations*. — Oxford University Press, Oxford.

Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. & Thomas, L. 2001: *Introduction to distance sampling: estimating abundance of biological populations*. — Oxford University Press, Oxford.

Burnham, K. P. & Anderson, D. R. 1984: The need for distance data in the transect counts. — *Journal of Wildlife Management* 48: 1248–1254.

Burnham, K. P., Anderson, D. R. & Laake, J. L. 1980: Estimation of density from line transect sampling of biological populations. — *Wildlife monographs* 72: 1–202.

Cederlund, G. 1981: Daily and seasonal activity pattern of roe deer in a boreal habitat. — *Swedish Wildlife Research* 1: 315–353.

Cederlund, G., Bergqvist, J., Kjellander, P., Gill, R., Gaillard, J. M., Boisaubert, B., Ballon, P. & Duncan, P. 1998: Managing roe deer and their impact on the environment: maximisin the net benefits to society. — In: Andersen, R., Duncan, P. & Linnell, J. D. C. (eds.), *The European roe deer: the biology of success*: 337–372. Scandinavian University Press, Oslo.

Costa, L. 1992: *Ecología del corzo en las montañas cantábricas. Modelo de gestión*. — Ph.D. thesis, Universidad de León, Spain.

Chapman, N. G., Claydon, K., Claydon, M., Forde, P. G. & Harris, S. 1993: Sympatric populations of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*): a comparative analysis of their ranging behaviour, social organization and activity. — *Journal of Zoology* 229: 623–640.

Danilkin, A. & Hewison, A. J. M. 1996: *Behavioural ecology of Siberian and European roe deer*. — Chapman and May, London.

Delibes, J. R. 1996: *Ecología y comportamiento del corzo (Capreolus capreolus L. 1758) en la Sierra de Grazalema (Cádiz)*. — Ph.D. thesis, Universidad Complutense de Madrid, Spain.

Diefenbach, D. R., Brauning, D. W. & Mattice, J. A. 2003: Variability in grassland bird counts related to observer differences and species detection rates. — *Auk* 120: 1168–1179.

Ellenberg, H. 1978: The population ecology of roe deer (*Capreolus capreolus* L. Cervidae) in central Europe. — *Spixiana* 2: 5–211.

Focardi, S., Isotti, R., Pelliccioni, E. R. & Iannuzzo, D. 2002: The use of distance sampling and mark-resight to estimate the local density of wildlife populations. — *Environmetrics* 13: 177–186.

Focardi, S., Montanaro, P., Isotti, R., Ronchi, F., Scacco, M. & Calmanti, R. 2005. Distance sampling effectively monitored a declining population of Italian roe deer Capreolus capreolus italicus. — *Oryx* 39: 421–428.

Fuller, T. K. 1990: Dynamics of a declining white-tailed deer population in north-central Minnesota. — *Wildlife Monographs* 110: 1–37.

Gaillard, J. M., Delorme, D., Boutin, J. M., Van Laere, G., Boisaubert, B. & Pradel, R. 1993: Roe deer survival patterns: a comparative analysis of contrasting populations. — *Journal of Animal Ecology* 62: 778–791.

Gazzola, A., Bertelli, I., Avanzinelli, E., Tolosano, A., Bertotto, P. & Apollonio, M. 2005: Predation by wolves (*Canis lupus*) on wild and domestic ungulates of the western Alps, Italy. — *Journal of Zoology* 266: 205–213.

Gill, R. 1990: *Monitoring the status of European and North American cervids*. — GEMS Information Series 8, UNEP, Nairobi.

Gill, R. M. A., Johnson, A. L., Francis, A., Hiscocks, K. & Peace, A. J. 1996: Changes in roe deer (*Capreolus capreolus* L.) population density in response to forest habitat succession. — *Forest Ecology and Management* 88: 31–41.

Gill, R. M. A., Thomas, M. L. & Stocker, D. 1997: The use of portable thermal imaging for estimating deer population density in forest habitats. — *Journal of Applied Ecology* 34: 1273–1286.

Gregory, R. D., Wilkinson, N. I., Noble, D. G., Brown, A. F., Robinson, J. A., Hughes, J. Procter, D. A., Gibbons, D. W. & Galbraith, C. A. 2002: The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002–2007. — *British Birds* 95: 410–448.

Heydon, M. J., Reynolds, J. C. & Short, M. J. 2000: Variation in abundance of foxes, *Vulpes vulpes*, between three

regions of rural Britain, in relation to landscape and other variables. — *Journal of Zoology* 251: 253–264.

Horcajada, F. 2007: Seguimiento de las poblaciones de corzo en el Parque Natural de Peñalara y Valle de El Paular. — In: Comunidad de Madrid (ed.), *Quintas jornadas científicas del Parque Natural de Peñalara y del Valle de El Paular*: 67–81. Consejería de Medio Ambiente y Ordenación del Territorio: Comunidad de Madrid, Spain.

Liu, Z., Wang, X., Teng, L., Cui, D. & Li, X. 2008: Estimating seasonal density of blue sheep (*Pseudois nayaur*) in the Helan Mountain region using distance sampling methods. — *Ecological research* 23: 393–400.

Marques, F. F. C. & Buckland, S. T. 2003: Incorporating covariates into standard line transect analyses. — *Biometrics* 59: 924–935.

Marques, F. F. C., Buckland, S. T., Goffin, D., Dixon, C. E., Borchers, D. L., Mayle, B. A. & Peace, A. J. 2001: Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. — *Journal of Applied Ecology* 38: 349–363.

Martin, R. D. 1990: *Primate origins and evolution: a phylogenetic reconstruction*. — Chapman and May, London.

Mateos-Quesada, P. 2002: *Biología y comportamiento del corzo ibérico*. — Servicio de Publicaciones de la Universidad de Extremadura, Cáceres.

Mateos-Quesada, P. 2005: Densidad poblacional y uso del espacio del corzo en el centro de la Península Ibérica. — *Galemys* 17: 3–12.

Mattioli, L., Capitani, C., Avanzinelli, E., Bertelli, I., Gazzola, A. & Apollonio, M. 2004: Predation by wolves (*Canis lupus*) on roe deer (*Capreolus capreolus*) in north eastern Apennine, Italy. — *Journal of Zoology* 264: 249–258.

Meriggi, A., Sotti, F., Lambert, P. & Gilio, N. 2008: A review of the methods for monitoring roe deer European populations with particular reference to Italy. — *Hystrix* 19: 103–120.

Norvell, R. E., Howe, F. P. & Parrish, J. R. 2003: A seven-year comparison of relative-abundance and distance sampling methods. — *The Auk* 120: 1013–1028.

Pedroli, J. C., Blant, M., Chappuis, F. & Maire, J. A. 1981: La biologie du chevreuil *Capreolus capreolus* (L.) dans le canton de Neuchätel. (Suisse). I. Recesement de la population: comparación de deux methodes. — *Mammalia* 45: 467–472.

Pollock, K. H. & Kendall, W. L. 1987: Visibility bias in aerial surveys: a review of estimation procedures. — *Journal of Wildlife Management* 51: 502–509.

Prior, R. 1995: *The roe deer. Conservation of a native species*. — Swan Hill Press, Shrewsbury.

Quang, P. X. & Lanctot, R. B. 1991: A line transect model for aerial surveys. — *Biometrics* 47: 1089–1102.

Radeloff, V. C., Pidgeon, A. M. & Hostert, P. 1999: Habitat and population modelling of roe deer using an interactive geographic information system. — *Ecological Modelling* 114: 287–304.

Rivas-Martínez, S. 1987: Nociones sobre fitosociología, biogeografía y bioclimatología. — In: Peinado, M. & Rivas-Martínez, S. (eds.), *La vegetación de España*: 19–46. Servicio de publicaciones, Universidad Alcalá de Henares, Madrid.

Sadlier, L. M. J., Webbon, C. C., Baker, P. & Harris, S. 2004: Methods of monitoring foxes (*Vulpes vulpes*) and badgers (*Meles meles*): are field signs the answer? — *Mammal Review* 34: 75–98.

Sáez-Royuela, C. & Tellería, J. L. 1991: Roe deer (*Capreolus capreolus*) distribution in Central Spain. — *Folia Zoologica* 40: 37–45.

San José, C., Braza, F., Aragón, S. & Delibes, J. R. 1997: Habitat use by roe and red deer in southern Spain. — *Miscellània Zoològica* 20: 27–38.

Schmidt, J. H., Rattenbury, K. L., Lawler, J. P. & Maccluskie, M. C. 2012: Using distance sampling and hierarchical models to improve estimates of Dall's sheep abundance. — *Journal of Wildlife Management* 76: 317–327.

Smart, J. C. R., Ward, A. I. & White, P. C. I. 2004: Monitoring woodland deer populations in the U.K.: an imprecise science. — *Mammalian Review* 34: 99–114.

Staines, B. W. & Ratcliffe, P. R. 1987: Estimating the abundance of red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.) and their current status in Great Britain. — *Symposium of the Zoological Society in London* 58: 131–152.

Thomas, L., Auckland, S. T., Burnham, K. P., Anderson, D. R., Laake, J. L., Borchers, D. L. & Strindberg, S. 2002: Distance sampling. — In: El-Shaarawi, A. H. & Piegorsch, W. W. (eds.), *Encyclopaedia of environmetrics*: 544–552. John Wiley & Sons, Ltd., Chichester.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., Bishop, J. R. B. & Marques, T. A. 2010: Distance software: design and analysis of distance sampling surveys for estimating population size. — *Journal of Applied Ecology* 47:5–14.

Verner, J. & Milne, K. A. 1989: Coping with sources of variability when monitoring population trends. — *Annales Zoologici Fennici* 26: 191–199.

Verner, J. 1985: Assessment of counting techniques. — *Current Ornithology* 2: 247–302.

Walter, M. J. & Hone J. 2003: A comparison of three aerial survey techniques to estimate wild horse abundance in the Australian Alps. — *Wildlife Society Bulletin* 31: 1138–1149.

Ward, A. I., White, P. C. L. & Critchley, C. H. 2004: Roe deer *Capreolus capreolus* behaviour affects density estimates from distance sampling surveys. — *Mammalian Review* 34: 315–319.

Wegge, P. & Storaas, T. 2009: Sampling tiger ungulate prey by the distance method: lessons learned in Bardia National Park, Nepal. — *Animal Conservation* 12: 78–84.

White, G. C. 2005: Correcting wildlife counts using detection probabilities. — *Wildlife Research* 32: 211–216.