Research Article

PELLET: An Excel®-based procedure for estimating deer population density using the pellet-group counting method

Salvador Mandujano[1]

[1] Red de Biología y Conservación de Vertebrados, Instituto de Ecología A. C, Km 2.5, Carret. Ant. Coatepec, Xalapa, Ver., México. salvador.mandujano@inecol.edu.mx

Abstract

Pellet-group counting (PGC) is a commonly used method for estimating the population density of various ungulate species. The method assumes a positive linear relationship between the number of animals and the number of pellet-groups. To estimate population density from PGC, three parameters must be determined: defecation rate, persistence time, and spatial pattern of pellet-groups. This article introduces PELLET, a semi-automatic procedure in Microsoft Excel® for estimating population density in deer. The purpose of PELLET is to support deer managers and studies that determine and compare densities in different types of habitats. The density calculation includes a range of variation in the defecation rate that eliminates the subjective practice of selecting one single defined value for this rate. The calculation also incorporates spatial variation and deposition time. PELLET comprises four Excel® worksheets, the choice of which depends on type of plot and number of field samples. As an example, I describe the application of this procedure in a case study. Spanish and English versions of PELLET are freely available online.

Keywords: monitoring, defecation rate, spreadsheet, linear model, probability distribution.

Resumen

El conteo de grupos fecales (CGF) es un método empleado comúnmente para estimar la densidad poblacional de varias especies de ungulados. Este método asume una relación lineal positiva entre el número de venados y el número de grupos fecales. Para convertir el CGF a número de animales, se requiere conocer tres parámetros: la tasa de defecación, el tiempo de permanencia y el patrón espacial de los grupos fecales. En este artículo se introduce PELLET un procedimiento semi-automatizado en Excel® para estimar la densidad de venados. El propósito de PELLET es apoyar a los manejadores y estudiosos de los venados para calcular y comparar las estimaciones en diferentes tipos de hábitats principalmente bosques densos en regiones tropicales y otras. El cálculo de la densidad se realiza incluyendo un rango de variación en la tasa de defecación lo cual elimina la subjetividad de seleccionar solo un valor determinado de la misma. Además, el cálculo incorpora la variación espacial y el tiempo de depósito de los excrementos. PELLET tiene cuatro hojas dependiendo el diseño de muestreo: tipo de parcelas y número de muestreos en campo. A manera de ejemplo, se presenta la aplicación de este procedimiento en un estudio de caso. PELLET está disponible gratis en línea en versión en español o inglés.

Palabras clave: monitoreo, tasa de defecación, hoja de cálculo, modelo lineal, distribución probabilística.

Introduction

Pellet-group counting (PGC) is one of the most commonly used methods for estimating the population density of various ungulate species, such as the white-tailed deer *Odocoileus virginianus* [1,2], mule deer *O. hemionus* [3], elk *Cervus canadensis* [4], moose *Alces alces* [5], fallow deer *Dama dama* [6], roe deer *Capreolus capreolus* [7], sika deer *Cervus nippon* [8], gray brocket *Mazama gouazoubira*, red brocket *M. americana* [9,10] and the kudu *Tragelaphus strepsiceros* [11], among other species in tropical regions [12]. In Mexico, the method has been used for the mule deer [13,14] and the white-tailed deer, mainly in temperate [15-22] and tropical dry [23-29] forests. The method also serves to estimate the population density of various species of leporids [30-34], kangaroos [35-39], elephants [40] and marmots [41]. The PGC method has been used as an indicator of population size for more than 50 years [42-44]. It is an index that correlates positively with other population estimates [2,23,45,46]; however, it is not exempt from potential errors that can introduce bias into estimates [47-50]. As a consequence, different sampling and data analysis schemes have been tested in order to evaluate the efficiency, precision, and accuracy of the method [1,27,46,51-55].

The general assumption underlying PGC is that accumulation of fecal groups is linearly related to population density, based on the daily production of pellet-groups per individual (defecation rate) and deposition time of the feces (or mean decay time) [43]. It is widely documented that this rate varies, depending mainly on the sex and age of the animals, habitat type, season, and plants consumed [56-62]. Rain and humidity affect the persistence of pellet-groups, which can also be a source of bias in field counts [27,63-67]. Depending on the defecation rate used and the deposition time of the feces, different density estimates will be obtained at the same site [50,55]. This complicates comparisons of densities among regions, but above all, it seriously limits the application of the method for management purposes, since it is necessary to determine the number of deer at the site as accurately as possible [23].

The main objective of this article is to introduce PELLET, a procedure for estimating deer population densities by applying the pellet-group counting method. PELLET is a semi-automatic Microsoft

Excel® spreadsheet for analyzing data. The purpose of PELLET is to support deer management and studies that require estimates in different habitat types such as dense forests in tropical regions. As an example, I apply this procedure in a case study of white-tailed deer monitoring in an area of the Tehuacán-Cuicatlán Biosphere Reserve. For convenience, PELLET version can be downloaded free in Spanish (http://www1.inecol.edu.mx/cv/CV_pdf/mandujano/PELLET_Espanol.rar) and English (http://www1.inecol.edu.mx/cv/CV_pdf/mandujano/PELLET_English.rar) from the website.

Methods

Model

When sampling pellet-groups, the question is, how many deer deposited the excreta that are counted? It is assumed that a higher quantity of pellet-groups implies a higher number of deer (Fig. 1a). In fact, pellet-groups can be used as an index of abundance [46,68]. This index can be very useful for monitoring the same population over a period of time, or for comparisons among different populations [69]. However, if this assumption of the relationship between deer and pellet-group numbers is violated, the pellet-group count could be an unreliable index of abundance [70]. It is also necessary to test whether the detectability of the excreta is constant and how this changes depending on sampling design [65]. Although this index is an indicator of habitat use [e.g., 71-74], the index (mean pellet-groups per sampling unit) is commonly converted into an estimate of density (number of deer per km^2) using the model or formula proposed by Eberhardt and Van Etten [43], which assumes that: 1) the average defecation rate is 12.7 fecal pellet-groups per individual per day, 2) the time that the pellet-groups have remained in the field is accurately known, and 3) all of the pellet-groups in the plot are correctly identified and have not been counted twice. The extent to which these assumptions are fulfilled or violated introduces corresponding levels of bias to the estimates produced [47,55].
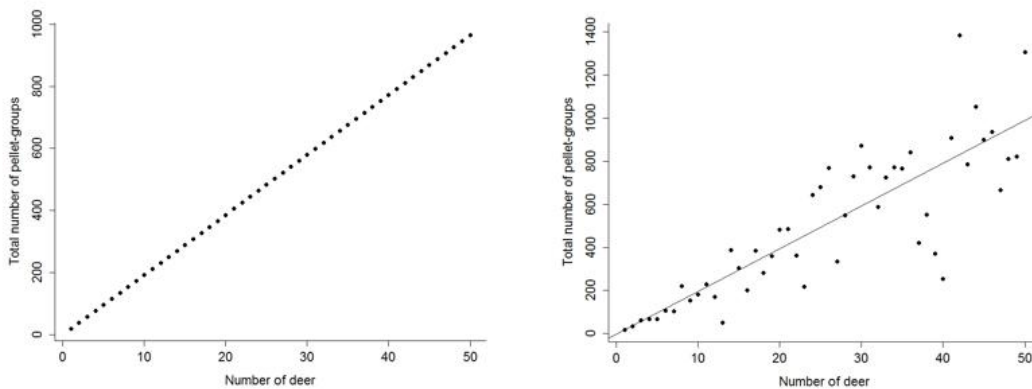
Fig. 1. (a) Positive linear relationship between number of deer and the defecated pellet-groups considering a fixed mean defecation rate of 19.3 pellet-groups/ind/day. (b) Simulation of the expected number of pellet-groups as number of deer increase considering a random defecation rate of 19.3 and variation of 7.3 pellet-groups/ind/day. In both examples, the days of defecation was not considered.

The formula or model for the estimation of density is:

$$D_{ind} = \frac{(D_{pg} \times Np)}{(Def \times Days)} \qquad \textbf{Equation 1,}$$

where: D_{ind} = the density of deer per km^2 (ind/km^2), D_{pg} = is the average density of pellet-groups per sampling plot, Np = number of sampling plots there are or that fit into one square kilometer, Def = defecation rate, and $Days$ = time (in days) since deposition of the excreta. The parameter D_{pg} is estimated differently depending on the sampling method: sampling in circular plots or in strip or line transects (Table 1). PELLET calculates D_{pg} for the first two methods, but the DISTANCE method [see 11,27] is used for the latter.

Table 1. Formulas to estimate the density of pellet-groups (D_{pg}), depending on sampling method: circular plots, strip transects and line transects.

Sampling method	Equation	Software
Circular plots	$D_{pg} = \dfrac{pg_{total}}{\sum_{i=1}^{n} \pi \cdot r^2}$	PELLET
Strip transects	$D_{pg} = \dfrac{pg_{total}}{2 \cdot L \cdot w}$	PELLET
Line transects	$D_{pg} = \dfrac{pg_{total} \cdot f(0)}{2 \cdot L}$	DISTANCE

Where: pg_{total} is the total number of fecal pellet-groups counted, depending on analysis type: grouping all transects or per separate transect, n the number of sampling units, π is the constant, r radius of the circular plots, L is transect length, w is width, and $f(0)$ is the probabilistic function of density at zero meters perpendicular distance. For r, L and w, it is important in every case to use the same metrics units. It is suggested that these should be in meters so that D_{pg} is expressed as the number of fecal pellet-groups per m^2.

Variation in the defecation rate

It is incorrect to assume that all deer defecate an average of 12.7 pellet-groups per day. This assumption introduces bias into the density estimate, since defecation rates can vary depending on such factors as the age and sex of each individual, quality of forage, condition of the animal, and environmental conditions [61,62]. According to Equation 1, estimates of density increase at lower defecation rates and *vice versa*. Consequently, generalized application of an assumed defecation rate in a study site will produce a biased result. While the recommendation has always been prior knowledge and application of the local defecation rate, the reality is that few data exist in this context, for which reason obtained estimates are inevitably biased by the application of an assumed defecation rate. It has been assumed that deer present local defecation rates, and that these vary

among sites (Table 2). Defecation rate even varies markedly in the same individual (8 to 25 pg/ind/day) [75].

Alternatively, deer may present a species-specific defecation rate that could vary markedly depending on several factors; however, more detailed studies are required to test this assumption. According to the findings of the studies cited in the Table 2, deer defecation rates can vary from 13 to 34 pg/ind/day, with an average of 19.3 and standard deviation (SD) of 7.1 pg/ind/day. PELLET uses these average and SD values to derive the density estimates. Considering this variation, the expected number of pellet-groups defecated varies randomly depending on the number of deer (Fig. 1b). An important aspect of the previous simulated graphic is that variation in the total defecated pellet-groups increases as the number of deer increase. This will have important consequences in the standard deviation estimation of the population density (see below).

Table 2. Variation in the defecation rate of white-tailed deer in different studies. (F) females (M) males. Defecation rate is expressed as pellet-groups/individual/day.

Defecation rate	Site	Condition	No. of deer /sex	Reference
34.0	USA	Free living	7F	[61]
26.9	USA	Captivity	1M, 3F	[62]
20.9	Mexico	Semi-captivity	3M, 3F	[76]
19.6	USA	Captivity	4F	[59]
17.0	Mexico	Captivity	3M, 3F	[75]
15.2	Mexico	Captivity	1M, 8F	[17]
14.0	Venezuela	Captivity	5M, 3F	[77]
13.7	USA	?	?	[78]
12.7	USA	Captivity	18M, 1F	[43]
19.3	Mean			
7.1	Standar deviation			

Time of pellet-group deposition

Pellet-group counting is conducted via two field procedures: 1) Fecal Standing Crop (FSC), which consists of estimating the density by considering all pellet-groups in the sampling plots, the daily defecation rate, and the persistence of the excreta; and 2) Fecal Accumulation Rate (FAR), in which density is estimated from the accumulation of new pellet-groups between sampling times, following prior removal of all excreta from the sampling sites [10]. The latter procedure produces less biased estimates, but requires at least two visits to each sampling plot, while the former is less costly since it needs only one visit to each sampling plot. PELLET can analyze data produced by either procedure.

Sampling transects

Field sampling of pellet-groups has been the subject of several studies that analyze the shape and size of the plots or sampling quadrants as well as the separation between them, in order to ensure independence of the data. Distance between sampling transects is also considered, in order to avoid counting the same individuals [e.g., 1,3,51, 53]. There has even been the application of techniques such as the line transect method [11,27,46,54,55], in which the program DISTANCE [79] is used to derive estimates of the average density and variation of pellet-groups in the transects.

Two possible sampling schemes are: 1) transects with circular plots (TCP) and 2) strip transects (ST). While this is not a rule, in practice, the use of TCP is efficient in sites with medium to high abundance of deer, whereas ST are more practical in sites with medium to low abundance of deer [27]. This is due to the fact that in sites of low abundance, the probability of counting pellet-groups in small plots is low, implying a small sample size and high variation. In such cases, ST are efficient in terms of accurately counting everything within the predefined width [79]. Nevertheless, because there is a high possibility of violating the assumptions of the ST, this scheme requires careful design and execution. The alternative is to use methods with no fixed sampling area, such as line transects [11,27,54].

Transects with circular plots (TCP).— These consist of transects 400 m in length with 40 separate 9.3 m^2 plots, located every 10 m along the length of the transect (Fig. 2a). With some variants, TCP are the most commonly used method (see references cited in the Introduction); however, increased distance between the plots may improve the independence of the data [50], and some studies (especially in arid zones) have used transects of 800 m, with separate plots every 20 m [14]. Density of the pellet-groups (D_{pg}) per plot is calculated according to the formula detailed in Table 1.

Strip transects (ST).— These consist of transects of 500 m in length by 2 m in width (1000 m^2), divided into 10 segments or plots of 100 m^2 (50 x 2 m) to facilitate counting of pellet-groups (Fig. 2b). Strip transects are easily applied in the field and increase the probability of counting more pellet-groups, thus improving the accuracy of the density estimate. While the use of a 2 m wide strip is suggested here in order to increase compliance with the assumptions of the method [27], some authors prefer to employ transects of up to 6 m in width [see 24]. In this method, density of pellet-groups (D_{pg}) is obtained following the formula detailed in Table 1. PELLET performs these calculations automatically.

400 m transect

40 circular plots of 9.3 m² spaced every 10 m

a)

500 m x 2 m strip transect

10 rectangular plots of 50 x 2 m (100 m²)

b)
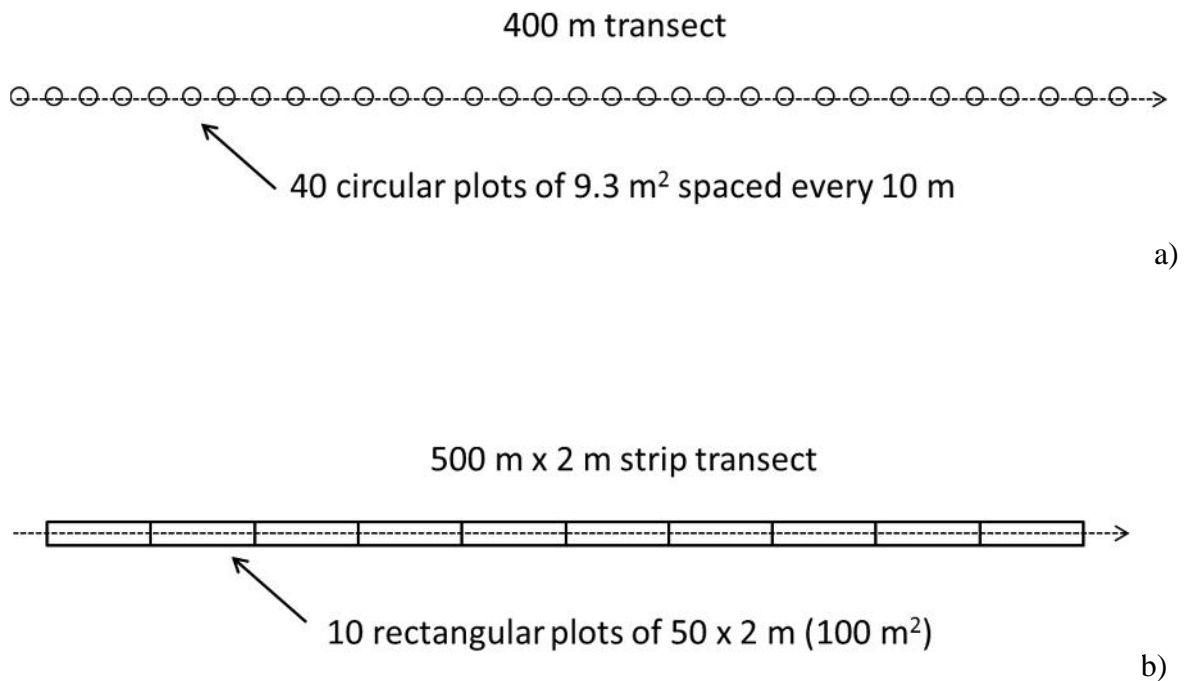
Fig. 2. Two sampling schemes used to count fecal pellet-groups in the field. (a) standard transect of 400 m in length and 40 circular plots of 10 m² each. (b) Strip transect of 500 m in length by 2 m in width, divided into 10 plots or sampling quadrants, each of 100 m².

A fundamental aspect of this type of study is to determine the appropriate number of transects to sample. This is a function of the size of the study and/or management area, the abundance of deer in the site, and the availability of time and resources to carry out the sampling, among other factors [27]. This number will also depend on the sampling technique employed (FSC or FAR). In general, transect sampling should be conducted in the dry season to avoid loss of excreta [15,27]. Destruction of excreta may occur during the wet season by the actions of the rain and beetles, among other factors. Dense understory vegetation can also impede detection of all the pellet-groups present within the sampling units. Another fundamental aspect to consider is the need to adequately differentiate each fecal group to avoid counting it more than once. Generally, the term "pellet-group" implies that all of the pellets are of equal color and of similar size and degree of dryness [43]. If there are several pellet-groups in the same plot (a frequent occurrence), the different groups must be clearly defined. This can be achieved using size, color, shape, and degree of dryness, among other criteria [e.g., 46]. Consequently, this method requires experience in the tracking of deer. This is crucial, because different observers may determine different numbers of pellet-groups in the same sampling units [50].

Spatial distribution of pellet-groups

The spatial distribution of pellet-groups is not homogeneous within sampling units. Most commonly, excreta are concentrated in a few plots while many plots have no excreta. This is due to the use and preference of the habitat and to social factors [80]. This distribution therefore does not follow a normal type, but instead can be described by other distribution models, such as the negative binomial [15,81-83]. Estimation of the variation of pellet-groups per plot must therefore be calculated from the distribution model that best fits the data [84]. In this case, the standard error (*SE*) is calculated as:

$$SE = \sqrt{\dfrac{\left(\dfrac{D_{pg} + D_{pg}^2}{k}\right)}{n}}$$

Equation 2,

where D_{pg} = average density of pellet-groups per plot, k = negative binomial parameter and n = number of plots. Specifically: $k = D_{pg}^2 / (S^2 - D_{gf})$, where S^2 is the variance of the number of pellet-groups per plot. Once the average of pellet-groups is known, the standard error must be added and subtracted in order to obtain an estimate of the variation within the sampling units. PELLET incorporates this variation in the calculations of density.

Procedure in PELLET

Conceptual model and mathematics

Implicit in the initial model of Eberhardt and Van Etten [43] is the assumption that, given an average rate of 12.7 pg/ind/day, a value of deer density (*D*) will be determined that depends on the average number of pellet-groups per plot and on the length of time that these have remained in the field. In this approach, therefore, the population parameter *D* only has one value, which is unknown but possible to infer using standard statistical procedures. However, considering that the defecation rate varies markedly among individuals, the population density in the determined place and time must therefore be considered in itself as a parameter with a probabilistic distribution. This is conceptually important and thereby differs from the "standard" approach. Given a certain number of pellet-groups, there will thus be a range of possible deer densities, and not simply one value of density as has been commonly assumed.

PELLET approaches the density calculation assuming that density has a probabilistic distribution depending on variation of the parameters of defecation rate, time of persistence of the fecal pellet-groups, and the pattern or spatial distribution of the fecal pellet-groups. This eliminates the subjectivity of selecting only one determined value for these parameters, but above all it incorporates the high uncertainty in the number of deer estimated by counting their pellet-groups (see Fig. 1b). PELLET therefore calculates density as:

$$D_{ind} = \left\{\frac{(D_{pg} \pm Se)}{(Def \pm Var) \times (Days \pm Range)}\right\} \times Np$$

Equation 3,

Note that *Np* (number of plots or sampling units in 1 km^2) is simply a factor for converting deer density per m^2 to density per km^2. Of greater importance is the incorporation of data pertaining to variation in the other parameters (*D$_{pg}$*, *Def* and *Days*). This aspect is significant and represents one of the main contributions of PELLET. Specifically, the probabilistic distributions proposed for each parameter are: 1) Poisson, for the count of pellet-groups, 2) negative binomial, to describe the pattern of the pellet-groups in the sampling plots, 3) normal, to describe the defecation rate, and 4) uniform, to determine the possible dates of deposition of the excreta in the field. Apart from the first distribution, PELLET uses a procedure to incorporate the other three distributions into the density calculation. However, in this case, there is no procedure of random sampling of the variables for each distribution. Instead, PELLET fixes these from the initial specific values of the variation of these parameters. The calculation is semi-automatic and the user therefore need not be concerned by this aspect. However, other procedures are currently in development using generalized linear mixed models (GLMM) to calculate deer population density, using estimation methods of maximum likelihood (MLE) and also using previously known information to define the *a priori* distribution using a Bayesian approach in R and WinBUGS [Mandujano, in preparation].

Procedure

Step 1.— Once field work is complete, data are entered into the PELLET calculation worksheet to perform the analysis. The number of pellet-groups counted in each of the plots on all transects is captured, along with the date on which each transect was sampled (Table 3). PELLET includes 40 columns (transects), but these can be modified using the "delete" and "insert" columns function if a higher or lower number of transects was sampled. The number of plots varies depending on whether a strip transect (*n* = 10 rectangular plots) or a standard transect (*n* = 40 circular plots) was used. In this case, the number of lines can also be modified by the insertion or deletion of lines, as dictated by the particular sampling scheme used in each study.

Table 3. Example demonstrating how to enter the data of number of fecal pellet-groups counted in the field using the ST-FSC worksheet. In this case, eight transects of 500 x 2 m were used, divided into 10 plots, each of 50 m. Note that in each plot or quadrant, the number of fecal pellet-groups is entered consecutively until the transect is completed. Red data to be entered for each particular case.

	A	B	C	D	E	F	G	H	I	J
1	Casa Blanca, Oax.		T1	T2	T3	T4	T5	T6	T7	T8
2	Dry season 2013	Sampling date of each transect >	01/05/2013	01/05/2013	08/05/2013	07/05/2013	09/05/2013	09/05/2013	01/05/2013	09/05/2013
3		0-50 m	0	1	0	0	0	0	0	0
4		51-100 m	3	3	7	3	8	3	3	3
5		101-150 m	0	1	0	0	0	0	0	0
6		151-200 m	7	1	7	7	7	3	7	7
7		201-250 m	1	1	5	1	1	1	1	1
8		251-300 m	0	0	0	0	0	0	0	0
9		301-350 m	0	1	4	0	0	0	0	0
10		351-400 m	0	0	0	0	0	0	0	0
11		401-450 m	0	0	0	0	0	0	0	0
12		451-500 m	0	1	3	0	0	0	0	0
13										

Step 2.— PELLET has four worksheets depending of the sampling scheme used (FSC or FAR) and the transect type employed (TCP or ST). Depending on these factors, the corresponding worksheet is selected. By way of example, the option of sampling in strip transects following the FSC technique is presented in this paper. In this case, the maximum and minimum probable dates of deposition of the excreta are incorporated.

Step 3.— Once all data are entered, the calculation worksheet will automatically generate the results of the population estimate. If the FSC technique was used, 18 density estimates will be obtained for each transect by combining three defecation rates, two deposition times, and three estimates of the number of fecal pellet-groups per plot. If the FAR sampling technique was used, however, there will be nine estimates of density per transect (three defecation rates by one deposition time by three estimates of the number of pellet-groups per plot). In both cases, the average of these estimates will be the density for that transect. For example, Table 4 presents the "hidden" formulas in each cell for the transect (T1).

Table 4. Semi-automatic formulas in PELLET. Examples are shown for transect 1 (T1), but the program can include different numbers of transects.

Step 4.— PELLET provides estimates of the average density, standard deviation and maximum and minimum values of deer density for the entire study area. With this information, 95% confidence intervals can be generated. For comparison, the estimate that would have been obtained using the original method of Eberhardt and Van Etten [43] is also presented.

Example of application

Below is presented an example of the procedure in PELLET. The corresponding cells for each datum and statistic are shown in parenthesis and bold type (Table 5). It should be noted that these cell coordinates will vary for some data depending on the number of transects sampled. In the community "Casa Blanca", in the Mexican state of Oaxaca, during the dry season of 2010 (**cells A1:A2**) a total of 108 pellet-groups (**K13**) were sampled in eight transects of 500 x 2 m divided into 10 sampling plots (**C3:J12**). Samples were taken between the 1st and 13th of June 2010 (**C2:J2**) and maximum (**A19**) and minimum (**A28**) dates were considered according with the last rainfall. This gives between 150 and 174 probable days of deposition (*Days*) (**C15:J16**). The number of pellet-groups in every plot of each transect is incorporated. For example, for transect 1 (T1), these were 0, 3, 0, 7, 1, 0, 0, 0, 0 and 0 (**C3:C12**) for a total of 11 pellet-groups for this transect (**C13**), and a D_{pg} of 1.1 (**C14**). The value of the coefficient of the negative binomial (*k*) was 0.142 (**O16**), suggesting a clustered pattern. Three defecation rates (*Def*) are used that represent the average of 19.3 pg/ind/day (**B22, B31**), 12.2 pg/ind/day, which is one standard deviation (SD) less than the average (**B19, B28**) and 26.4 pg/ind/day, which is one SD (**B25, B34**) higher than the average.

Table 5. Complete example for estimating the population density (ind/km²) of the white-tailed deer in the locality of "Casa Blanca", in the Mexican state of Oaxaca, from sampling eight strip transects of 500 x 2 m during the dry season 2013.

With this procedure, PELLET produces 18 estimates of density per transect; producing a total of 144 values of density (**C19:J36**), considering the eight transects sampled. A histogram of frequencies was generated with the estimates of the densities obtained for all transects to visualize the variation in density (Fig. 3). The results of the estimates are provided in the yellow box (**N18:Q33**) in PELLET. In this example, the average density for the study area was 4.75 deer/km^2 (**O26**), with a standard deviation of 2.4 (**O27**). In comparison, the density estimated under the model of Eberhardt and Van Etten was 6.8 deer/km^2 (**O32**) (Fig. 3).
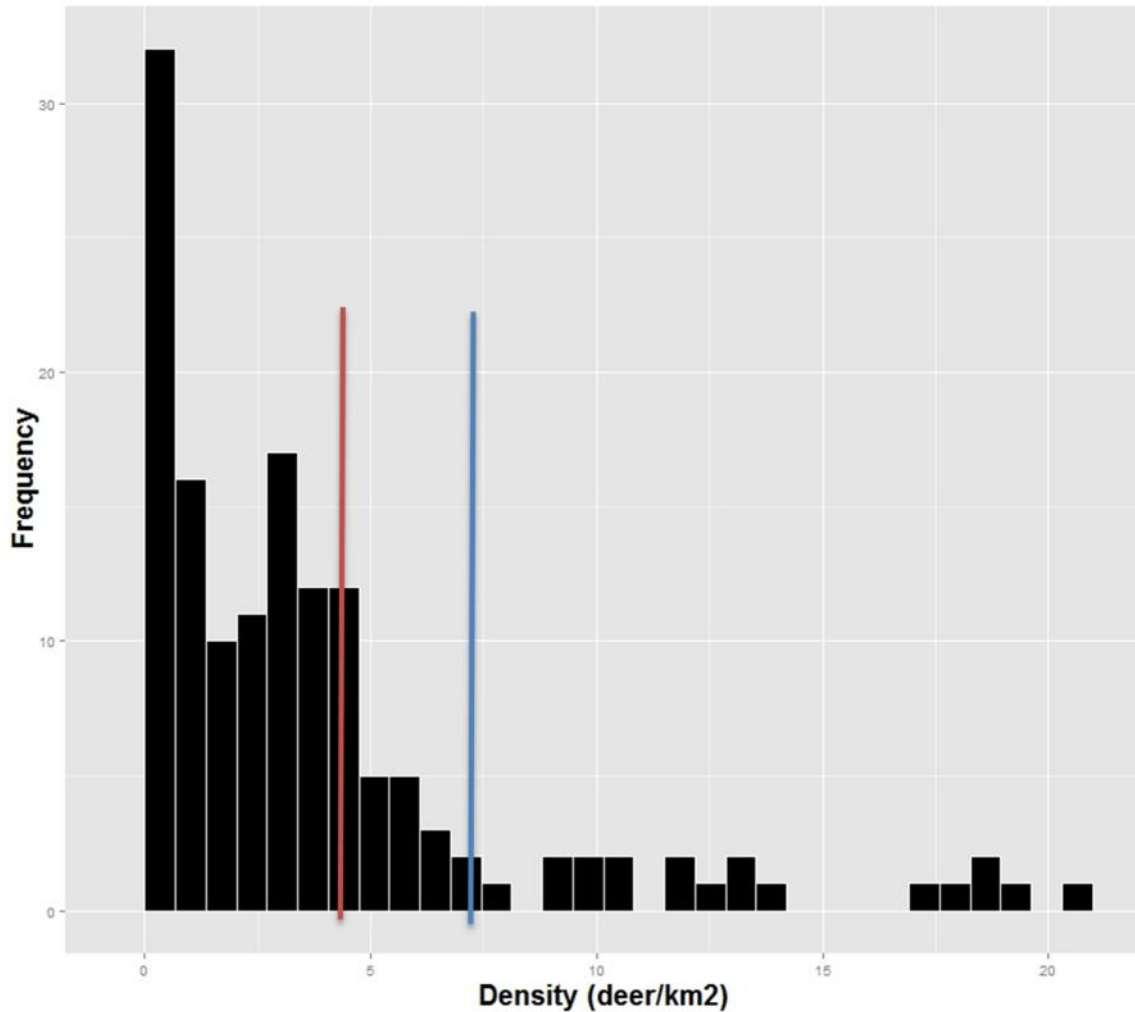
Fig. 3. Frequency distribution of estimates of population density of the white-tailed deer in the community of "Casa Blanca" in the Mexican state of Oaxaca, during the dry season of 2013. The average estimate produced by following the PELLET protocol is shown in red, and the estimate obtained by the original model of Eberhardt and Van Etten [43] is shown in blue.

Implications for conservation

PELLET is mainly designed to support decision making in deer management, since it calculates population density in a relatively simple manner using semi-automatic calculations on a spreadsheet that features different options depending on the particular sampling scheme. This allows valid comparisons to be made between population trends at the same site over time, as well as comparisons of density among populations that inhabit different geographical areas, which is important in order to standardize monitoring protocols [85]. However, as with any program, PELLET will be modified as more situations, featuring aspects not currently considered, are applied.

PELLET is a relatively simple alternative procedure for calculating deer population densities from counts of fecal groups. The proposal includes estimation of density based on variation in three parameters: defecation rate, time of permanence of the excreta, and the spatial variation of fecal groups within the sampling units. There are two aspects to highlight as a consequence: first, the procedure eliminates the subjectivity inherent in having to select just one defined defecation rate, which has been the general rule in the majority of studies that have used this method. It has been deemed necessary to know the specific defecation rate of the deer in the study area. However, the evidence clearly indicates that, even in the same site, defecation rate can vary markedly among individuals and even in the same individual over time. For this reason, we must consider the possibility that a specific defecation rate does not exist, but is instead a variable that is determined by the physiological process of ingestion and excretion in the species. Defining a single defecation rate in order to convert counts of fecal groups within sampling areas to the population density of deer per unit area will therefore inevitably produce biased estimates. PELLET therefore proposes consideration of the defecation rate as a parameter of the species, assuming a normal type distribution model, where the tendency of the population will be to defecate at rates that are around the mean but with a wide range of variation.

Second, the consequence of assuming a mean and a wide variation, such as that presented in Table 2, is that this procedure produces a wide range of density estimates (see Fig. 1b, 3). This is the inevitable cost that must be accepted given the uncertainty in the conversion of an indirect index, in this case the density of excreta per sampling plot, to an estimate of population density (number of deer/km^2).

Acknowledgements

References

[1] Mooty, J. J., P. D. Karns y D. M. Heisey. 1984. The relationship between white-tailed deer track counts and pellet-group surveys. *J. Wildl. Manage.* 48: 275-279.

[2] Batcheler, C. L. 1975. Development of a distance method for deer census from pellet groups. *J. Wildl. Manage.* 39: 641-652.

[3] Freddy, D. J. y D. C. Bowden. 1983. Sampling mule deer pellet-group densities in juniper-pinyon woodland. *J. Wildl. Manage.* 47: 476-485.

[4] Rowland, M. M., G. C. White y E. M. Karlen. 184. Use of pellet-group plots to measure trends in deer and elk populations. *Wildl. Soc. Bull.* 12: 147-155.

[5] Härkönen, S. y R. Heikkilä. 1999. Use of pellet group counts in determining density and habitat use of moose *Alces alces* in Finland. *Wildl. Biol.* 5: 233-239.

[6] Bailey, R. E. y R. J. Putman. 1981. Estimation of fallow deer (*Dama dama*) populations from faecal accumulation. *J. Appl. Ecol.* 18: 697-702.

[7] Acevedo, P., J. Ferreres, R. Jaroso y M. Durán. 2010. Estimating roe deer abundance from pellet group counts in Spain: An assessment of methods suitable for Mediterranean woodlands. *Ecol. Ind.* 10: 1226-1230.

[8] Marques, F., Buckland, S.T., Goffin, D., Dixon, C.E., Borchers, D.L., Mayle, B.A. and Peace, A.J. 2001. Estimating deer abundance from line transect surveys of dung: sika deer in sourthern Scotland. *J. Appl. Ecol.* 38: 34-363.

[9] Rivero, K., D. I. Rumiz y A. B. Taber. 2004. Estimating brocket deer (*Mazama gouazoubira* and *M. americana*) abundance by dung pellet counts and other indices in seasonal Chiquitano forest habitats of Santa Cruz, Bolivia. *Eur. J. Wildl. Res.* 50: 161-167.

[10] Periago, M. E. y Gerardo C. Leynaud. 2009. Density estimates of *Mazama gouazoubira* (Cervidae) using the pellet count technique in the arid Chaco (Argentina). *Ecol. Austral* 19:73-77.

[11] Ellis, A. M. y R. T. F. Bernard. 2005. Estimating the density of kudu (*Tragelaphus strepsiceros*) in subtropical thicket using line transect surveys of dung and DISTANCE software. *Afri. J. Ecol.* 43: 362-368.

[12] Koster, S. H. y J. A. Hart. 1988. Methods of estimating ungulate populations in tropical forests. *Afri. J. Ecol.* 26: 117-126.

[13] Gallina, S., P. Galina-Tessaro y S. Álvarez-Cárdenas. 1991. Mule deer density and pattern distribution in the pine-oak forest at the Sierra de La Laguna in Baja California Sur, Mexico. *Ethol. Ecol. Evol.* 3: 27-33.

[14] Sánchez-Rojas, G. y S. Gallina 2000. Mule deer (*Odocoileus hemionus*) density in a landscape of the Chihuahuan Desert, Mexico. *J. Arid Environ.* 44:357-368.

[15] Ezcurra, E. y S. Gallina. 1981. Biology and population dynamics of white-tailed deer in northwestern Mexico. In: *Deer Biology, Habitat Requirements and Management in Western North America*, eds. P. F. Ffolliott and S. Gallina, pp. 77–108. Instituto de Ecología, A.C. México, D.F.

[16] Valenzuela, D. 1994. Estimación de la densidad y distribución de la población del venado cola blanca en el bosque La Primavera, Jalisco, México. In: *Ecología y Manejo del Venado Cola Blanca en México y Costa Rica*. Ch. Vaughan y M. Rodríguez (eds.), Pp. 247-262. EUNA, Universidad Nacional, Costa Rica.

[17] Zavala, G. 1992. Estimación poblacional del venado cola blanca (*Odocoileus virginianus*) en la Estación Científica Las Joyas, Reserva de la Biosfera Sierra de Manantlán, Jalisco. Tesis Licenciatura, Universidad de Guadalajara, Jal.

[18] Ortiz-Martínez, T., S. Gallina, M. Briones-Salas & G. González. 2005. Densidad poblacional y caracterización del hábitat del venado cola blanca (*Odocoileus virginianus oaxacensis*, Goldman y Kellog, 1940) en un bosque templado de la Sierra Norte de Oaxaca, México. *Acta Zool. Mex. (n.s.)* 21: 65-78.

[19] Medina-Torres, S. M. 2008. El venado cola blanca de Coues *Odocoileus virginianus couesi* y su hábitat en la Sierra del Laurel, Aguascalientes. Tesis Doctorado, Colegio de Postgraduados, Campus Montecillo, Texcoco, Edo. México.

[20] Sánchez-Rojas, G., Aguilar-Miguel, C. & Hernández-Cid, E. 2009. Estudio poblacional y uso de hábitat por el Venado Cola Blanca (*Odocoileus virginianus*) en un bosque templado de la Sierra de Pachuca, Hidalgo, México. *Trop. Conser. Scie.* 2: 204-214.

[21] Beltrán, C. Y. y A. D. Díaz. 2010. Estimación de la densidad poblacional del venado cola blanca texano (*Odocoileus virginianus texanus*), introducido en la UMA "Ejido de Amanalco" Estado de México. *Ciencia Ergo Sum* 17: 154-158.

[22] Flores-Armillas, V. H., F. Botello, V. Sánchez-Cordero, R. García-Barrios, F. Jaramillo & S. Gallina. 2013. Caracterización del hábitat del venado cola blanca (*Odocoileus virginianus mexicanus*) en los bosques templados del Corredor Biológico Chichinautzin y modelación de su hábitat potencial en Eje Transvolcánico Mexicano. *Therya* 4: 377-393.

[23] Mandujano, S y S. Gallina. 1995. Comparison of deer censusing methods in tropical dry forest. *Wildl. Soc. Bull.* 23:180-186.

[24] Villarreal-Espino, O. 2006. *El venado cola blanca en la Mixteca Poblana; Conceptos y métodos para su conservación y manejo*. Benemérita Universidad Autónoma de Puebla; Fundación PRODUCE Puebla, A. C.; Mazamiztli, A. C. 199 pp.

[25] López- Tellez, M.C., Mandujano, S. y G. Yañez. 2007. Evaluación poblacional del venado cola blanca en un bosque tropical seco de la Mixteca Poblana. *Acta Zool. Mex. (n.s.)* 23: 1-16.

[26] Corona, P., S. Gallina y A. Contreras. 2010. El aprovechamiento del venado cola blanca en una UMA de la Sierra de Huautla, Morelos. In: *Uso y manejo de la fauna silvestre en el norte de Mesoamérica*, M. Guerra-Roa, S. Calmé, S. Gallina y E. J. Naranjo (eds.), pp. 263-296. Secretaria de Educación de Veracruz, Xalapa. Ver.

[27] Camargo-Sanabria, A. y S. Mandujano. 2011. Comparison of pellet-group counting methods to estimate population density of white-tailed deer in a Mexican tropical dry forest. *Trop. Conser. Scie.* 4: 230-243.

[28] Ramos-Robles, M. I., S. Gallina y S. Mandujano. 2013. Habitat and human factors associated with white-tailed deer density in the tropical dry forest of Tehuacán-Cuicatlán Biosphere Reserve, Mexico. *Trop. Conser. Scie.* 6: 70-86.

[29] Mandujano, S., Yañez-Arenas, C., González-Zamora, A. y A. Pérez-Arteaga. 2013. Habitat-population density relationship for the white-tailed deer *Odocoileus virginianus* during the dry season in a Pacific Mexican tropical dry forest. *Mammalia* 77: 381-389.

[30] Wood, D. H. 1988. Estimating rabbit density by counting dung pellets. *Aust. Wildl. Res.* 15: 665-673.

[31] Iborra, O. y J. P. Lumaret. 1997. Validity limits of the pellet group counts in wild rabbit (*Oryctolagus cuniculus*). *Mammalia* 61: 205-218.

[32] Prugh, L. R. y C. J. Krebs. 2004. Snowshoe hare pellet-decay rates and aging in different habitats. *Wildl. Soc. Bull.* 32: 386-393.

[33] Murray, D. L., J. D. Roth y E. Ellsworth. 2002. Estimating low-density snowshoe hare populations using fecal pellet counts. *Can. J. Zool.* 80: 771-781.

[34] Murray, D., E. Ellsworth y A. Zack. 2005. Assessment of potential bias with snowshoe hare fecal pellet-plot counts. *J. Wildl. Manage.* 69: 385-395.

[35] Coulson, G. M. y J. A. Raines. 1985. Methods for small-scale surveys of grey kangaroo populations. *Aust. Wildl. Res.* 12: 119-125.

[36] Perry, R. J. y M. L. Braysher. 1986. A technique for estimating the numbers of eastern gray kangaroos, *Macropus giganteus*, grazing a given area of pasture. *Aust. Wildl. Res.* 13: 335-338.

[37] Hill, G. J. E. 1981. A study of grey kangaroo density using pellet counts. *Aust. Wildl. Res.* 8: 237-243.

[38] Johnson, C. N. y P. J. Jarman. 1987. Macropod studies at Wallaby Creek. *Aust. Wildl. Res.* 14: 139-145.

[39] Vernes, K. 1999. Pellet counts to estimate density of a rainforest kangaroo. *Wildl. Soc. Bull.* 27: 991-996.

[40] Barnes, R. F. W. 2001. How reliable are dung counts for estimating elephant numbers? *Afr. J. Ecol.* 39: 1-9.

[41] Karels, T. J., L. Koppel y D. S. Hik. 2004. Fecal pellet counts as a technique for monitoring an alpine-dwelling social rodent, the hoary marmot (*Marmota caligata*). *Arctic, Antarctic, and Alpine Res.* 36: 490-494.

[42] Bennett, L. J., P. F. English y R. McCain. 1940. A study of deer populations by use of pellet-group counts. *J. Wildl. Manage.* 4: 398:403.

[43] Eberhardt, L. y Van Etten, R.C. 1956. Evaluation of the pellet group count as a deer census method. *J. Wildl. Manage.* 20: 70-74.

[44] Rogers, G., O. Julander y W. L. Robinette. 1958. Pellet-group counts for deer census and range-use index. *J. Wildl. Manage.* 22: 193-199.

[45] McCaffery, K. R. 1976. Deer trail counts as an index to populations and habitat use. *J. Wildl. Manage.* 40: 308-316.

[46] Forsyth, D. M., R. J. Barker, G. Morriss y M. P. Scroggie. 2007. Modeling the relationship between fecal pellet indices and deer density. *J. Wildl. Manage.* 71: 964-970.

[47] Van Etten, R. C. y C. L. Bennett Jr. 1965. Some sources of error in using pellet-group counts for censusing deer. *J. Wildl. Manage.* 29: 723-729.

[48] Neff, D. J. 1968. The pellet-group count technique for big game trend, census, and distribution: a review. *J. Wildl. Manage.* 32: 597-614.

[49] Fuller, T. K. 1991. Do pellet counts index white-tailed deer numbers and population change? *J. Wildl. Manage.* 55: 393-396.

[50] Galindo-Leal, C. 1992. Overestimation of deer densities in Michilia Biosphere Reserve. *Southwes. Nat.* 37: 209-212.

[51] Smith, R. H. 1968. A comparison of several sizes of circular plots for estimating deer pellet-group density. *J. Wildl. Manage.* 32: 585-591.

[52] Freddy, D. J. y D. C. Bowden. 1983. Efficacy of permanent and temporary pellet plots in juniper-pinyon woodland. *J. Wildl. Manage.* 47: 512-516.

[53] Drummer, T. D., A. R. Degange, L. L. Pank y L. L. McDonald. 1990. Adjusting for group size influence in line transect sampling. *J. Wildl. Manage.* 54: 511-514.

[54] Campbell, D., Swanson, G.M. y Sales, J. 2004. Comparing the precision and cost-effectiveness of faecal pellet group count methods. *J. Appl. Ecol.* 41: 1185-1196.

[55] Smart, J. C. R., A. I. Ward y P. C. L. White. 2004. Monitoring woodland deer populations in the UK: an imprecise science. *Mammal Rev.* 34: 99-114.

[56] Smith, A. D. 1964. Defecation rates of mule deer. *J. Wildl. Manage.* 28: 435-444.

[57] Dinerstein, E. y H. T. Dublin. 1982. Daily defecation rate of captive axis deer. *J. Wildl. Manage.* 46: 833-835.

[58] Miquelle, D. 1983. Summer defecation-urination rates and volumes of moose. *J. Wildl. Manage.* 47: 1230-1233.

[59] Rollins, D., Bryant, F.C., and Montandon, R. 1984. Fecal pH and defecation rates of eight ruminants fed known diets. *J. Wildl. Manage.* 48:807-813.

[60] Mitchell, B., J. J. Rowe, P. Ratcliffe y M. Hinge. 1985. Defecation frequency in roe deer (*Capreolus capreolus*) in relation to the accumulation rates of faecal deposits. *J. Zool.* 207: 1-7.

[61] Rogers, L.L. 1987. Seasonal changes in defecation rates of free-ranging white-tailed deer. *J. Wildl. Manage*. 51: 330-333.

[62] Sawyer, T.G., Marchinton R.L. y Lentz, W.M. 1990. Defecation rates of female white-tailed deer in Georgia. *Wildl. Soc. Bull.* 18: 16-18.

[63] Wallmo, O. C., A. W. Jackson, T. L. Hailey y R. L. Carlise. 1962. Influence of rain on the count of deer pellet groups. *J. Wildl. Manage.* 26: 50-55.

[64] Harestad, A. S. y F. L. Bunnell. 1987. Persistence of black-tailed deer fecal pellets in coastal habitats. *J. Wildl. Manage.* 51: 33-37.

[65] Lehmkuhl, J. F., C. A. Hansen y K. Sloan. 1994. Elk pellet-group decomposition and detectability in coastal forests of Washington. *J. Wildl. Manage.* 58: 664-669.

[66] Massei, G., P. Bacon y P. V. Genov. 1998. Fallow deer and wild boar pellet group disappearance in a Mediterranean area. *J. Wildl. Manage.* 62: 1086-1094.

[67] Hemami, M. R. y P. M. Dolman. 2005. The disappearance of muntjac (*Muntiacus reevesi*) and roe deer (*Capreolus capreolus*) pellet groups in a pine forest of lowland England. *Eur. J. Wildl. Res.* 51: 19-24.

[69] Caughley, G. 1977. *Analysis of vertebrate populations*. Wiley-Interscience publication, London and New York.

[70] Dietrich, U. 1991. Densidad poblacional de algunas especies cinegéticas en el noreste de México. IX Simposio de Fauna Silvestre. UNAM, Edo. México.

[70] Thompson, W. L., White, G. C., & Gowan, C. 1998. *Monitoring vertebrate populations*. Academic Press, San Diego. CA.

[71] Papageorgiou, N. K. 1978. Use of forest openings by roe deer as shown by pellet group counts. *J. Wildl. Manage.* 42: 650-654.

[72] Rost, G. R. y J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. *J. Wildl. Manage.* 43: 634–641.

[73] Collins, W. B. y P. J. Urness. 1981. Habitat preferences of mule deer as rated by pellet-group distributions. *J. Wildl. Manage.* 45: 969-972.

[74] Skarin, A. 2007. Habitat use by semi-domesticated reindeer, estimated with pellet-group counts. *Rangifer* 27: 121-132.

[75] Pérez-Mejía, S., Mandujano, S. and Martínez-Romero, L. E. 2004. Tasa de defecación del venado cola blanca, *Odocoileus virginianus mexicanus*, en cautividad en Puebla. *Acta Zool. Mex. 8n.s.)* 20: 167-170.

[77] Correa-Viana, M. 1991. Abundancia y manejo del venado caramerudo en Venezuela: evaluación inicial. In: *El venado en Venezuela: conservación, manejo, aspectos biológicos y legales*. Pp. 29-39, Memoria Simposio (FUDECI, PROFAUNA, and FEDECAVE, eds.). Raúl Clemente Editores CA, Valencia, Venezuela.

[78] McCullough, D. R. 1982. White-tailed deer pellet-group weights. *J. Wildl. Manage.* 46: 829-832.

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

[80] Marchinton, R. L. & D. H. Hirth. 1984. Behavior. In: *White-tailed deer: ecology and management*, L. K. Halls (ed.), pp. 129-168, Stackpole Bokks, Harrisburg, PA.

[81] Bowden, D. C., A. E. Anderson y E. Medin. 1969. Frequency distributions of mule deer fecal group counts. *J. Wildl. Manage.* 33: 895-905.

[82] Stormer, F. A., T. W. Hoekstra, C. M. White y C. M. Kirkpatrick. 1977. Frequency distribution of deer pellet groups in southern Indiana. *J. Wildl. Manage.* 41: 779-782.

[83] White, G. C. y L. E. Eberhardt. 1980. Statistical analysis of deer and elk pellet-group data. *J. Wildl. Manage.* 44: 121-131.

[84] Royle, J. A. y R. M. Dorazio. 2008. *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. Academic Press, London, UK.

[85] Thompson, E. L. 2004. *Sampling rare or elusive species: concepts, designs and techniques for estimating population parameters*. Island Press, Washington, D.C.