A method to estimate roe deer (*Capreolus capreolus*) density at various spatial scales in a fragmented landscape

Daniele Iannuzzo, Stefano Focardi, Elisabetta Raganella-Pelliccioni & Silvano Toso

ISPRA Istituto Superiore per la Protezione e la Ricerca Ambientale,

via ca’ Fornacetta, 9 I-40064 Ozzano dell'Emilia, Italy.

Corresponding author: Stefano Focardi: stefano.focardi@isprambiente.it

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Abstract

The estimate of density of wildlife populations is still a difficult task, especially when working with spatially-open populations when one must relax the assumption of closure, which is at the base of most methods currently used. Further difficulties arise to obtain density estimates at small spatial scales. Using eight years (1996-2003) of monitoring data from a roe deer (*Capreolus capreolus*) population, living in a sub-Mediterranean environment in central Italy, we were able to estimate local density (at a spatial scale of one home range) using a large sample of radio-marked animals. Local density estimates could be obtained only in zones where radio-marked deer were available in sufficient number. To estimate local density over the whole study area, we developed a calibration model which allowed us to infer density where radio-marked deer were absent or scarce. To do this, we compute the mark-resight density estimates (using radio-marked animals) and we relate these estimates to linear and non-linear functions of animal count and surface area of fields, to obtain a set of density estimators. Then we select a linear combination of such estimators, whose quality was assessed by cross-validation. Our results show that the method we propose can be effective to investigate small-scale spatial structure of density in a roe deer population. There are several potential applications of this method for both research and management.

Introduction

The estimation of population abundance is a fast-developing issue. Several approaches are now available for closed populations such as distance-sampling and capture-mark-recapture (Borchers et al. 2002). The estimate of spatially-open population size is still a difficult task, especially if one is interested in densities rather than abundances.

For spatially closed populations, to estimate animal numbers or densities is equivalent, since area size is fixed. But this is not true for spatially-open populations, that are the rule, rather than the exception, in wildlife management. A solution is provided by radiotelemetry, as shown by Eberhardt (1990) and White & Shenk (2001), Density estimates using radiotelemetry were calculated successfully for bears (Miller et al. 1987, Miller et al. 1997), goshawks (Kenward et al., 1981), roe deer (Focardi et al. 2002a, Hewison et al. 2007) and small rodents (Efford, 2004). Distance sampling as well can provide population density estimates (Buckland et al. 2001, Focardi et al. 2006).

For spatially open populations, such methods remain reliable, provided the survey is very fast so that one obtains a snapshot estimate (but see Kenward et al. 1981, for another approach to relax closure assumption). Focardi et al. (2002a) estimated density of the roe deer population at Tredozio (central Italy) at a 200 hectares scale by mark-resighting, calculating then the average density with a maximum likelihood approach pooling four count sessions (White 1996). The assumption was that even if some movement occurred across the border, it was negligible, given the small border-area ratio. However, during counts at Tredozio, some radio-marked deer, detected outside just before the survey, were subsequently sighted during the two-hours trial. This problem, probably neglectable at a large spatial scale, may become relevant at small scale when border-area ratios increase.

The importance of investigating ecological patterns at various spatial scales is reviewed by Ray & Hastings (1996). Local density, i.e. density at a very small scale, is recognized as more and more important. For roe deer in particular, the importance of local density was shown by Pettorelli et al. (2005), who detected an influence of environmental variables on fawn survival at the scale of a single home range. Moreover, local density can be used to estimate large scale density, if necessary, while the inverse, of course, does not hold.

Local density estimation is a relatively novel issue, with theoretical questions still unaddressed. One major point is that for local density estimation the closure assumption does not hold. Each individual inhabiting the surveyed zone has a given probability (usually <1) to stay in at each time. Density can be redefined as the average number of individuals inside the surveyed zone. Of course if closure assumption is valid, i.e. the probability of stay in is one, this interpretation is completely consistent with the usual definition of density.

Exploiting an idea from Kenward et al. (1981), Focardi et al. (2002b) relaxed the assumption of spatial closure and were successful at estimating roe deer density at a very small scale (ca 10 hectares) by combining mark—resight techniques with radiotelemetry. However, since the size of the count unit was in this case very small, many zones contained too few marked animals or none at all, simply by chance. Accordingly, the estimates obtained by Focardi et al. (2002b), were scattered across the study area (24 reliable estimates out of 45 surveyed zones), concentrated in areas with the highest presence of marked animals. This outcome was unfortunate, since lacking local density estimates for the whole study area, we could not analyze the effect of local density on roe deer demography. The aim of this paper is to develop further the work of

Focardi et al. (2002b) and to present a method amenable to estimate local density even in areas without marked animals.

Basically, our method stems from sightability models which have been often used to estimate the size of ungulate populations (see e.g. Poole 2007, Freddy et al. 2004, and White & Schenk 2001 for a summary). In sightability models the detection probability is computed using a trial survey where detectability of radio-marked animals is modeled as a function of environmental variables in a logistic regression framework. Once sightability is computed, one can derive population size (Borchers et al. 2002).

Central to this work is the idea that individual sightability is influenced by population density, vegetation openness and fragmentation. We suppose that biological and geometrical issues can influence the rate at which deer can be seen at a survey point. An example of a biological reason could be that at higher densities deer can be forced to show in open areas by food shortage; a geometrical reason could be that the edge of a survey area grows as the square root of its extension. These relations have a non-linear form, and we expect other relations of this type to influence deer sightability.

More specifically, we derive a calibration model using local density estimates, computed with mark-resight (Focardi et al. 2002b), as the dependent variable and linear and non-linear functions of counted animals and survey zone area as regressors.

Materials and Methods

Study area

The study area extends over approximately five km^2 of a hilly landscape in north-central Italy (44°04’37”N, 11°44’30”E), with woods covering 47% of the whole surface. Woods are predominantly coppice (deciduous oak, hornbeam, chestnut, ash, maple) and coniferous plantations (mostly pine) with a few cultivated chestnut and old woods.

Open vegetation covers 48% of the whole, consisting mostly of cultivated fields (hay, cereals, sunflower, pastures), with a significant portion of abandoned fields.

A stream and an adjoining paved road divide the study area into two subareas. The subareas (Monti, south-eastern side, and Collinaccia, north-western side) share most of their relevant characteristics, for vegetation composition of woods and types of cultivations, nonetheless the average open field area is six hectares for Collinaccia and eleven hectares for Monti.

Climate in the study area is favorable for roe deer. Average monthly temperature never drops below 0°C, and there was no snow cover during the surveys, since snow cover in March is occasional and short lasting.

Roe deer captures and radiotracking

Roe deer were captured by driving, using falling long-nets, during autumn-winter. Captured deer were sexed and aged and fitted with Televilt TXE3 radiocollars. Newborns were captured and fitted with Televilt TXH2 radiocollars, during the hiding period (end of May through 10th of June, Raganella Pelliccioni et al., 2004).

Animal handling was performed according to present regulations relative to animal welfare and with constant veterinary assistance. Upon capture all animals were fitted with a soft mask (to reduce the animal’s distress) but which allowed deer to breathe normally. Deer were positioned on the right side to avoid ruminal meteorism which might reduce respiratory efficiency. A total of 220 roe deer were captured between 1996 and 2003.

Each deer was localized 12 times per month with a time-stratified sampling distributed across 24 hours.

Single operators equipped with a receiver (Advanced Telemetry Systems, mod. R2000 or Wildlife Materials RX 1000 S) collected at least three azimuths per fix.

Animal location was computed with software LOCATE (Nams, 1990) that uses a maximum likelihood criterion to estimate the position of the radio source.

Surveys of roe deer population

Surveys were performed at the end of March (green-up season in the study area) from 1996 to 2003. Observers were trained operators equipped with binoculars and telescopes to be able to read the numbers of the collars, to individually identify the marked deer. Counts were performed in four consecutive occasions at dawn and dusk. Observers were located in vantage points (Mayle et al. 1999) such as farmyards, hunting hides, roads. Each observation session lasted 2-hour, just after dawn or before dusk. Number of vantage points ranged 19-29 per year, in response to changes in the surveyed area or personnel availability. Operators were located to achieve a full visual coverage of all fields. Accordingly, while one field could be monitored by a single operator, sometimes two or more operators could survey the same field, as well as a single operator could cover two or more field portions. Where necessary, operators talk by radio to avoid double counts. Sixteen to nineteen fields were surveyed each year, for a total of 135 fields.

Statistical methods

The method consists of four steps: (a) we compute the mark-resight density estimates to be used as a set of reference densities, (b) we relate these estimates to linear and non-linear functions of animal count and surface area of fields, to obtain a set of density estimators, (c) we select a linear combination of such estimators based on a set of statistical criteria (d) we cross-validate the selected model to test whether the selected model is able to predict densities at three different spatial scales: the whole study area, sub-areas and small plots, the size of a single home range.

(a) The reference density estimates at small scale were obtained using the method described by Focardi et al. (2002b). The number of deer associated with each field was estimated by mark-resight (White & Schenk 2001) using the software NOREMARK (White 1996). Density was computed correcting for a factor accounting for the fraction of time each animal spent inside the field (Kenward et al. 1981) and divided by the area of the field. In this way we obtained *M* reference density estimates, representing our sample units, each of which pertains to a given field in a given year.

Subareas densities were obtained with the same procedure. The whole area densities are the average of subareas densities, weighted for subareas extension.

(b) Two variables were used to account for deer density: the number of counted deer, O_i, and the field area A_i, with i=1,…,M. O_i was computed as the mean number of deer recorded in a given field during the four count sessions. A_i is the area of the horizontal projection of the surveyed field, computed with a GIS (Arc-View, ESRI, 1996).

Let us define $\rho(O,A)$ a generic function such that $\sum_{i=1}^{M}(\bullet_i - D_i)^2$ be minimum, where D_i is the estimated density in the i^{th} count zone. There is no *a priori* reason to select a certain function as ρ. A graphical exploration of the relationships among *D*, *A* and *O* allowed us to select a certain number of candidate models (e.g. linear, exponential, hyperbolic etc.).

The fitting of non-linear functions was made using PROC NLIN of SAS, (SAS Institute Inc., 2000). We obtained *G* different models ($\rho^1, \rho^2, ..., \rho^g ,..., \rho^G$) where each ρ^g is an estimator of density *D*.

All the regressors are some function of O_i and A_i. For a more intuitive understanding of their biological meaning, we put $E_i=O_i/A_i$ and $U_i=E_i/D_i$. E_i is an apparent density, while U_i is the ratio between E_i and the CMR-estimates of density in a given field and hence it represents the intensity of use of open fields by roe deer. In Table 1 we report the regressors we used, the function that was fitted to compute parameter values, and the function that was used as regressor.

(c) We then exploited all of these estimators to compute a best linear function, $R(\rho^1, \rho^2,\ldots, \rho^G)$. The fitting, computed such that $\sum_{i=1}^{M}(R_i - D_i)^2$ be minimum, was performed with PROC REG (SAS Institute Inc., 2000). All possible models were evaluated. We obtain one model with G regressors, G models with G-1 regressors, $G(G$-1)/2 models with G-2 regressors,…, G models with one regressor. We discarded all of the models that were not full-rank (i.e., at least one regressor was a linear combination of the others), and then we ranked the remaining models according to the Akaike Information Criterion (AIC). Finally, we tested for collinearity among regressors, discarding the models in which at least one regressor had Variance Inflation Factors (VIF) greater or equal 10 (Belsey et al. 1980). The model with the best AIC and VIF < 10 for each ρ^g is selected.

The final model reads: $R=s^1b^1\rho^1+ \ldots + s^gb^g\rho^g + \ldots + s^Gb^G\rho^G + c$, where s^g=0 if ρ^g was discarded, and s^g=1 if ρ^g entered the model. b^g is the coefficient of ρ^g and c is the intercept.

(d) To evaluate the performance of the estimator R, we compared R_i with D_i. We evaluated first the significance of the model used (Fisher F-test). The level of precision attained by the model was described computing the median absolute error, which is reported in percentage of the reference density, D, and its interquartile variation, where D is scaled to 0. Then we test for the presence of a significant bias of the predictor (Student's t-test), comparing model estimates with reference densities. Finally the Pearson correlation (r) between R and D, is an index of a model's sensitivity or, in other words, a measure of how *R* is able to detect a trend. Finally we cross-validated the model. We divided our data set into years and subareas, then we recursively calibrated the model excluding one stratum, which was then used to test the performance of the model itself. In such a way, we tested the robustness of the method with respect to different environmental and temporal conditions. Note that *R* estimates at subarea and at whole area scales are computed by averaging field estimates.

Results

The model for the whole data set

We do not show here the outcome for each of the parameters of the regressors. In figure 1 we report the plots of some of the relations that were minimized to compute regressors, to provide an intuitive look of the fits. In figure 1A, we plot apparent density *U* as a function of field area. Clearly, the relationship is not linear. In this example we have fitted a hyperbole to the data. Note how *U* decreases as the field area increases. In figure 1B, we plot density *D* against *O*. Again, the relationship looks non linear. In the figure we minimize a Holling type-2 function. The point is that density is not usually a linear function of the number of observed animals.

Two regressors were included in the selected model (Table 2) which is highly significant ($F_{3,60}$=18.0, P<0.0001, R^2=0.47).

In Table 3 we report how the estimator (*R*) was good at fitting the reference density *D* at three different spatial scales. The estimates are unbiased and their precision is good at all scales. At large and medium scale the error is well below 20%. As expected the error decreases at increasing scale . No significant bias is evident at any scale. The correlation indicates that model sensitivity is quite good for small and medium scales, suggesting efficient trend detection. The apparent lack of correlation for the large scale is possibly an effect of the reduced data set characterising this spatial scale.

Cross validation

The models used for the cross-validation per year are reported in Table 4, while results are reported in Table 5. The results are qualitatively very similar to the ones previously described for the complete model (Table 3) suggesting that one can obtain reliable density estimates for one year, using a model developed for different years. The bias is always non-significant at all scales and remarkably low at the small scale. In particular the correlations relative to small and medium scales appear to be high, while the performance is lower at the large spatial scale.

Finally (Tables 6 and 7) we investigated whether one can use a model developed in one subarea to estimate density in the other subarea, i.e. how much our model can be exported. These results (when compared to the previous cross-validation per year) exhibit a lower precision at medium scale, which remains below 20%, while the precision at small scale is even better than in the case of cross-validation per time (cf. table 5). Bias is always not significant. Correlations are good at both scales.

Looking in particular at the small scale, correlation between true density and our estimates is always very significant ($P<0.01$, cfr. Tables 3, 5, 7), while precision is always around 25%.

Our experience showed that the use of both AIC and VIF for model selection improved sensibly the cross-validations between subareas with respect to the use of AIC only.

The cross-validation by year (Table 5) is comparable with the whole data set model (Table 3) and the difference is partly due to the reduced data set used to calibrate the model. Overall, the results shown in Tables 3 and 5 suggest that the method is very reliable to estimate local density even in years following the model's calibration or in different subareas.

Discussion

The basic message of this work is that it is possible to use calibration models with simple and cheap data as inputs (in our case field area and the number of counted roe deer) to estimate density at different scales, provided reliable density data are available, e.g. by mark-resight. Results are also encouraging if one wants to predict density using data collected in different years within the same area. Errors are usually lower than 20% which are acceptable in most of applications.

Our modelling approach is purely pragmatic in the sense that the functions used (the ρs) has no specific mechanistic interpretation. In this paper we used a sort of "blind" calibration of our density estimates. Usually calibration is defined as the reverse process to linear regression, by deducing an unknown value of the dependent variable (density) given known independent variables. However, given the complexity of factors linking sightability, habitat structure and density, we do not expect their relationship to be linear. In fact even in sightability models non-linear (exponential) functions are used to predict animal abundance. The use of non-linear relationships is in fact commonplace when modelling animal detectability (White & Schenk 2001). A non-linear relationship between population indices and population abundance was also found by Morellet et al. (2007) for the roe deer population of Dourdan (France). In distance sampling non linear detectability functions are used to account for different detection patterns (Buckland et al. 2001). Thus our choice of ρs is arbitrary (i.e it is not derived by mechanistic considerations) but it is empirically useful and justified from the literature. The method proposed has the potential to be used for validating population indices, such as the kilometric index of abundance (KIA), which are often used as management tools for roe deer populations through Europe (Vincent et al 1991). Recently the use of KIA was extended to other species of ungulates as well: Maillard et al (2001) supported its use for detecting population trends in an African ecosystem, while Acevedo et al. (2008) showed that the KIA was well correlated with line-transect density-estimates of red deer populations in Spain.

We argue that our method was very successful at estimating local density of roe deer. We expected to obtain the best results for the estimates at larger scales than at a small scale. While this turned out to be true for the precision of our estimates, that was very good at intermediate and large scales, correlation and accuracy were worse at the larger scale. We suppose that this unexpected result is caused by the reduced data set available when spatial scale increases, but density differences between fields and woods may also play a role.

Results confirm the usefulness of our method both for research and management.

For research our method can provide reliable local density estimates where a radiomarked set of roe deer is available. It allows insights in population dynamics and regulation, mainly by providing the researcher with information about the spatial structure of density.

Note also that the information on density in an area can be extended to zones where animals were not captured, provided the model is used only for zones similar to those where the model was calibrated. This result was achieved by testing for collinearity (VIF analysis). In a preliminary phase of our work we saw that estimators obtained only with AIC are biased when used to estimate density between subareas. Interestingly only in one case a single regressor was the best solution (cf Table 6). In all other cases a combination of regressors performed better than any single one. This supports our choice of using a multiple regression framework.

In management the use of simple counts may determine the adoptions of harvesting quotas which are inappropriate to fulfill the aims of management. Integrating field counts with a zone-specific method calibrated in place, game managers can smooth steep interannual variations of counts, gaining trust among hunters and allowing more stable game returns.

The application of the method relies on appropriate calibrations. Wildlife managers should invest resources (at least for some years) to radio-mark animals. Alternatively, it could be interesting to investigate the use of surface density modelling based on distance sampling survey (Buckland et al. 2004, Focardi et al. 2006) as a base for the calibration model. Distance sampling surveys could be performed for some years at relatively low costs (Franzetti & Focardi 2006). Although we have not yet tried to develop this approach, we think the outcomes could be very fruitful.

Finally, these results will allow us to test the relevance of local density upon roe deer population dynamics in the same population described in Focardi et al. (2002a and 2002b). We will investigate the scale at which density is relevant to shape life history traits.

Although our method is quite specific for our needs, we think that the general framework can be adapted to other species and environments.

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Table 1. List of the regressors for the density estimation model. The functions on the second column are obtained by expliciting density *D* in the equation reported in the first column and replacing it with ρ. *A*=field area; *O*=counted deer; $E=O/A$; $U=E/D$; *a*, *b*, *c*, *d*, and *k* are parameters computed by least squares.

Fitted functions	Regressor functions
$U=a+b/(k+A)$	$\rho_1=(kO+AO)/((ak+b)A+aA^2)$
$U=a+b/Di$	$\rho_2=O/aA-b/a$
$D=O^a+b$	$\rho_3=O^a+b$
$D=E^a+b$	$\rho_4=E^a+b$
$D=aAO^b$	$\rho_5=aAO^b$
$D=a(AO)^b$	$\rho_6=a(AO)^b$
$D=a+(AO)^b$	$\rho_7=a+(AO)^b$
$D=aO+c$	$\rho_8=aO+c$
$D=aE+c$	$\rho_9=aE+c$
$D=aO$	$\rho_{10}=aO$
$D=aE$	$\rho_{11}=aE$
$D=aO+bA+c$	$\rho_{12}=aO+bA+c$
$D=aE+bO+c$	$\rho_{13}=aE+bO+c$
$D=aA+bO+cE+d$	$\rho_{14}=aA+bO+cE+d$
$D=a+bO/(c+O)$	$\rho_{15}=a+bO/(c+O)$
$D=a+bE/(c+E)$	$\rho_{16}=a+bE/(c+E)$
$D=bAO/(c+AO)$	$\rho_{17}=bAO/(c+AO)$

Table 2. We report the coefficients of the regressors (•$_1$ and •$_7$) entered in the selected model for the whole data set, standard errors, Student's t tests for difference from 0 and the variance inflation factors (VIF).

Regressors	Parameter estimate	Standard error	t	Pr>t	VIF
Intercept	179.71	40.20	4.47	<0.0001	/
ρ_1	1.31	0.18	7.29	<0.0001	2.22
ρ_7	-4.44	1.08	-4.13	0.0001	2.22

Table 3. Precision and bias of the estimator calibrated upon the whole data set, and correlation between the estimator, *R*, and reference density, *D*, at three different spatial scales: small (• 10 ha), medium (• 200 ha) and large (• 400 ha). The median error is computed using the absolute value of the difference between the estimates derived from the model and the reference density. The percentile error is computed considering the percentage deviation from the reference density. The Student's t-tests for the presence of a bias are performed with N-1 degrees of freedom. Significant correlations are indicative of a good trend detection.

		Precision			Bias		Correlation	
Scale	N	Median error (%)	Percentile error 25th	Percentile error 75th	t	Pr>t	Pearson's *r*	Pr>*r*
small	64	23.60	-14.78	40.53	0.00	1.00	0.69	<0.0001
medium	15	10.96	-16.49	7.04	1.48	0.16	0.71	0.003
large	7	7.25	-29.33	4.36	1.01	0.35	0.24	0.61

Table 4. Cross-validation per year. The year reported in first column refers to the data predicted by the procedure of cross-validation, which were hence excluded by model's computation. For each year of study we report the selected model (upper line), F-test and adjusted R^2 (lower line) for the selected model.

Year	F	Pr>F	adj-R^2
1996	$R = 161.27 + 3.88\rho_3 - 1.16\rho_6 - 5.83\rho_7$		
	$F_{3,58}=12.54$	<0.0001	0.45
1997	$R = -31.82 + 0.99\rho_{16} + 0.83\rho_{17}$		
	$F_{2,51}=22.89$	<0.0001	0.43
1998	$R = 162.54 + 1.41\rho_1 - 4.28\rho_7$		
	$F_{2,55}= 32.79$	<0.0001	0.43
1999	$R = -27.92 + 0.97\rho_{16} + 0.71\rho_{17}$		
	$F_{2,49}= 29.44$	<0.0001	0.43
2000	$R = 287.74 - 6.79\rho_7 + 1.39\rho_1$		
	$F_{2,47}= 21.35$	<0.0001	0.45
2001	$R = 279.89 - 6.86\rho_7 + 1.40\rho_1$		
	$F_{2,52}=26.09$	<0.0001	0.48
2002	$R = 147.84 + 1.21\rho_1 - 3.48\rho_7$		
	$F_{2,55}=23.30$	<0.0001	0.44
2003	$R = 179.64 + 1.20\rho_1 - 4.17\rho_7$		
	$F_{2,56}=25.69$	<0.0001	0.46

Table 5. Cross-validation per year (cf. Table 4). Precision, bias and correlation between the estimator and reference density, at three different spatial scales: small (• 10 ha), medium (• 200 ha) and large (• 400 ha). The median error is computed using the absolute value of the difference between the estimates derived from the model and the reference density, *D*. The percentile error is computed considering the percentage deviation from the reference density. The Student's t-tests for the presence of a bias are performed with N-1 degrees of freedom. Significant correlations are indicative of a good trend detection.

		Precision			Bias		Correlation	
Scale	N	Median error (%)	Percentile error		t	Pr>t	Pearson's *r*	Pr>*r*
			25^{th}	75^{th}				
small	64	27.03	-13.13	39.60	-0.15	0.88	0.64	<0.0001
medium	15	9.74	-19.34	8.87	1.35	0.20	0.66	0.0074
large	7	7.77	-29.16	5.44	0.92	0.39	0.19	0.68

Table 6. Cross-validation per subarea.We report the selected model (upper line) and F-test and adjusted R^2 (lower line) for the cross-validation models by subareas. The selection procedure is performed on our data set removing data relative to the subarea reported in the first column.

Subarea	F	Pr>F	adj-R^2
Monti		$R = \bullet_{13}$	
	$F_{1,36}$=36.92	<0.0001	0.49
Collinaccia		$R = 55.24 - 3.63\bullet_{7} + 1.96\bullet_{3} + 1.24\bullet_{12}$	
	$F_{3,22}$=6.71	0.0022	0.41

Table 7. Cross-validation by subarea (cf. Table 6). Precision, bias and correlation between the estimator and reference density, at two different spatial scales: small (• 10 ha) and medium (• 200 ha) (note that the large scale can not be evaluated in this analysis). The median error is computed using the absolute value of the difference between the estimates derived from the model and the reference density, *D*. The percentile error is computed considering the percentage deviation from the reference density. The Student's t-tests for the presence of a bias are performed with N-1 degrees of freedom. Significant correlations are indicative of a good trend detection.

		Precision			Bias		Correlation	
Scale	N	Median error (%)	Percentile error		t	Pr>t	Pearson's *r*	Pr>*r*
			25^{th}	75^{th}				
small	64	22.81	-11.44	49.80	-0.81	0.42	0.63	<0.0001
medium	15	14.66	-14.66	19.35	0.70	0.50	0.49	0.02

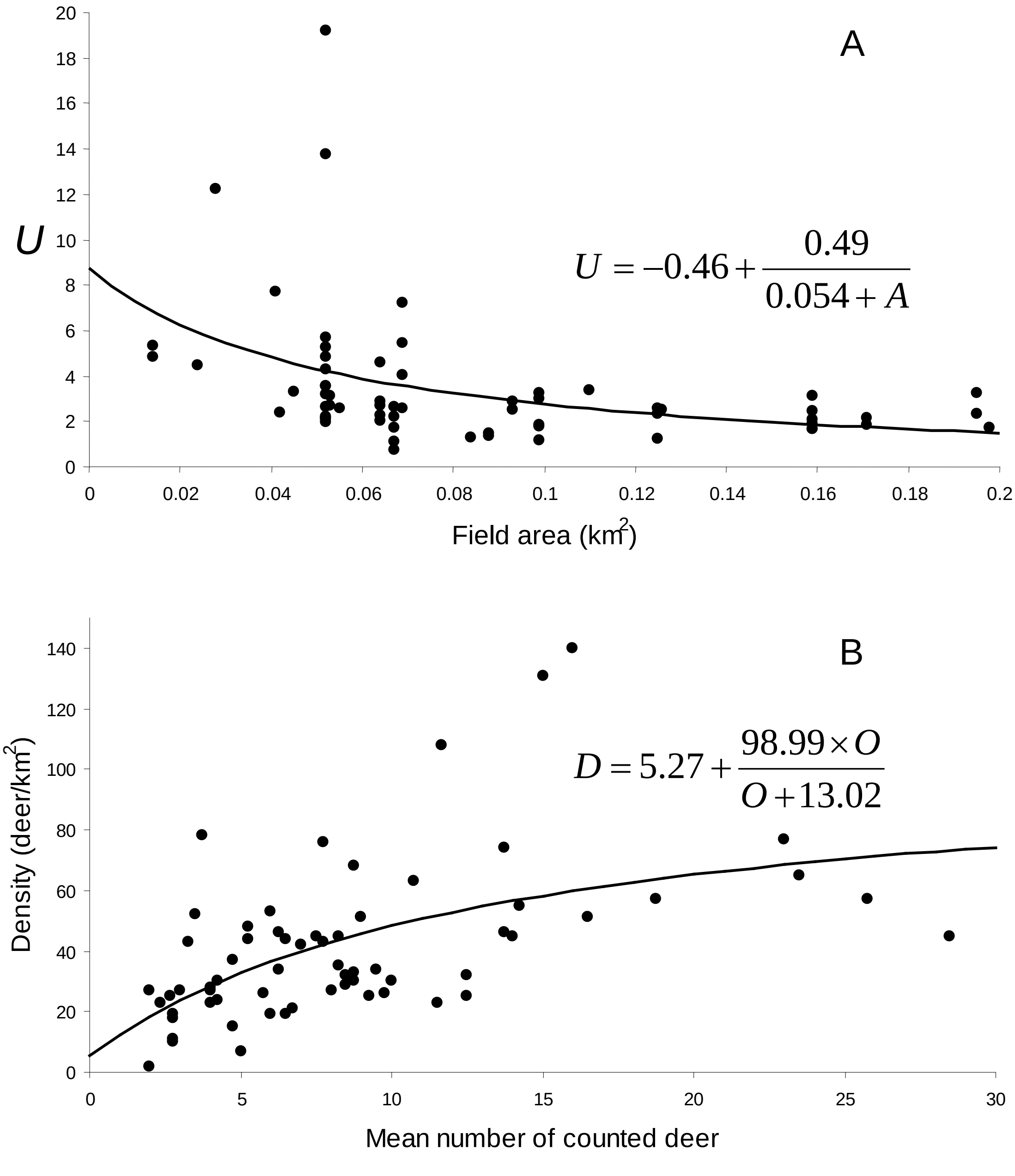

Figure 1. Two examples of non-linear relations that were minimized to estimate the ρs. (A) the use of fields has an hyperbolic relation with the field area. (B) the relationship between *D* and *O* is Holling-type 2. The parameters of the equations were estimated from the whole data set. *U* is the ratio between apparent and true densities.