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How many are there? Multiple-covariate distance sampling for monitoring pampas deer in Corrientes, Argentina

Talía Zamboni[A,D], *Alicia Delgado*[B], *Ignacio Jiménez-Pérez*[B] and *Carlos De Angelo*[C]

[A]Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Avenue. Haya de la Torre s/n, CP 5000, Córdoba, Argentina.
[B]The Conservation Land Trust Argentina, Scalabrini Ortiz 3355, 4° J, CP 1425, Buenos Aires, Argentina.
[C]National Scientific and Technical Research Council (CONICET); Instituto de Biología Subtropical, Facultad de Ciencias Forestales, Universidad Nacional de Misiones; Asociación Civil Centro de Investigaciones del Bosque Atlántico; Bertoni 85, N3370BFA, Puerto Iguazú, Misiones, Argentina.
[D]Corresponding author. Present address: Alejandro Korn 3189, CP 5016, Córdoba, Argentina. Email: taliazamboni@gmail.com

Abstract

Context. The pampas deer (*Ozotoceros bezoarticus*) is an endangered species in Argentina. Scarce information exists about one of the four last populations that survive in Corrientes province, where direct counts estimated a population of <500 individuals.

Aims. To evaluate the status of the pampas deer population in Corrientes by applying a standardised methodology and to develop methodological recommendations for future deer monitoring.

Methods. We conducted six population censuses between 2007 and 2010, using line transects placed on roads throughout 1200 km^2 of grasslands in the Aguapey region, Corrientes, Argentina. From a moving vehicle, we counted every pampas deer group observed along transects. We used Distance 6.0 and its multiple-covariate distance sampling engine to estimate deer density, while exploring the potential effect of roads, habitat type, hour, season, observer experience and survey effort on deer occurrence and density estimation.

Key results. The occurrence of pampas deer was irrespective of transect location (minor or major road) but a greater number of animals was detected over transects in minor roads and in areas covered by grasslands with young pine plantations. We estimated a density of 1.17 individuals km^{-2} (s.e. = 0.52), and habitat type was the most important covariate for density estimation. We estimated a total population of 1495 deer (95% CI = 951–2351, CV = 23.27%) for the Aguapey region in Argentina.

Conclusions. Corrientes hosts one of the largest populations of pampas deer in Argentina, with ~1000 individuals. The fact that we estimated a larger population than did previous studies could be explained either by actual population growth during the past 10 years, or by the use of more exhaustive and sophisticated sampling design and data analysis.

Implications. Population surveys using covariate distance sampling on ground line transects can provide more realistic population estimates than do other simpler methods. Our population estimates and methods can be used as a baseline for future monitoring of this population, as long as factors such as sampling effort, type of roads for locating transects, and habitat type are considered in future analysis.

Additional keywords: habitat type, line transects, *Ozotoceros bezoarticus*, roads, survey effort.

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Introduction

Until livestock arrival, the pampas deer (*Ozotoceros bezoarticus*) was the dominant ungulate over most of the vast plain areas of Brazil, Bolivia, Paraguay, Uruguay and Argentina (González *et al*. 2010; Miotto *et al*. 2012). Originally distributed throughout the Argentinean grasslands, the pampas-deer population has suffered a dramatic decline within this country as a result of habitat loss and fragmentation, hunting and probable competition with livestock for forage (Jackson and Giulietti 1988; Demaría *et al*. 2004). Despite being considered internationally a nearly threatened species (González and Merino 2008), the pampas deer is considered endangered in Argentina; therefore, precise estimates about its population status are needed (Díaz and Ojeda 2000; Pastore 2012).

Of the four pampas deer populations remaining in Argentina, one is located on the Aguapey basin (Corrientes province, north-eastern Argentina; Fig. 1) and belongs to the *O. b. leucogaster* subspecies (Goldfüss 1817). As in other populations of the species in Argentina, the one in Corrientes is isolated and with scarce protection (Merino and Beccaceci 1999; Parera and Moreno 2000; Jiménez Pérez *et al*. 2009). Hunting pressure and competition with cattle have historically threatened pampas deer in Corrientes (Merino and Beccaceci 1999; Parera and Moreno 2000). However, since the end of the last century, habitat loss through forest plantations, which had occupied 24% of deer's available habitat by 2008, has been considered a major threat to this population (Jiménez Pérez *et al*. 2009). Although deer may utilise regions with young pine plantations and even browse on them (Parera and Moreno 2000), old pine plantations do not seem to represent a suitable habitat for pampas deer, considering it is a species that has evolved for open habitats (González *et al*. 2010). These growing threats have led government and NGOs to seek urgent conservation actions; either *in situ* protection or the translocation of individuals to establish a new population within Iberá Nature Reserve, located adjacent to Aguapey's population (Fig. 1). This has accentuated the need for having precise estimates of population size and trends to support these management actions.

Aerial and terrestrial surveys combined with interviews of local people were previously conducted to assess the number of pampas deer present within the Aguapey region (Merino and Beccaceci 1999; Parera and Moreno 2000; Jiménez Pérez *et al*. 2009). By the end of the last century, the total estimated population of pampas deer in Corrientes ranged from 130 to 500 individuals (Merino and Beccaceci 1999; Parera and Moreno 2000). These were isolated surveys that used different methodologies and survey designs, hindering the opportunity of using the data in population monitoring.

Biased results or high variation in population estimates prevent the detection of changes within populations over time and reduce the possibility of finding differences when comparing among populations (Conroy and Carroll 2009). Among the survey techniques used for non-volant mammals, line-transect distance sampling has been increasingly used because of its ability to estimate the detection probability of animals, which is essential for accurate population estimation (Buckland *et al*. 1993; Rudran *et al*. 1996; White 2005). This survey technique is one of the recommended methods for monitoring deer in open areas (Andriolo *et al*. 2010) and is already being used to estimate

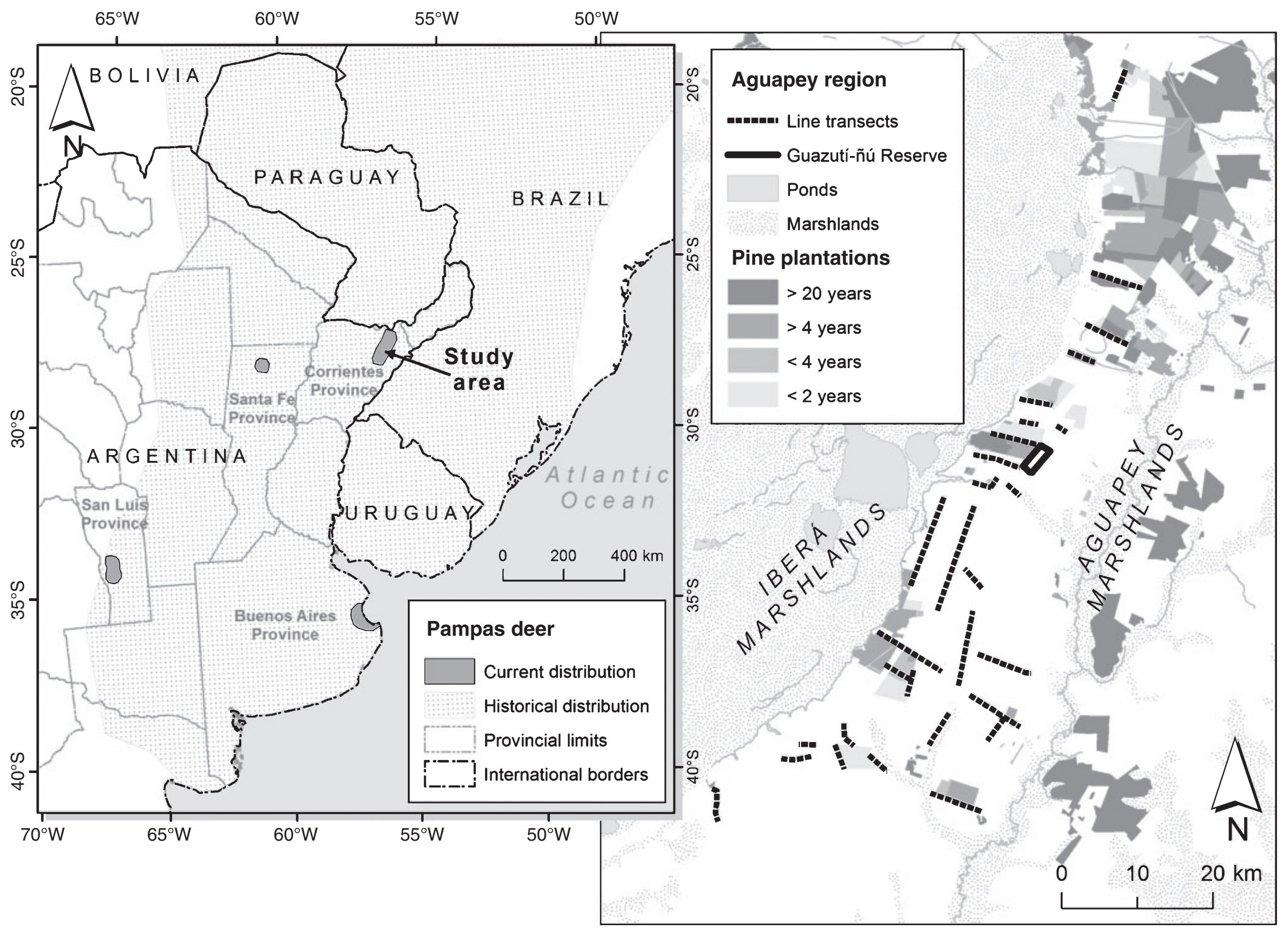

Fig. 1. Location of the pampas deer remaining populations in Argentina (left) and detailed map of the Aguapey region in Corrientes Province, where the study was conducted (right). The later map shows the location of line transects used to estimate deer abundance between 2007 and 2010, and the distribution of pine plantations among the grasslands and marshlands that historically covered the area.

population size for different species of South American deer (Mourão *et al*. 2000; Tomás *et al*. 2001). Additionally, the analysis capabilities for distance-sampling data are also advancing, making it possible to deal with factors other than distance that could affect animal detection (Buckland *et al*. 2004).

A variety of factors such as the transect location, the sighting time, or the environmental heterogeneity could all influence the number of animals detected on surveys (Buckland *et al*. 1993; Rudran *et al*. 1996). Many times, transects are located in existing roads and trails because it is the most efficient or the only way to survey certain areas (Gill *et al*. 1997). Road-based sampling may bias population estimates because of, for instance, the fact that roads may not be randomly distributed in relation to the density of animals (Buckland *et al*. 1993), or to their influence on animal behaviour. For example, some animals may avoid roads on account of their association with humans or for other habitat factors (Rost and Bailey 1979; Ward *et al*. 2004); in contrast, some species may be attracted by road-side clearings (Varman and Sukumar 1995). Daily activity pattern of animals may also influence our capacity of detecting animals during surveys (Gill *et al*. 1997). In heterogeneous areas, habitat preferences and different detectability conditions can also have a great impact on animal census (Putman *et al*. 2011). Additionally, observer expertise and survey effort should also be considered when analysing census data (Jachmann 2002). Pampas deer, for example, are rather cryptic, hindering their detection by unexperienced observers (González *et al*. 2010). So as to obtain more accurate results, all or at least some of these factors should be considered when analysing data and estimating parameters, especially when dealing with heterogeneous data (Putman *et al*. 2011). Solid survey design and data analysis are crucial to obtain unbiased and precise estimates, which are essential for monitoring endangered populations or species (Thomas *et al*. 2010; Porteus *et al*. 2011; Oedekoven *et al*. 2013).

Our main objective was to assess the use of multiple-covariate distance sampling to obtain precise abundance estimations for pampas deer in Corrientes, Argentina, and make recommendations for their long-term population monitoring.

Materials and methods

Study site

The Aguapey River basin is located in the north-east of Corrientes province, Argentina. Our study area comprised 1278 km^2 of grasslands located between the Paraná River in the north, the Iberá Marshlands in the west and the Aguapey River in the east (central coordinates 28°04′2.89″S, 56°32′46.69″W) (Heinonen Fortabat *et al*. 1989; Fig. 1). The landscape was composed of natural humid grasslands sites on flat lowlands, locally known as '*malezales*' (Carnevalli 1994; Di Giácomo *et al*. 2010). These grasslands are characterised by the predominance of one or few species of tall grasses (mainly *Andropogon lateralis* and *Sorghastrum setosum*) from 1 to 1.2 m high, that grow over soils covered with 30–70 cm of water most of the time (Arbo and Tressens 2002; Etchepare *et al*. 2013). The deficient superficial drainage and slow movement of masses of water in the flat lowlands yield to a permanent or temporary flood of more than 70% of their surface, with a fluctuant stage that oscillates up to 1 m in depth (Ferrati *et al*. 2005).

The region comprises private properties, generally larger than 10 000 ha, that are dedicated to extensive cattle ranching (Parera and Moreno 2000). Starting in the 1980s, timber plantations became established in the region and it is estimated that they have already substituted 24% of natural grasslands within the Aguapey basin, and their range is still increasing (Srur *et al*. 2009). The Aguapey basin is adjacent to the 1.3 million ha Iberá Provincial Reserve, and it currently lacks any formal conservation status.

Surveys

We conducted six successive surveys between 2007 and 2010 (Table 1). Surveys consisted of linear transects placed across the west of the Aguapey basin (Fig. 1). Flooded terrain conditions, along with the great extension of the area, made it impracticable to implement random transects. In addition, grassland height was in most cases more than 1 m, thus making it difficult to detect deer while walking transects on foot, with the average shoulder height of deer being ~70 cm. Transect location over roads is sometimes the only possible means to perform a survey with a sufficient number of sightings for density estimation (>60 sightings, Buckland *et al*. 1993). Considering this, transects were placed over random straight sections of existing main dirt roads and minor roads inside private lands over the whole area, with only two exceptions of transects that included one curve along the transect (Fig. 1). Surveys were conducted by two observers in the back of a pick-up truck moving at ~20 km h^{-1}, looking for deer on both sides of the line. The back of the vehicle led observers to perform transects from a considerable height, thus allowing them

Table 1. Description of the six surveys performed for pampas deer monitoring in Corrientes, Argentina
These surveys were developed using main and minor dirt roads to locate transects, and were conducted between 2007 and 2010. L, Total line length

Survey	Number of transects	Survey effort (km)	Total number of deer observed	Number of individual sightings	Number of cluster sightings	Mean cluster size	Encounter rate (*n*/L)	Encounter rate 95% CI
A (spring 2007)	17	123.24	22	7	5	1.67	0.11	0.04–0.27
B (autumn 2008)	26	170.74	73	7	18	3.00	0.14	0.07–0.29
C (spring 2008)	26	169.25	31	16	6	1.41	0.13	0.07–0.22
D (winter 2009)	22	142.75	23	6	7	1.77	0.09	0.04–0.18
E (spring 2009)	10	79.95	28	7	8	1.80	0.19	0.03–1.06
F (spring 2010)	20	89.45	32	13	7	1.60	0.13	0.05–0.32
Total	123	775.48	209	56	51			
Mean	20.5	129.24	34.8			1.91		
s.e.	2.26	19.85	7.8			0.16		

to detect deer over tall grasses, particularly near the transect line, as recommended by Buckland *et al*. (1993). Main dirt roads were ~10 m wide and had light traffic, comprising mainly slow vehicles and some people riding horses, whereas minor roads were ~5 m wide and showed minimal traffic, either vehicles or horses.

Where possible, all selected transects were travelled for each survey, with a minimum of 10 and a maximum of 26 transects surveyed each time, totalling an average survey effort of 129.3 km. Each survey took approximately a week to complete (4–7 days per survey). To achieve independence between transects within each survey, transects were placed at least 5 km apart from each other (straight line), along the same road or over a different road.

For each deer observation, we recorded the perpendicular distance from the animal or cluster of animals to the transect (approximate distance estimated by a trained observer), the cluster size, the type of habitat and the time of sighting. The habitat was categorised into grasslands, grasslands with cattle presence, grasslands with pine plantations younger than 4 years old, and pine plantations older than 4 years old. So as to avoid double counts, the same area was never surveyed twice within the same survey and all neighbouring transects were surveyed during the same day.

Considering that animals may tend to avoid or be attracted by roads and their surroundings (Varman and Sukumar 1995; Tomás *et al*. 2001), we evaluated differences in deer detection on transects located on main versus minor roads. We also evaluated the difference in the number of deer observed in different habitat types. For both analyses, we performed a chi-square (χ^2) test using R ver. 2.15.0 (R Development Core Team 2012), following procedures recommended by Logan (2010). Additionally, the same software was used to develop an odds-ratio test, so as to explore which combinations of habitat categories contribute most to the differences in deer observations among habitat types.

To estimate deer density, we analysed the data using Distance 6.0 software (Thomas *et al*. 2009), where 5% of the data were right truncated, as recommended by Buckland *et al*. (1993). A visual analysis of q-q plots showed a trend of rounding distances (Buckland *et al*. 2004), and, therefore, grouping data into intervals was necessary. Data were grouped into distance intervals in nine different combinations (different interval number and width, including equal interval widths), and we used the chi square goodness-of-fit values to select the interval combination with the lowest chi square value that showed the best fit to our data (Buckland *et al*. 2004).

We considered the six surveys as strata and we used the multiple-covariate distance sampling (MCDS) engine of Distance to estimate the detection function separately for each covariate value. The four covariates analysed were habitat type, road type where the transect was located (main dirt road or minor road), sighting time and season. The most influential covariate or combination thereof was selected as the model with the minimum value for Akaike's information criterion (AIC, Buckland *et al*. 2004). For habitat type, we grouped the different types into the following two categories of habitat according to their potential effect on deer detectability: open (including grassland, grassland with cattle, and grasslands with pine plantations younger than 4 years old) and closed (pine plantations older than 4 years old). For sighting time, we differentiated sightings that occurred during the morning (AM) and in the afternoon (PM). Because the surveys were developed in different years and in different seasons (autumn, winter and spring), we included season as a covariate because of the potential differences in the behaviour of deer and deer detectability among seasons. The detection functions obtained with the chosen covariates were used for the estimation of the final density of deer in the study area. For mean cluster size and detection-function estimation, data from all strata (i.e. survey) were used together because of the low number of observations for each individual survey, assuming that those parameters did not vary among surveys. However, considering season as a covariate, we observed the potential variation in detection function caused by differences among seasons.

After selecting the best model for density estimation, the overall encounter rate was the average of encounter rates for each survey, weighting each of them by survey effort. We calculated the density for each stratum, which were averaged as well as the encounter rate for obtaining the mean density. Overall population size was obtained by extrapolating overall density over the complete study area. We used Spearman's rank correlation to analyse the potential effect of survey effort (measured as the total of kilometres surveyed and the number of transects included in each survey) and the previous experience of the observers in relation to the coefficient of variation of the density estimate.

Results

In all, 123 transects were travelled, totalling 777.5 km of surveying effort (mean = 129.2 km per survey, s.e. = 15.9). We observed a total of 209 deer grouped in 56 individual sightings and 51 clusters, with an average of 34.8 deer per survey (s.e. = 7.8, Table 1).

The detection of deer (presence/absence) was independent of transect location over main or minor dirt roads ($\chi^2 = 0.02$, $P = 0.886$). However, the frequency of deer observed in transects located over main roads (total $n = 41$, 0.15 individuals km^{-1}) was lower than expected by the proportional survey effort for each type of road (minor road total $n = 168$, 0.32 individuals km^{-1}; $\chi^2 = 8.95$, $P = 0.003$). Pampas deer were observed more frequently than expected by the proportional survey effort in grasslands with young pine plantations ($\chi^2 = 9.76$, $P = 0.021$), and the probability of observing deer was higher in these areas than in other habitat types (Table 2).

Estimates of population density and abundance

The best grouping option for our data was seven unequal intervals with increasing widths according to the distance to the transect. Hazard rate key function with cosine adjustment terms was selected for our analysis using minimum AIC (Fig. 2). The estimated mean density for each survey without covariates varied between 0.74 and 1.84 individuals km^{-2} (Fig. 3), with a mean cluster size of 1.91 deer per cluster (s.e. = 0.16). Encounter rates were similar among surveys (high overlap among their confidence intervals, Table 1), but the density estimate from spring of 2009 (survey E) showed an extremely high s.e. (1.28 individuals km^{-2}; Fig. 3), mostly explained by the high variability observed in its encounter rate. This value could be explained by the scarce number of transects performed during that survey

Table 2. Differences in the number of deer observed among the habitat-type categories surveyed in the Aguapey region, Corrientes, Argentina, between 2007 and 2010

Odds-ratio values lower than 1 indicate that the proportion within the first compared category is lower than that within the second one, and values greater than 1 indicate the opposite. The *P*-value corresponds to a chi-square test (Logan 2010). Significant ($P < 0.05$) comparisons are shown in bold type. The type of habitat considered were as follows (*n* describes the total number of deer observed in each type): Grasslands (open habitat; $n = 93$); G & cattle: grassland with cattle (open habitat; $n = 29$); G & pine < 4: grasslands with pine plantations with less than 4 years old (open habitat; $n = 43$); and G & pine > 4: grasslands behind which are located pine plantation older than 4 years old (closed habitat; $n = 40$)

Comparison	Estimate	95% CI	*P*
Grasslands vs G & cattle	1.1	0.7–2.0	0.654
Grasslands vs **G & pine < 4**	**0.4**	**0.2–0.8**	**0.004**
Grasslands vs G & pine > 4	0.8	0.5–1.4	0.534
G & pine < 4 vs **G & cattle**	**2.6**	**1.3–5.3**	**0.006**
G & pine < 4 vs **G & pine > 4**	**2.0**	**1.0–3.9**	**0.048**
G & pine > 4 vs G & cattle	1.3	0.7–2.6	0.379

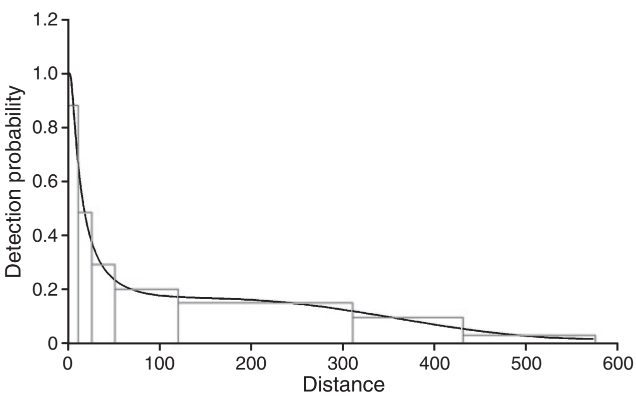

Fig. 2. Detection probabilities as a function of the distance without including covariates for estimates of pampas deer density in the Aguapey region, Argentina, between 2007 and 2010.

(10 vs 17–26 from other surveys) owing to adverse climatic conditions during the survey, added to the fact that of the 15 overall detections (individuals and clusters) in Survey E, 13 were achieved over one transect only.

Considering potential covariates that may affect the detection function, the model that obtained the highest support from our data was the one containing the habitat type as covariate (Table 3). As expected, a higher detection probability was observed at greater distances in open habitats, whereas in closed habitats, the detection probability fell abruptly after 25 m (Fig. 4*a*, *b*). The type of road where transects were located also showed a relatively high support (third position in the ranking), but with a lower support than the habitat type covariate and the simplest model without covariates (Table 3). However, the detection probability plots of the transects in the two types of roads (Fig. 4*c*, *d*) showed that few deer were observed close to major roads, indicating that this type of road may affect not only the detection function but also the encounter rate.

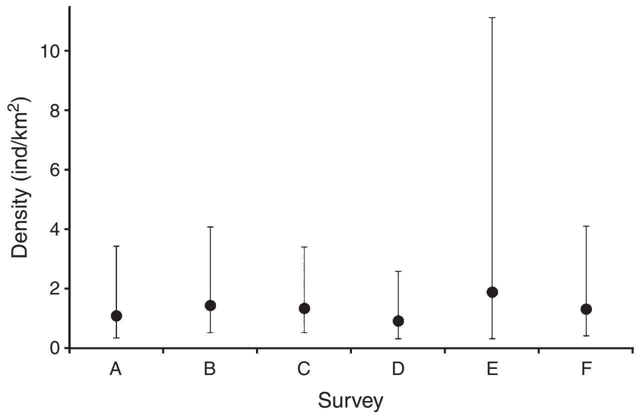

Fig. 3. Estimates of pampas deer density for six line-transect surveys developed in the Aguapey region in Argentina (black dots) between 2007 and 2010. Error bars indicate the confidence intervals for each density estimation. See Table 1 for details of each survey.

Looking for more accurate pooled estimates of pampas deer density, we recalculated deer density using the selected model from Table 3, but exploring the following three different alternatives: (1) excluding Survey E; (2) excluding major roads; and (3) excluding both (Table 4). Only the exclusion of the Survey E reduced the variance of the overall density estimate in relation to the selected model, with a mean density estimate for the study period of 1.17 individuals km^{-2} (s.e. = 0.52 individuals km^{-}). Extrapolating this density to our study area (1278 km^2), we obtained an abundance of 1495 individuals (95% CI of 951–2351, CV = 23.27%) estimated for the Aguapey region.

With and without considering Survey E, a reduction of the estimation variability was observed when increasing the survey effort either measured as the total kilometres travelled during the survey ($\rho = -0.886$, $P = 0.017$ and $\rho = -0.800$, $P = 0.067$, with and without Survey E, respectively) or the number of transects travelled in each survey ($\rho = -0.886$, $P = 0.017$ and $\rho = -0.800$, $P = 0.067$, with and without Survey E, respectively, Fig. 5). However, we did not find the effect of the observers previous experience ($\rho = 0.543$, $P = 0.879$ and $\rho = 0.3$, $P = 0.742$, with and without Survey E, respectively).

Discussion

Population status of the pampas deer in Corrientes

Our 4-year survey using distance sampling showed that the pampas deer population in Aguapey, Corrientes, is currently larger than 1000 individuals. This indicates a potential increase in the number of individuals of this population in relation to previous estimates. Merino and Beccaceci (1999) performed two surveys by airplane, which consisted of 300-m fixed-width double-sided line transects, covering an area of 108.2 km^2. These authors assumed total detectability of animals within each transect and used the Jolly method (Jolly 1969) to estimate a population of 127 pampas deer for the whole Aguapey region. Parera and Moreno (2000) performed aerial counts by helicopter, travelling 13 east–west transects with a fix width of 200 m on each side, which covered an area of 108.6 km^2. They estimated a population of 200–500 individuals, although

Table 3. Comparison among the different models evaluated for estimating the detection function for pampas deer in the Aguapey region, Argentina, between 2007 and 2010

m, number of parameters in the model; *P*, probability of detection; ESW, effective strip width; *D*, estimate of the density of animals; CV, coefficient of variation of the parameter; LCL, lower 95% confidence limit of the parameter; UCL, upper 95% confidence limit of the parameter

Model	*m*	AIC	Delta AIC	*P*	*P* CV%	ESW	ESW CV%	*D*	*D* LCL	*D* UCL	*D* CV %
Habitat group	4	358.51	0.00	0.18	14	105.99	14.3	0.99	0.61	1.61	24.8
No covariates	3	364.50	5.99	0.14	42	81.39	42.4	1.30	0.54	3.16	47.1
Road type	4	364.87	6.36	0.14	25	80.14	24.9	1.31	0.71	2.44	32.1
Road type and habitat group	5	366.87	8.36	0.14	25	80.14	25.2	1.31	0.70	2.45	32.4
Road type and time of the day	5	369.11	10.60	0.15	24	84.05	24.4	1.24	0.67	2.29	31.8
Season	5	371.05	12.54	0.14	19	81.35	18.9	1.49	0.87	2.57	27.8
Time of the day[A]	6	372.01	13.50	0.28	10	158.30	9.7	0.65	0.42	1.02	22.5
Season and habitat group	6	373.05	14.54	0.14	20	81.35	19.5	1.49	0.86	2.58	28.2
Season and time of the day	6	373.05	14.54	0.14	20	81.35	20.2	1.49	0.86	2.61	28.7
Season and road type	6	373.05	14.54	0.14	19	81.35	19.4	1.49	0.87	2.58	28.1
Time of the day and habitat group	5	380.00	21.49	0.15	15	86.08	14.9	1.25	0.77	2.05	25.2

[A]Model had different adjustment parameters because of lack of convergence.

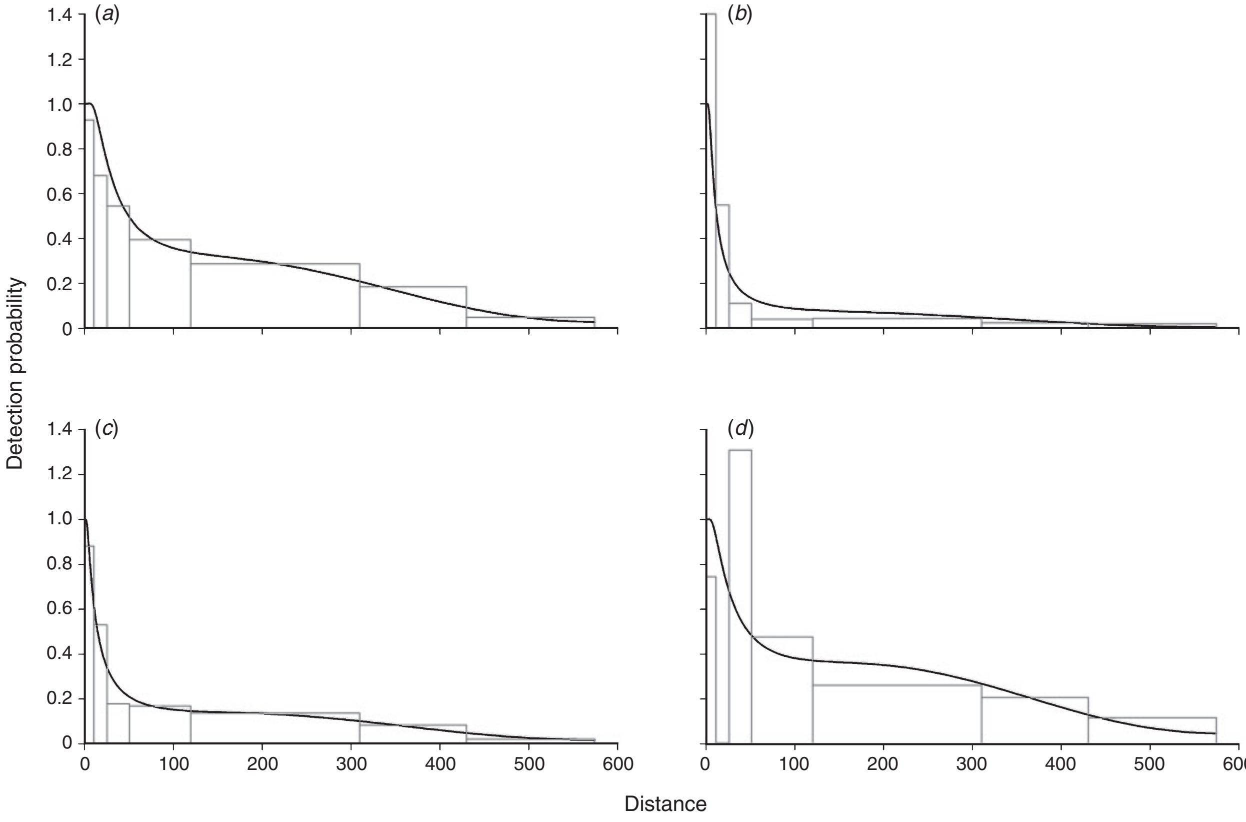

Fig. 4. Detection probabilities as a function of the distance, including covariates for estimates of pampas deer density in the Aguapey region, Argentina, between 2007 and 2010. The histograms for the detection function that includes habitat group as a covariate, for (*a*) open habitats: grassland, grassland with cattle and grassland with young pines; and (*b*) closed habitats: grassland with old pine plantations. The histograms for the detection function that includes road type as a covariate for (*c*) minor roads and trails; and (*d*) major dirt roads.

they did not show the calculations behind these numbers. In both cases, Merino and Beccaceci (1999) and Parera and Moreno (2000) also performed terrestrial surveys, but did not use this information for population estimation. More recently, Jiménez Pérez *et al*. (2007) performed a terrestrial survey in 2006 within the same area as in the previous studies, with a higher survey effort (additional transects within main and secondary roads), although they did not use any formal sampling design or method of analysis. They observed a total of 106 individuals and agreed with previous authors in their estimates of population size. Even using our most conservative density estimate (the first option evaluated in Table 4 that showed the lowest coefficient of

Table 4. Mean pampas deer densities estimated by Distance multiple-covariate distance sampling engine engine for the Aguapey region in Corrientes, Argentina, between 2007 and 2010

These three alternatives were explored to assess the potential effect of excluding Survey E or main roads from the analysis to increase density estimates precision and accuracy. *D*, estimate of density of animals; CV, coefficient of variation of the parameter; *N*, number of individuals; LCL, lower 95% confidence limit of the parameter; UCL, upper 95% confidence limit of the parameter

Selected model	*D*	*D* LCL	*D* UCL	*D* CV%	*N*	*N* LCL	*N* UCL	Effort (transects)
(1) Habitat group, excluding Survey E	1.17	0.74	1.84	23.3	1495	951	2351	105
(2) Habitat group, excluding major roads	1.36	0.77	2.41	29.0	1736	980	3075	92
(3) Habitat group, excluding Survey E and major roads	1.49	0.90	2.47	25.9	1908	1153	3158	86

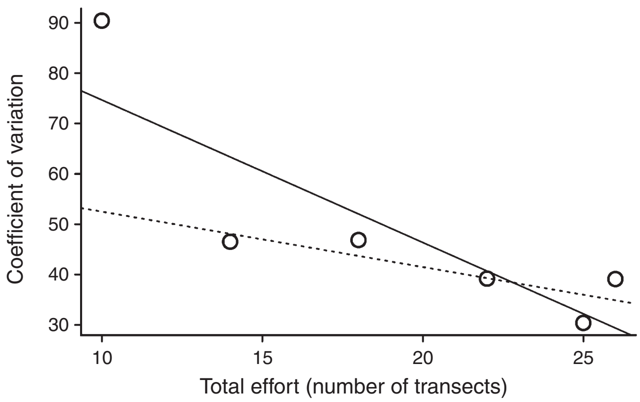

Fig. 5. Relationship between coefficient of variation (CV expressed in percentage) of density estimation in each survey (circles) and the survey effort (expressed as the number of transects for each survey) for pampas deer monitoring in the Aguapey region, Argentina. Both relations are shown, including all surveys (continuous line; rho = –0.886, $P = 0.017$) and excluding Survey E that presented an extreme CV (discontinuous line; rho = –0.800, $P = 0.067$).

variation), all these previous estimates are below our estimated 95% confidence interval for the population density of pampas deer in the Aguapey region.

Differences in population estimates could be explained by differences in sampling design and analysis, or by an actual increase on abundance during the past years. Even though the total number of deer observed in each of our surveys was lower (34.8 ± 7.8 deer per survey) than the number reported by Jiménez Pérez *et al*. (2007), the ability to estimate the detection probability and correct for unseen animals allowed us to obtain more reliable and higher abundance estimates than in any of the other previous studies. These differences in methodologies would be enough to explain differences in density estimates, and therefore they hinder any reliable comparison between studies, to ascertain an actual increase in population abundance through the past 10 years. However, qualitative data from researchers with years of experience in the area (Alejandro Giraudo and Marcelo Beccaceci, pers. comm.) and local ranchers support the idea that there has recently been an increase in the pampas deer population in Corrientes.

Several factors could explain this increase during the past few years. First, the species was declared a Natural Monument in Corrientes province in 1992 (Law No. 22.351), which prohibited and fined its hunting. Also, cattle ranchers have ended traditional open-access policies to their properties, thus limiting entrance by hunters. In addition, during the past two decades, the government of Argentina has implemented stricter controls on cattle management and vaccination campaigns, so as to prevent outbreaks of diseases such as foot-and-mouth (Saraiva 2004). These preventative measures probably had a positive effect on pampas deer, as seems to be the case with its relative, the marsh deer (*Blostocerus dichotomus*), the populations of which have experienced a sharp increase in Corrientes during the past two decades (De Angelo *et al*. 2011). Finally, several years of educational campaigns directed to increase awareness of pampas deer conservation may have had a positive change on the way landowners and their employees see and care about this species.

Within Argentina, density estimated for the Corrientes deer population in the present study (1.17 individuals km^{-2} considering major roads but not considering Survey E, Table 4) does not differ greatly from the other two other main populations of pampas deer in the country, although estimation methods differ for each population, and animal distribution is not homogeneous. The population densities of *O. bezoarticus celer* from Bahía Samborombón, Buenos Aires (Fig. 1), range from 0.51 ± 0.29 (range = 0.18 to ~1.46) to 1.38 ± 0.36 (range = 0.4 to ~1.83) individuals km^{-2} for coastal and inner strata, respectively (Vila 2006). Meanwhile, Dellafiore *et al*. (2003) estimated a density between 0.43 and 0.83 individuals km^{-2} for a population of the same subspecies located in San Luis Province (Fig. 1). Merino *et al*. (2011) estimated a density of 1.95 ± 0.25 individuals km^{-2} for the largest pampas deer nucleus in the same population of San Luis Province. Most of these density values are included in the confidence-interval estimates for Corrientes (Table 4). Deer density of the *O. b. leucogaster* subspecies population located in Santa Fe Province is uncertain (Fig. 1); however, only scarce sightings have been recorded (Pautasso *et al*. 2002) and population size would not be greater than 50 individuals (González *et al*. 2010). From all the studies mentioned, the only one that applied the distance-sampling method was Merino *et al*. (2011), although they used conventional distance sampling without the inclusion of covariates.

Compared with other pampas deer population densities estimated by distance sampling, the population of Corrientes has a relatively low density. Rodrigues (1996) estimated for the Brazilian Emas National Park population a density of 1 individual km^{-2}, but for populations located in the Brazilian Pantanal, Tomás *et al*. (2001) estimated a density of 9.8 ± 3.8 individuals km^{-2}, implementing the same methodology as used in our study. Simultaneously, these authors surveyed parallel transects by foot each year, estimating lower and more precise densities than the global estimation obtained by road-located transects (6.85 ± 1.43 individuals km^{-2} and 4.99 ± 0.7 individuals km^{-2} for both years, respectively). The survey method of transects travelled by foot was also applied by Moraes Tomas *et al*. (2004) for another area in the Pantanal, where they estimated a density of 2.5 ± 0.6 individuals km^{-2} and by Desbiez *et al*. (2010) who estimated densities from 0.2 to 6.0 individuals km^{-2} for different habitats in Pantanal. These last three studies were undertaken for *O. b. leucogaster* populations, the same subspecies as inhabiting Corrientes, and they showed similar or higher densities than our estimates.

Surveying and monitoring the pampas deer

The present study is one of the first implementations of distance sampling to estimate population size of pampas deer within Argentina, and the first to include covariates in distance sampling for this species. This method is widely recommended because of the ability to determine the precision of estimates and for allowing data stratification and the addition of covariates to improve the precision (Buckland *et al*. 1993). The technique also takes into account the two major sources of variation for obtaining unbiased estimations, namely, spatial variation and detectability (Yoccoz *et al*. 2001). Another important issue for population monitoring is to standardise the sampling over time, which allows the detection of population variation over several years. Karanth and Nichols (2002) suggested that for monitoring large herbivores, estimates should have a coefficient of variation of ~15%, so as to detect significant population changes over time. Even if our study represents 4 years of population survey, the final abundance estimate had a coefficient of variation of 23%, indicating that greater efforts are needed to reduce the factors that affect data variability, so as to achieve a more sensitive monitoring. In this sense, the main factors that we recognised that are influencing the variability in density estimation of pampas deer are the potential seasonal variations among surveys, the location of transects (minor vs main roads, Fig. 4*c, d*), the habitat type (Tables 2, 3, Fig. 4*a, b*) and the survey effort (Fig. 5).

Pooling data from several surveys developed in different seasons may help explain the high variability in our results, because potential changes in deer behaviour among seasons and differences in survey conditions can affect the detection probability, cluster size and encounter rates. We assessed the effect of seasons in detection probability including it as a covariate, but its effect was relatively lower than was the effect of habitat and road type, and even lower than the effect of the time of the day (Table 3). Encounter rates showed high variation in each survey, but their differences among surveys were not significant considering the high overlap in their confidence intervals (Table 1). The cluster size also showed low variation among surveys (Table 1), except for Survey B (autumn) where cluster size was considerably higher, probably owing to seasonal social behaviour (post-breeding). The relative contribution of this component to the total variance in each survey was less than 2% along all surveys in relation to the contribution of the detection probability and the encounter rate. Therefore, although it is important to consider potential seasonal biases in future surveys, and it is recommended to develop the surveys in the same season every year (e.g. spring), our results indicated that other factors could be more important for improving the accuracy and precision of pampas deer density estimates.

Because the encounter rate component accounts for most of the overall density variance (Fewster *et al*. 2009), factors affecting that variance should be particularly considered. Line placement within the survey region is one of the main components of that variance, as systematic line placement tends to reduce variance compared with random placement, mostly for strong spatial trends in animal density (Fewster *et al*. 2009). In our surveys, transect placement depended mainly on road location, which in most of the cases implied a directional east–west systematic location, but does not necessarily account for systematic placement considering deer presence or density (i.e. location over high or low deer-density patches). In our density estimates, a high variance could be the result of the lack of randomness in transects location considering deer density. Encounter rates did not vary much among surveys (Table 1), but they showed wide confidence intervals, suggesting that the source of variance may be more related to variability among transects rather than among surveys or seasons. Obtaining density estimates with a different survey design or method (such as aerial surveys) that does not use roads would be an important comparison with our density estimates, to evaluate the potential bias caused by using roads to locate transects (Tomás *et al*. 2001; Porteus *et al*. 2011).

Another factor to take into account when using roads for transect placement is the uniformity assumption required for line-transect sampling (Fewster *et al*. 2008). The uniformity results when distance from the line to the object distributes uniformly over the area, considering that lines are located randomly. Within the study area, terrain conditions hindered implementation of random transect locations in this and previous studies, making roads (main and minor) the only possible way of implementing terrestrial surveys within the region. As it was suggested by Fewster *et al*. (2008), the more suitable option in this case was the implementation of systematic transects with a random starting point, assuming roads have a systematic location over the area. However, road-based transects have previously not been recommended for pampas deer survey because of avoidance response by animals towards roads, as was described by Tomás *et al*. (2001). These authors truncated all the observations up to 100 m from the road because few deer were observed close to the road, contrasting with the data obtained from the surveys conducted on foot. Their density estimates on roads were higher and had less precision than those obtained from foot surveys in systematic line transects (Tomás *et al*. 2001). The high variance in density estimates along roads was associated by the authors with the lack of randomness of road distribution in relation to deer. Although detection probabilities and encounter rates were not presented in their work, similar number of clusters per kilometre indicates that the cluster encounter rates were similar among both survey methods (Tomás *et al*. 2001). Therefore, the higher densities estimated in road-based transects may be a consequence of underestimation of the detection probability (Porteus *et al*. 2011), possibly derived from left truncation of deer observations that resulted from the road avoidance by deer. Within cervids, a tendency to avoid roads with more traffic than those with less traffic has been found also in other species, for example, in mule deer (*Odoicoileus hemionus*) and elk (*Cervus canadensis*) (Rost and Bailey 1979). This trend may lead to underestimation of the encounter rate, leading, in turn, to underestimation of density (Porteus *et al*. 2011). In our surveys in Corrientes, we did not perceive this effect of road avoidance in relation to transects located in minor roads (Fig. 4*c*). Additionally, road type was not selected as an important covariate for detection probability (Table 3). However, the higher frequency of deer observed from minor roads in our surveys than from transects located in main roads, along with a lower number of animals detected near main roads (Fig. 4*d*), could indicate that major roads are negatively affecting the encounter rate of pampas deer and, therefore, affecting density estimation. Accordingly, the density estimate was higher when transects located in main roads were excluded from the analysis (Table 4). Considering the low performance of main-road surveys and the possible bias caused by main roads, in future surveys, much more effort should be made to locate transects only in minor roads, so as to reduce the effect of roads on density estimate.

Regarding habitat type, we found a higher number of deer than expected on grasslands with young pine plantation, which may imply that this environment could be positively selected by deer. Parera and Moreno (2000) mentioned this pattern for the same pampas deer population in 1998. Conversely, in adult pine forest we observed animals mostly over the internal roads or only in grassland areas surrounding plantations, suggesting that even if animals tend to avoid being inside the forest, they use part of this habitat at a certain level. This should be taken into account, mainly by land owners and forest companies, so as to perform a sustainable management of their plantations with deer presence. These results are important not only for understanding the species habitat use, but also to obtain a proper estimate of the available habitat for estimating the total population size. The potential differences in density of deer within pine plantations of different ages or management may be another factor affecting the variability in our density estimates. Underestimation of detection probability can be caused by these differences in habitat type, and this can lead to overestimation of the density (Porteus *et al*. 2011). Better understanding of deer habitat use in these landscapes will help improve density estimates and, therefore, management and conservation of this population.

Finally, our results showed a clear relationship between survey effort and the coefficient of variation (Fig. 5), a relationship that is expected in this kind of field survey (Plumptre 2000; Buckland *et al*. 2004). However, the increased importance of survey effort in relation to other factors (e.g. the previous experience of observers) can help inform decision making for future monitoring. For example, creation of a new survey team, including new observers, to increase the survey effort (particularly increasing the number of transects) would be preferable to surveying with only one group of experienced observers, who could not achieve the same level of survey effort.

Conclusions

Our results have brought new light to the conservation significance of the pampas deer population in Corrientes, compared with the other three remnant populations in Argentina. Santa Fe harbours a population not greater than 50 individuals (Pautasso *et al*. 2002; González *et al*. 2010). The population estimate for Buenos Aires Province was 247 ± 61 individuals (Vila 2006), and conversations with local experts indicated a decrease in numbers during recent years (Mario Beade, pers. comm.) Finally, Merino *et al*. (2011) estimated 731 ± 121 individuals for the main population nucleus in San Luis Province, and M. L. Merino (pers. comm.) gave an approximate estimate of 1000 pampas deer in the whole population. With this new data, Corrientes would be hosting the largest or second-largest population of pampas deer in Argentina, with an estimated number of 951–2351 individuals. Although these results should be corroborated with other census methods and further repetitions of the same transects, our findings concur with recent genetic analysis that identify the Corrientes population of pampas deer as the one maintaining the highest genetic diversity in Argentina (Raimondi 2013).

During the past 20 years, habitat loss through pine plantations has become the main potential threat for the species conservation within the region (Parera and Moreno 2000; Jiménez Pérez 2006; Jiménez Pérez *et al*. 2007; Srur *et al*. 2009). However, this has not hampered what appears to be a recovering population, most likely because of major improvements in law enforcement, private control of poachers, and human disease-prevention campaigns. Other *in situ* conservation measures are currently being undertaken, such as the creation of a private reserve (Guazutí-Ñú) of 535 ha (Fig. 1), acquired for pampas deer conservation by a conservation NGO (Fundación Flora y Fauna Argentina) in 2008. Along with this, conservation NGOs and the government are promoting the awareness of land owners and workers within the region, as well as producing a public awareness campaign about the species status and conservation (Jiménez Pérez *et al*. 2009; Dirección de Parques y Reservas 2011).

Additionally, since 2009, the organisation Conservation Land Trust has established a second population of pampas deer in Corrientes province, but inside a private reserve (San Alonso Reserve, 10 000 ha) located in the middle of the Iberá Nature Reserve and separated from the Aguapey region by 90 km of flooded lands. This reintroduced population was made up of animals translocated from the Aguapey. By October 2013, it was composed of 34–37 animals and it was rapidly increasing (Zamboni *et al.* 2015). Our results regarding the status of the Aguapey deer population and the recommendations for its monitoring will help evaluate *in situ* management actions and future decisions on the management and/or establishment of new pampas deer populations within other regions of Corrientes.

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