



Does the interface with plantation forests provide suitable habitat for axis deer (*Axis axis*) to avoid systematic hunting pressure in a protected area of north-eastern Argentina?

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Abstract

Axis deer (*Axis axis*), an introduced invasive species of growing concern around the globe, have rapidly expanded through the southern cone countries in South America. Despite increasing culling efforts over 14 years, axis deer remained abundant at El Palmar National Park in north-eastern Argentina. We tested whether this continued abundance possibly reflected control failures as a result of adjacent plantation forests providing a safe-haven refuge for deer. We carried out a cross-sectional survey of deer faecal pellet groups and tracks in 77 matched pairs of 25 m² plots deployed at random over the park–plantation interface and assessed the presence of deer trails along the 14.2-km wire fence between both land-use types. The relative odds of having at least one pellet group (occupancy) were 4.5 (95% CI 1.5 to 18.3) times higher among park plots than plantation plots. Using generalized linear mixed models, the relative odds of occupancy decreased significantly with increasing distance to the main permanent water course, but it was 83% lower in plantation plots than in the park plots. Principal component analysis of shrub cover, plant structure and plant height revealed greater shelter within the park. Deer trails were spatially aggregated up to 2300 m and were directly associated with deer occupancy. These results indicate that, in El Palmar National Park interface, plantation forests do not provide a refuge or selected habitat, and suggest instead that the environmental characteristics and diversity of habitats within the protected area are relevant for the effectiveness of the exotic ungulate management program.

Keywords Axis deer · Plantation forest · Habitat use · Invasive species · Protected areas · Spotted deer · Chital

Introduction

Biological invasions and habitat fragmentation are important drivers of global biodiversity loss (Mooney 2005). Human-dominated landscapes are more prone to disturbances, providing opportunities for new invasion events and facilitating the spread of established exotic populations (With 2002). Both factors may interact multiplicatively, making their simultaneous study relevant (Brook et al. 2008). In the case

of family Cervidae or cervids, one of the mammalian taxa with the highest proportion of successful invaders globally (Clout and Russell 2008), several species preferentially utilize plantations or disturbed forests rather than other natural habitats (Lantschner et al. 2013; Tejada-Cruz et al. 2009).

Tree plantations or plantation forests are considered one of the largest novel terrestrial ecosystems in the world (Lindenmayer et al. 2015). The Food and Agriculture Organization registered a worldwide increase of 55.8 million ha in the period 1990–2020

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for this land-use type (FAO 2020). As a result, several assessments evaluated the impact of tree plantations on biodiversity, particularly mammals (Coelho et al. 2014; Cravino and Brazeiro 2021; Iezzi et al. 2018, 2020; Ramesh et al. 2016; Ramírez-Mejía and Sánchez 2016). Red deer (*Cervus elaphus*) and fallow deer (*Dama dama*), two mixed-grazer species, made greater utilization of plantation forests in their early-to-medium stages (e.g. establishment, open-thicket, pre-thicket) and unplanted areas, such as firebreaks in the plantation forests of Europe (Borkowski and Pudielko 2007; Catt and Staines 1987; Latham et al. 1996; Staines and Welch 1984).

Axis deer, also known as chital or Indian spotted deer, have been widely introduced around the globe (Long 2003). It reached the status of an invasive species and a cause of concern in Hawaii and Australia (Page et al. 2008) and is considered of moderate risk in Europe (Nentwig et al. 2017; Scalera et al. 2020). Axis deer were categorized as an invasive species in the Andaman Islands (India), where they caused negative impacts on seedling and sapling survival and vegetative cover, particularly of the understory (Ali 2004; Ali and Pelkey 2013). Axis deer have a large capacity to adapt to variable environments and take advantage of landscape heterogeneity (e.g. a forest-grassland mosaic) for shelter against predators and forage (Bhattarai and Kindlmann 2012; Moe and Wegge 1994; Tak and Lamba 1984). Hence, they are typically described as an edge species (Dinerstein 1980).

The distribution of axis deer mainly depends on water courses (Mishra 1982; Forsyth et al. 2019). They typically spend most of their time budget in riparian forests and move daily between grassland and forest habitats through the same paths, leaving evidence of their passage through tracks and formation of trails (Graf and Nichols 1966; Mishra 1982; Tak and Lamba 1984). Axis deer are mixed grazer–browsers (Ahrestani et al. 2016); they consume tender shoots and short grasses (Graf and Nichols 1966), and selectively use grassland patches subjected to disturbances that keep the grass short (Mishra 1982; Moe and Wegge 1997). Like many other deer species (VerCauteren et al. 2006), axis deer movement is not restricted by livestock fences (Graf and Nichols 1966).

Axis deer are the exotic cervid with the highest number of location records in the Neotropics (da Rosa et al. 2020), with recent establishment in southern Brazil (da Rosa et al. 2017) and range expansion in Argentina (Tellarini et al. 2019) and Uruguay (Pereira-Garbero et al. 2013). This region has suffered a severe land-use conversion from native forests or grasslands to plantation forests of pine and eucalyptus over the last 30 years (Kröger 2012; Miñarro and Bilenca 2008). Little is known about the relationship between axis deer and plantation forests in both its native and exotic ranges (see Graf and Nichols 1966 and Mathur et al. 2011 for eucalyptus plantations), unlike for other forest-dwelling deer whose diet, abundance, and habitat use in plantation forests have been extensively investigated (Latham et al. 1996; Borkowski and Pudielko 2007).

Axis deer were first introduced to southern Argentina in 1930 (Chebez and Rodríguez 2014), and apparently reached El Palmar National Park (hereafter the park) in the north-east region over the early 1980s. Wild boar (*Sus scrofa*), another exotic species in the park, posed a serious threat to the conservation of yatay palm trees (*Butia yatay*) as it consumes its seeds, saplings and fruits (Ballari et al. 2015). The concern for these species is no surprise: a recent systematic review of the global impacts of alien ungulates, 26 of the 27 species established worldwide caused harmful effects on the ecosystem (Volery et al. 2021). Consequently, the park initiated a long-term management program involving the lethal removal of both exotic ungulates. Control actions mainly included controlled still shooting from elevated hunting blinds distributed uniformly across the protected area, hunting with dogs and occasional shooting from vehicles from 2006 on (Gürtler et al. 2017). These efforts effectively reduced and then kept wild boar at low population abundance compatible with minimum levels of damage to soil structure (rooting), while the relative abundance of axis deer continued to increase throughout the decade (Gürtler et al. 2017, 2018).

The park's borders contain firebreaks with short grass along both sides of the fence line, which divides two land-use types differing in hunting pressure and environmental characteristics. Axis deer may seek shelter from hunting pressure in adjacent plantation forests and then return to forage within the park; if so, plantation forests may play a role in the steady population increase of axis deer within the park. However, the relative occurrence of axis deer within plantation forests has not been assessed. Local foresters frequently complained to us about axis deer functioning as a magnet for illegal hunters who used firearms with or without dogs and eventually created fire hazards (e.g. campfires). Given the apparent selectivity of axis deer for using disturbed (Moe and Wegge 1997) and forest-mosaic landscapes (Bhattarai and Kindlmann 2012), a robust understanding of their habitat use patterns may contribute to better management practices in protected areas.

Here, we assessed axis deer habitat use (indexed by faecal pellet groups, tracks and trails) in the interface between the park and adjacent plantation forests. We define deer occupancy as the presence of at least one faecal pellet group per plot following Lele et al. (2013). We hypothesize that the interface is an optimal edge habitat for axis deer by providing easy access to shelter (e.g. plantation forests) and forage (e.g. park) (Moe and Wegge 1994), as seen for other deer species (Hanley 1983), and predict that (1) deer occupancy will decrease with greater distance from the fence, and (2) occupancy will reach similar values in both land-use types since the fence used to contain livestock does not to restrict deer movement (VerCauteren et al. 2006). Second, we hypothesize that habitat use in the interface was similar to the one described in its native range (i.e. Mishra 1982;

Tak and Lamba 1984; Moe and Wegge 1994), and predict that (3) axis deer occupancy will peak in proximity to permanent water courses (Forsyth et al. 2019), and (4) axis deer will mainly occupy more than one habitat type (e.g. forests and grasslands) based on their typical occurrence in a forest-grassland mosaic (Bhattarai and Kindlmann 2012). We also test whether the spatial distribution of axis deer trails along the fence is clustered, uniform or random.

Methods

Study area

El Palmar National Park approximately spans 8500 ha with one of the largest areas of yatay palm trees (*Butia yatay*) in Argentina (Batista et al. 2014). Following the suppression of spontaneous fires and exclusion of cattle in 1970, several exotic tree species and native shrubs increasingly expanded, up to covering approximately 3800 ha, most of which are over a 2-km-wide stretch on the eastern section. The park is enclosed by the Uruguay River, a highway (route 14), crop fields (e.g. soybean, corn and sorghum) and plantation forests on the southern and northern borders. The current study site is the northern interface (hereafter interface; Fig. 1) between the park and plantation forests, which are divided by a wire fence. According to the Köppen-Geiger classification, the area is in a subtropical region with no dry season (Peel et al. 2007). The annual mean temperature is moderate (17.9 °C) although it can reach

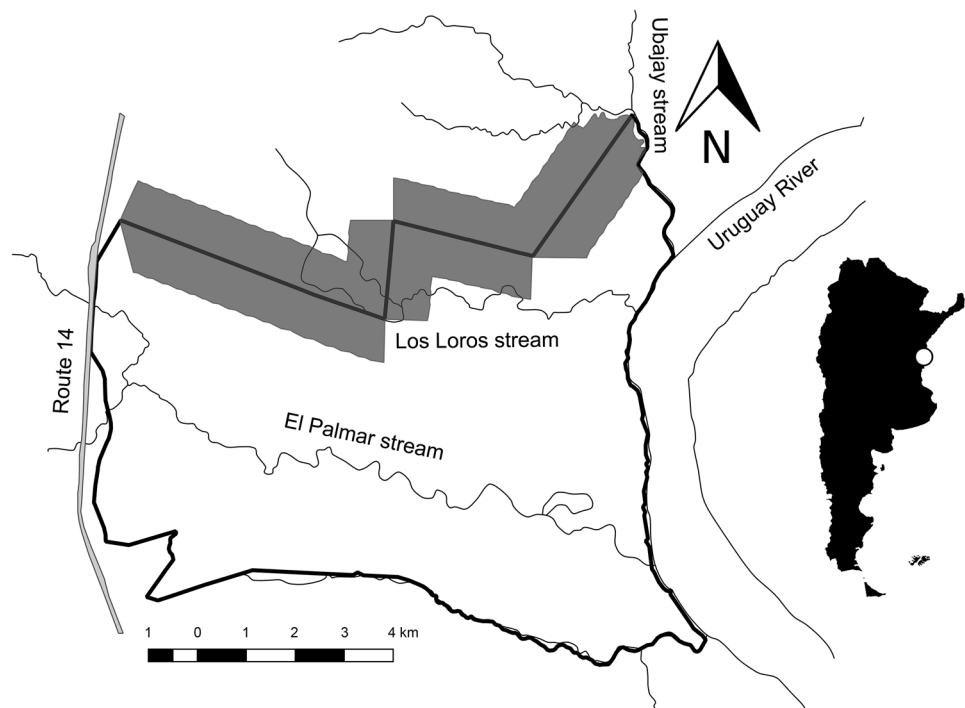
38.2 °C (maximum recorded) in summer and −4.2 °C (minimum recorded) in winter based on the park's weather station records (period 2015–2018). Rainfall occurs throughout the year (annual mean precipitation over 2015–2018, 1375 mm). Fieldwork was carried out in January–February 2019 during an intense El Niño cycle with slightly milder temperatures than in previous years.

Most of the plantation forests consisted of *Eucalyptus grandis* (occasionally *E. dunnii*) interspersed with grasslands used by cattle. The youngest plantations (less than or equal to 1 year old at the time of the survey) were hybrids of *E. grandis* and *E. camaldulensis*. There were a few fields planted with mature *Pinus taeda* or *P. elliotii*. Cattle was used to keep the grass short to prevent fires; they usually grazed in the firebreaks or unplanted fields and were rarely seen inside mature plantations. Within the park, the northern section mainly consisted of grasslands and shrublands, and in the eastern section exotic-dominated forests prevailed (hereafter mixed forests). The fence between park and plantations consisted of 6–8 wire strands (1 or 2 were barbed wires) held in place with wooden poles (approximate height, 1–1.5 m).

Study design and data collection

We carried out a cross-sectional survey of deer faecal pellet groups and tracks in 77 matched pairs of 25 m² plots deployed over the park–plantation interface, which covered approximately 2174 ha. The area of the plantation forests was divided into a grid of 5 by 5 m² plots using QGIS Development Team (2018) and classified into four strata: mature

Fig. 1 Location of El Palmar National Park. Fieldwork was conducted in the grey area, which comprised the interface between the park and the plantation forests



plantations of eucalyptus or pine trees (70.4% cover of plantation forest section); plantations of eucalyptus less than or equal to 1 year of age (6.7%); firebreaks (8.5%); and natural fields, mainly containing grasslands or shrub lands grazed by cattle (14.4%). Dirt roads and firebreaks were considered as one stratum as they were long and narrow landscape units between or within plantations. Then, we selected a simple random sample of plots. Each selected plot located in the plantation forests was matched to another unit within the park located at the same minimum distance (north–south or east–west) to the fence using QGIS Development Team (2018). We used a matched pair design (Morrison et al. 2008) to control for potential effects of distance to the fence as a confounding factor. The first three plots surveyed did not perfectly match the paired unit as we used field reference points to reach them. Subsequent plots were located with a GPS.

Plots were surveyed for axis deer faecal pellets and tracks using the “standing crop” method (Putman 1984) in January–February 2019. Control actions of axis deer and wild boar had been halted as of December 20, 2018 because of summer holidays. Faecal pellets were recorded as a group when they contained six or more droppings. Axis deer faecal pellet groups are typically small, bullet shaped and end in a rounded tip. Individual deer tracks were considered as a one-detection event. Another sympatric deer species in the park, the smaller brown brocket deer (*Mazama gouazoubira*), has tracks and faecal pellets hard to distinguish from those of axis deer fawns. However, brown brocket deer have smaller tracks, use latrines, and its abundance was at least two orders of magnitude lower than that of axis deer as determined by sighting and camera-trap surveys (Nicosia et al. 2021).

We measured four environmental variables at each plot location. Habitat type took into account the predominant vegetal physiognomy and type of management (particularly important for plantation forests). Plant structure was measured by vertical plant cover following Nudds (1977). Horizontal or ground plant cover (hereafter plant cover) and plant height were measured by the pin-point method (Mateucci and Colma 1982). The pin could fall in any of the following ground cover categories: bare ground, leaf litter, grass, herbaceous species, woody species, palm tree, fern, shrub and road. Distance from the plots to the nearest stream, the Uruguay River and the fence were measured with QGIS using the NNJoin complement.

The 14.2-km-long north fence was surveyed for axis deer trails by a team of three people on horseback in January 2019. Trails were only considered when they crossed the fence at an approximately right angle and continued on both sides. Trampled grass, faecal pellets, hair or mud stuck to the wire were used as supplementary evidence of crossings. Deer trails were georeferenced with a Garmin GPS and the assumed direction noted. The narrow portion of the tracks pointed to where the deer was heading (directionality).

Data analysis

We assessed the association between the presence of axis deer sign (tracks versus faecal pellet groups) within the same plot and the presence of axis deer pellet groups by land-use type (park versus plantation forests) using a two-tailed McNemar's χ^2 test. The strength of the association was measured by means of the odds ratio (OR) for a matched paired study design and its 95% confidence interval (CI). The observed frequency distribution of faecal pellet groups was fitted to a Poisson and negative binomial distribution, and a likelihood ratio test was used to decide which distribution fitted the data best.

We used generalized linear mixed models (GLMM) with binomial distribution to assess the relation of deer occupancy as a function of distance to the fence, Uruguay River and the nearest stream, habitat type, and land-use type. The response variable was a binary variable rather than the number of pellet groups per plot as few plots had more than one pellet group. Faecal pellet groups have frequently been used as an index of habitat use in several deer species (Neff 1968; Putman 1984). Although the interpretation of deer pellet groups has been somewhat controversial, there is some consensus that they usually indicate places where individuals spend more time (Neff 1968). We chose not to use deer tracks as a habitat-use index because plant cover and habitat type affected differentially the chance of recording any deer track (see “Results”).

The first model only included habitat type and each pair of plots as a random factor. We excluded from this analysis two categories (natural fields, flood-prone lowlands) that did not record any pellet group, and used Tukey's test to contrast habitat types by pairs. The second model included land-use type (park versus plantation forests), distance to the fence, distance to the Uruguay River and distance to the nearest stream. Distance variables were standardised prior to analysis. Each pair of plots was included as a random factor. The goodness of fit of both models to the data was measured by the percentage of explained deviance and Hosmer–Lemeshow test.

A principal component analysis (PCA) was performed with nine plant cover categories, plant height (averaging the measurements recorded by the pin-point method per plot), and plant structure in order to better describe land-use types (plantation forests and park). All variables were standardised before analysis. The original matrix had a dimension of 154 by 11, and the correlation matrix was 11 by 11.

The spatial distribution of axis deer trails along the fence was assessed as a point pattern on a line using Ripley's K global function for one dimension. Point pattern analysis along lineal networks has been used for investigating wildlife collisions in highways and railways (Neumann et al. 2012); it can be used to identify hotspots and provides useful

information for management (Clevenger et al. 2001). For the determination of the scale at which the estimated K was compatible with a clustered, uniform or random distribution of trails, K values were calculated for 10,000 Monte Carlo iterations based on a homogeneous Poisson process.

We described the spatial association between faecal pellet groups in plots and trails through the fence. We used QGIS to obtain a heat map of the probability of occupancy across the whole study area. We used an inverse distance weighting (IDW) interpolation with a weighting factor of 3. The input for this analysis was the GLMM-based predicted probabilities of pellet group presence in all 154 plots.

All statistical analyses were carried out in the R environment (R Core Team 2020). The following packages were used: lme4 v. 1.1.23 (Bates et al. 2015), ResourceSelection v. 0.3.5 (Lele et al. 2019), multcomp v. 1.4.13 (Hothorn et al. 2008) for parametric models; MASS v. 7.3.53 (Venables and Ripley 2002), lmtest v. 0.9.38 (Zeileis and Hothorn 2002) for comparing fits to Poisson and negative binomial distributions; vegan v. 2.5.6 (Oksanen et al. 2019) for PCA analysis; rgdal v. 1.5.16 (Bivand et al. 2018), maptools v. 1.0.2 (Bivand and Lewin-Koh 2019), spatstat v. 1.64.1 (Baddeley and Turner 2005), riverdist v. 0.15.3 (Tyers 2017) for spatial analysis of trails; and ggeffects v. 0.16.0 (Lüdecke 2018a), sjPlot 2.8.4 (Lüdecke 2018b), ggplot2 v. 3.3.2 (Wickham 2016) for graphics; and QGIS Development Team 3.2 (2018) for maps and interpolation analysis.

Results

Deer occupancy on the interface

Most of the plots with any deer sign registered faecal pellet groups and no tracks (*McNemar's test*: $\chi^2 = 3.90$, 1 *df*, $p = 0.048$; Fig. 2). At least one pellet group but no deer tracks occurred in 21 plots; the reverse was recorded in 10 plots; both types of sign co-occurred in 5 plots, and none in 118 plots. The relative odds of having a pellet group relative to a deer track were 2.1 (95% CI 0.95 to 4.99) times higher across all study plots. In total, 23.4% of the 154 plots inspected had either pellet groups, deer tracks or both. The mean number of pellet groups per 25 m² plot was 1.79 (SE 1.30). The negative binomial distribution with parameter $k = 0.05$ (SE 0.01) fitted the number of pellet groups per plot better than a Poisson distribution (*Likelihood ratio test*: Poisson LogLik = -1049.6, negative binomial LogLik = -135.0, $p < 0.001$).

The relative odds of having a pellet group were 4.5 (95% CI 1.5 to 18.3) times higher among park plots than plantation plots. The percentage of plots with at least one faecal pellet group present was highly significantly greater in the park (26.0%) than in adjacent plantation forests (7.8%) (*exact McNemar's test*: 1 *df*, $p = 0.004$; Table 1).

The percentage of plots with faecal pellet groups substantially varied with habitat type (Fig. 3). Mixed forests had the

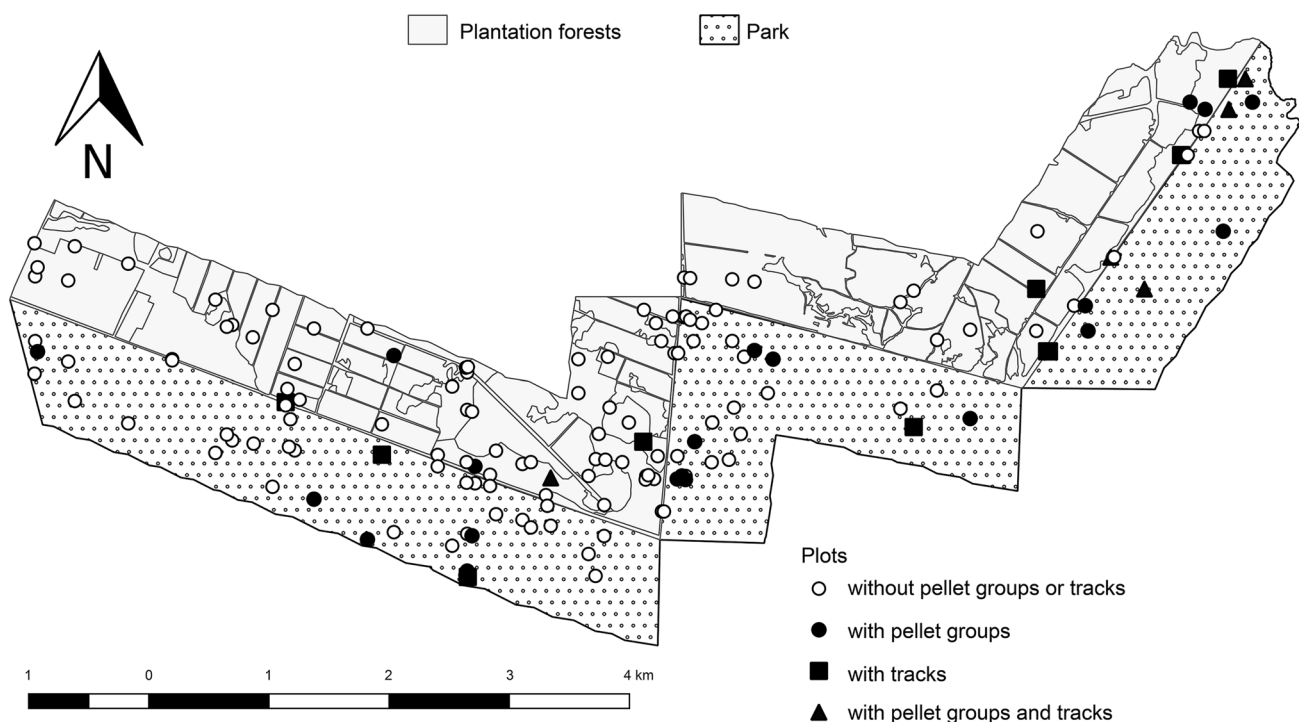


Fig. 2 Location of plots with type of sign recorded in the park–plantation forest interface

Table 1 Association between the presence/absence of deer pellet groups in matched pairs of plots and land-use type

Park	Plantation forests (%)		
	No	Yes	Total
No	53 (68.8)	4 (5.2)	57 (74.0)
Yes	18 (23.4)	2 (2.6)	20 (26.0)
Total	71 (92.2)	6 (7.8)	77

maximum percentage of occupied plots (mean \pm SE 60 ± 22), followed by grasslands (26 ± 8) and shrublands (25 ± 8), all within the park. Other habitat types, all within plantation forests, followed in decreasing order: firebreaks (17 ± 9), young plantation forests (10 ± 7) and mature plantation forests (4 ± 4). Natural fields and flood-prone lowlands had no plot with a deer pellet group. When these two apparently unused habitats were excluded from the analysis, the model explained 17.9% of the deviance and had evidence of poor fit (*Hosmer–Lemeshow test*: $\chi^2 = 34.5$, $df = 8$, $p < 0.001$). No significant differences were found between categories (*Tukey's test*: $p > 0.05$).

Using GLMM, deer occupancy significantly decreased with distance from the Uruguay River but increased with distance from the nearest minor stream, and overall was 83% lower in plantation forest plots (Fig. 4; Table 2). The odds ratio for the distance to the fence of each pair of plots was not significantly different from 1 (Table 2). This model explained 19.1% of the deviance and did not show evidence of poor fit (*Hosmer–Lemeshow test*: $\chi^2 = 8.96$; $df = 8$, $p = 0.35$). None of the six possible two-way interaction terms were significant at the 0.05 alpha level.

The first four components of the PCA explained 58% of the existing variation in environmental variables. The

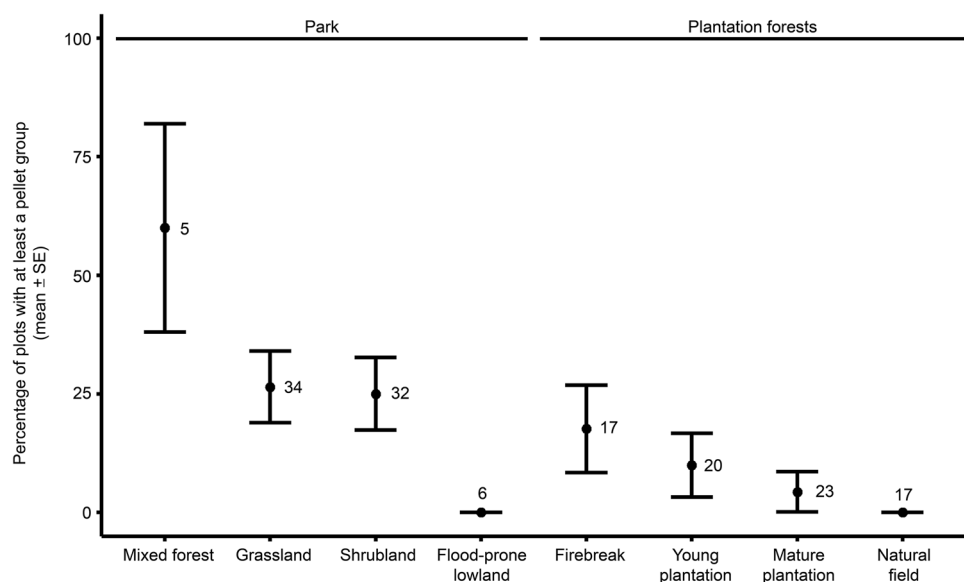
ordering of plots according to measured environmental variables was consistent with the land-use type in which the plots were located (Fig. 5). The first component contributed the most to the separation of these two groups and explained 21% of the variance; it was positively correlated with plant height, plant structure and shrub cover, and negatively associated with bare ground and leaf litter cover. In general, the park presented denser plant structure, higher plant height, greater shrub cover, less bare ground and less leaf litter cover compared to plantation forests.

Movement through the fence

A total of 75 axis deer trails were recorded along the 14.2 km fence (mean, 5.3 trails per km). Trails with a large number of deer tracks and no grass indicated more intensive use (10.7% of the total). Twenty-seven (36%) trails had tracks directed exclusively into the plantation forests; 24 (32%) had tracks in both directions; 22 (29%) had tracks directed exclusively into the park, and in 2 (3%) cases the assessment was inconclusive.

Deer trails were clustered up to 2300 m according to Ripley's K global analysis for one dimension and were distributed uniformly between 4700 and 5800 m (Fig. 6a). The histogram of distances between all deer trails displays a similar pattern (Fig. 6b), with groups of trails at regular intervals of 5000–8000 m; within these clusters distances between trails were less than 1000 m apart.

Deer occupancy (described by faecal pellet groups) and trails were spatially associated (Fig. 7). The probability of occupancy was greater where most trails were, particularly in the eastern section, which contained 45% of all trails. This association was heavily influenced by park occupancy values rather than by those in adjacent plantation forests, which always displayed a lighter colour (Fig. 7).

Fig. 3 Percentage of plots that had at least one deer faecal pellet group (mean) according to habitat type. Error bars represent the standard error (SE) of proportion multiplied by 100. The numbers associated with the bars represent the number of sampled plots per habitat type

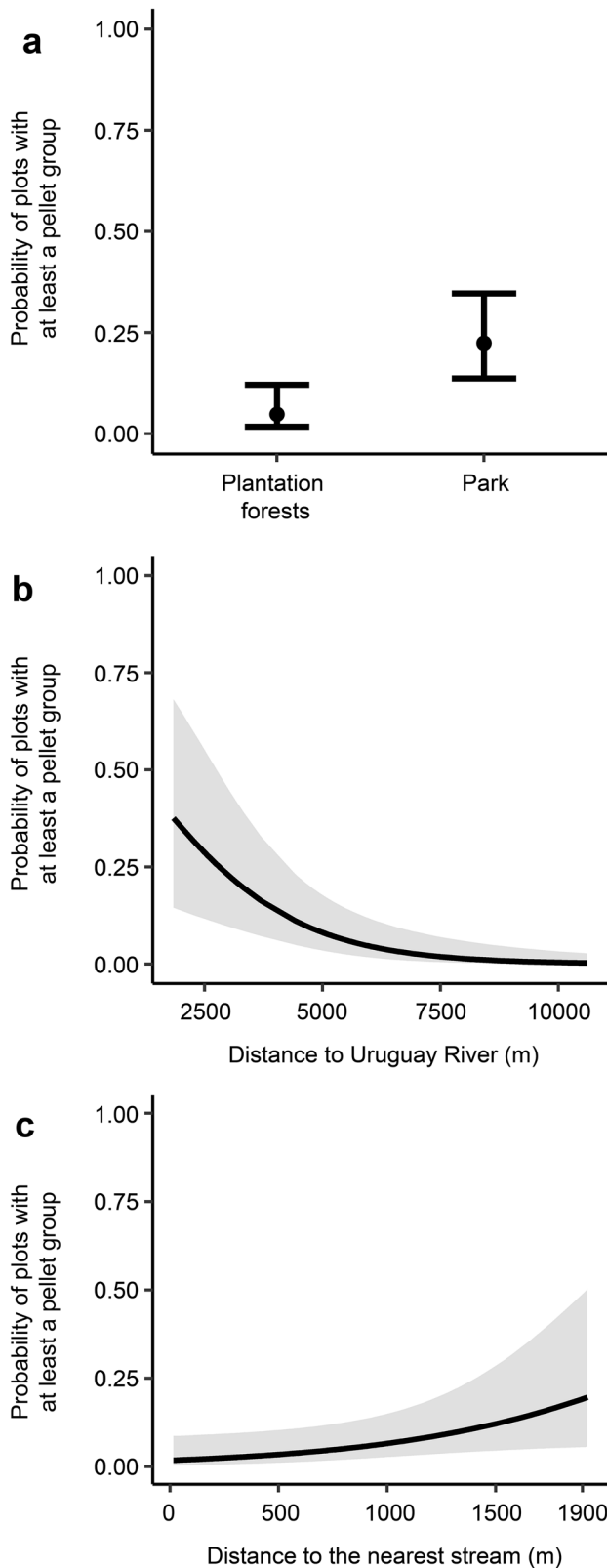


Fig. 4 Predicted values and 95% confidence intervals obtained from the generalized linear mixed model of the probability of finding at least one deer faecal pellet group per 25 m²-plot as a function of: **a** land-use type (plantation forests versus park), **b** distance to the Uruguay River and **c** distance to the nearest stream

Table 2 Generalized linear mixed model with binomial probability distribution and plot pair as a random factor. The response variable was the presence of at least one deer faecal pellet group per 25 m² plot (i.e. occupancy). Distance variables were standardised. The reference level in land-use type is plantation forest

Predictors	OR (95% CI)	<i>p</i>
Intercept	0.29 (0.14–0.51)	<0.001
Distance to nearest stream	1.99 (1.04–3.91)	0.038
Distance to Uruguay River	0.26 (0.11–0.52)	<0.001
Distance to fence	1.33 (0.83–2.27)	0.244
Land-use type	0.17 (0.05–0.49)	0.002

Discussion

Our study documents that deer occupancy was five times greater within the protected area than in adjacent plantation forests, and distance to the fence was not associated negatively with occupancy. Both findings reject the hypothesis that the interface may provide optimal edge habitat for axis deer (predictions 1 and 2). Second, deer occupancy was positively associated with proximity to the main permanent water course, supporting prediction 3. Third, occupancy apparently differed between habitat types: both mixed forests and grasslands were the most frequently occupied types,

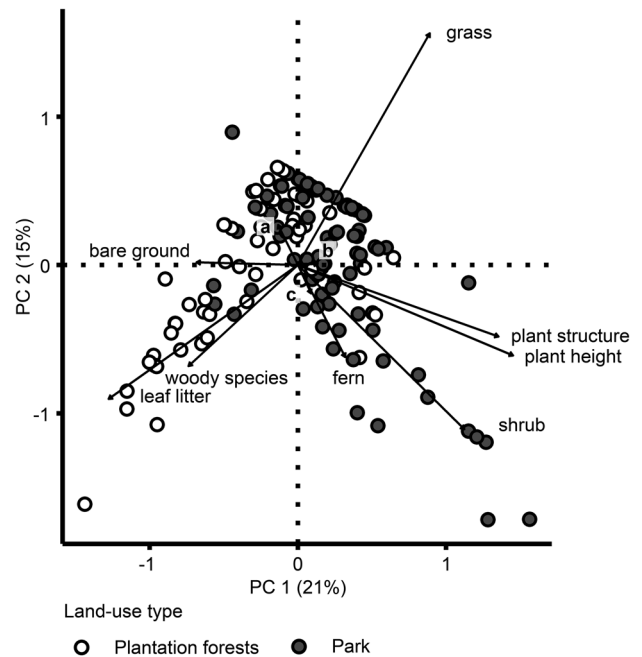
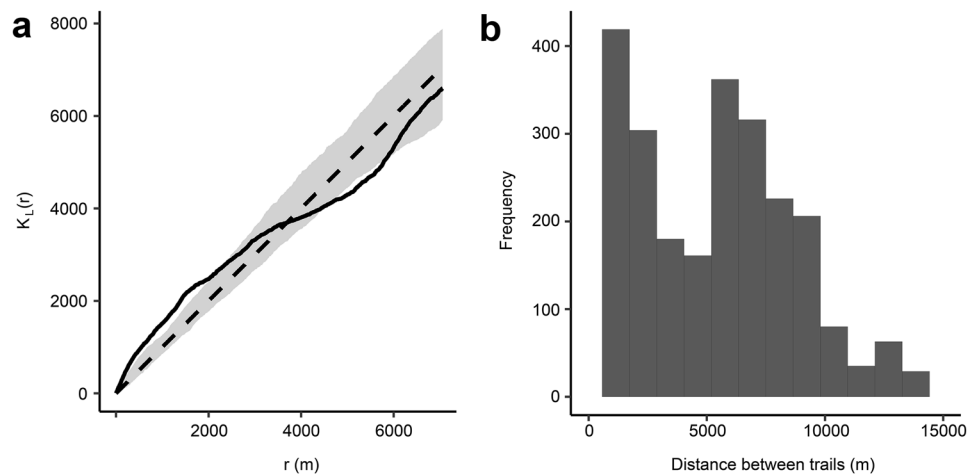


Fig. 5 Biplot for the two first main axes (PC1 and PC2) obtained from the principal component analysis of the matrix ($n=154$, circles), and loadings (arrows) showing the relative contribution of selected environmental variables ($p=11$). The letters correspond to the following ground cover categories: (a) road, (b) palm tree and (c) herbaceous species

Fig. 6 **a** One-dimension global spatial analysis for deer trails along the fence. The black line represents the observed statistic, the dashed line represents the expected value from complete spatial randomness, and the grey area the confidence envelope from 10,000 iterations. **b** Distribution of distances between deer trails along the fence.



although not significantly so, providing partial support for prediction 4.

Our results clearly contrast with habitat use by other exotic cervids under hunting pressure. In New Zealand, the abundance of red deer decreased in zones where they were more vulnerable to the hunting method used (Challies 1977), whereas in Australia, the frequency of sambar deer (*Rusa unicolor*) pellets was half as much in sections closer to the hunting epicentre (Bennett et al. 2015). In Japan, native sika deer (*Cervus nippon*) decreased in the centre of the study area under culling operations (Enoki et al. 2016); and in Scotland, red deer abundance was negatively related to

culling (Latham et al. 1997). In contrast, our study shows that axis deer preferentially used habitats within the park despite systematic hunting pressure and increasing harvest over more than a decade. The current systematic hunting pressure and methods have been insufficient to hold deer densities at current levels, let alone reduce them (i.e. the culling rate appears to be less than the population growth rate).

Park premises and plantation forests mainly differed in plant structure and cover, with greater shrublands and vertical cover within the park. These variables imply shelter availability (e.g. Mishra 1982; Tak and Lamba 1984; Graf

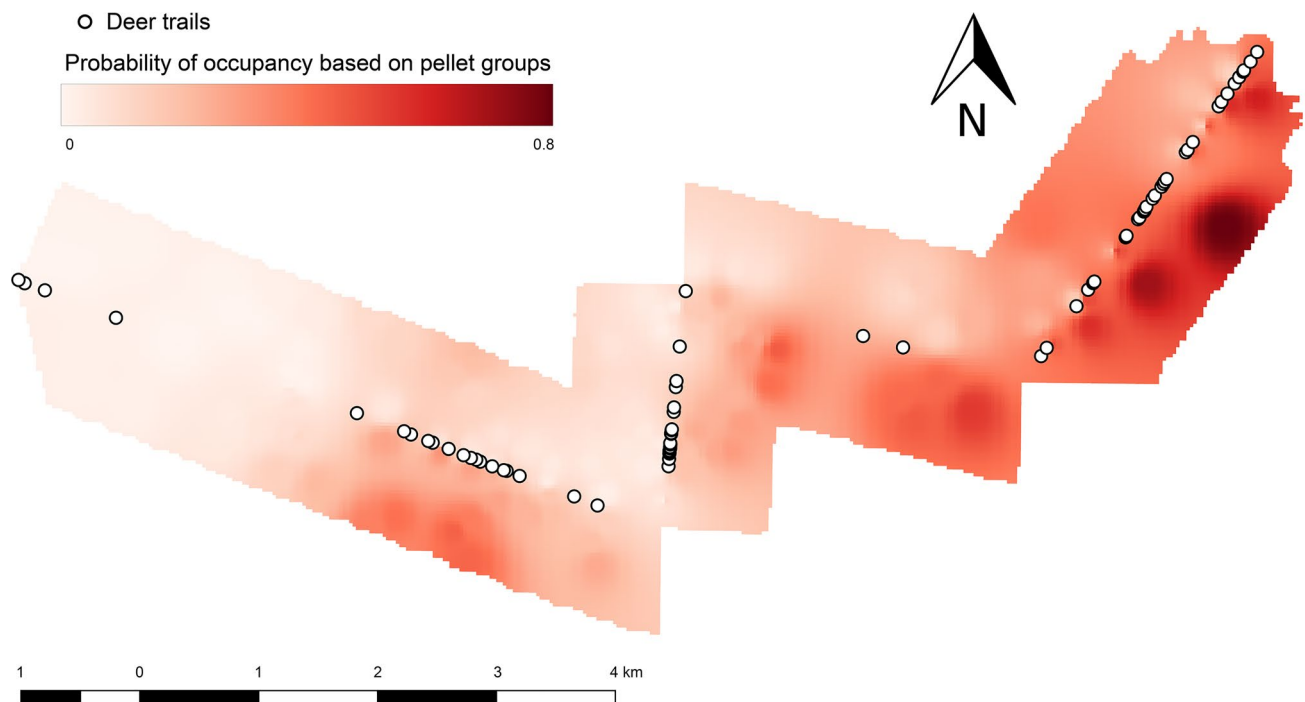


Fig. 7 Heat map with the probability of occupancy based on pellet groups across the interface and location of deer trails (white dots)

and Nichols 1966). Forage availability, which in studies elsewhere has sometimes explained deer occupancy (Kiffner and Lee 2019), was qualitatively greater within the park. In Europe, red deer and fallow deer utilized early-to-medium-stage plantation forests and unplanted areas more often than any other habitat type, including mature plantation forests and closed-canopy habitats (Borkowski and Pudelko 2007; Catt and Staines 1987; Latham et al. 1996; Staines and Welch 1984). In the Mediterranean, red deer selected shrublands and avoided eucalyptus plantations (Alves et al. 2014), whereas in Uruguay, axis deer under hunting pressure used natural forests more often than eucalyptus plantations (Ruiz 2017).

Deer occupancy peaked within park premises; this puts the park, with its diversity of suitable habitats, at the centre of the problem of invasive exotic ungulates. The park has undergone a several-decades-long process of lignification mainly due to the steady expansion of exotic trees and shrubs following the suppression of disturbance regimes that had prevented the palm tree savannah from turning into a dense shrubland or forest (Rolhauser et al. 2011). These processes provided axis deer with suitable shelter habitats adjacent to grasslands and mixed shrublands, especially on the eastern section by the Uruguay River, where axis deer were more abundant as determined by hunting-based indices and camera-trap surveys (Nicosia et al. 2021). Figure 7 also shows an increasing trend in the density of deer pellet groups and trails with decreasing distance to the Uruguay River. At a regional level, large-scale landscape shifts to plantation forests have provided corridors along water courses, which likely facilitated the expansion of axis deer through north-eastern Argentina (Tellarini et al. 2019).

We recorded a positive association between deer occupancy and proximity to the Uruguay River but not to permanent streams. Although both variables describe distances to permanent water courses, they were measured at different spatial scales. The distance to the Uruguay River is directly correlated with the humidity gradient that influences habitat types and plant communities. Although little represented within the interface, the natural forest was one of the habitats most used by axis deer elsewhere (e.g. Mishra 1982; Graf and Nichols 1966) and fully covered the eastern section of the park by the Uruguay River. The positive association between axis deer and water courses in the park is also consistent with evidence recorded elsewhere within its native (Mishra 1982) and exotic ranges (Graf and Nichols 1966; Forsyth et al. 2019). Furthermore, the park's boundary to the West is a high-traffic flow highway, which axis deer may avoid, as reported for other deer species (D'Amico et al. 2016).

The negative association between axis deer occupancy and proximity to permanent streams occurred on a local scale. The main water courses ran from West to East whereas secondary, smaller streams ran from north to south (Batista

et al. 2014). This pattern partly occurred in the interface, especially in the north-eastern section. The secondary streams have no defined channel, and the surface run-off to permanent water courses creates flood-prone lowlands in which no plot contained a deer pellet group. Thus, distance to the nearest streams was spatially associated with flood-prone lowlands. Perhaps the detectability or durability of deer pellet groups in flood-prone lowlands was lower than in other habitat types, or axis deer likely avoided lowlands as in its native range (Moe and Wegge 1994).

The movement of axis deer through the fence was evinced by conspicuous, multiple deer trails; whether the fence exerted a partial deterrent effect remains to be determined. This pattern is consistent with the characteristic behaviour of cervids in relation to livestock fences (VerCauteren et al. 2006). Because most deer trails occurred in sites where the fence was maintained in good condition, clustering of trails was more likely related to both the social nature of axis deer (Tak and Lamba 1984) and the habitat types at both sides of the fence. Surprisingly, we recorded fewer deer trails close to natural fields (with plenty of forage available) than expected based on their relative availability, whereas trails occurred more often than expected in the neighbourhood of firebreaks and young plantation forests. Although a substantial fraction of deer trails (36%) went inside them, the plantation forest plots rarely had pellet groups. Whether the deer directly passed through these forests and their rate of movement across the fence remains unknown.

Our analysis of deer habitat use is limited by the fact that it is based on pellet-group presence/absence, not absolute deer abundance. Although the occurrence of deer pellet groups can be affected by differential decay rates with varying rainfall, habitat type, diet and deer species (Davis and Coulson 2016; Neff 1968; Putman 1984), the use of faecal pellets implicitly widened the time window of observations as they may last several months. For present purposes, absolute estimates of deer density may be considered “unnecessary luxuries” (Caughley 1977), whereas faecal-pellet counts correlated closely with other indices (Nicosia et al. 2021) and provided a reasonable proxy for deer abundance. Although there were obvious differences in forage availability between the park and plantation forests, future studies should quantify it. Another limitation of our cross-sectional study is that it returned a snapshot of a dynamic system that may display seasonal or multi-year variations. Using a stratified sampling design would have allowed us to obtain more precise estimates of deer occupancy by type of habitat at the expense of a substantial increase in field labour.

Management implications

Adjacent plantation forests did not provide axis deer a major haven from long-term, systematic culling operations in the park. To substantially reduce their abundance to any defined

target level, the management programme needs to determine ways of increasing the effectiveness of deer removal methods and ideally combine them with habitat restoration practices and management of invasive exotic trees and shrubs.

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Declarations

Ethics approval Not applicable.

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