

# Differential long-term impacts of a management control program of axis deer and wild boar in a protected area of north-eastern Argentina

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**Abstract** Exotic ungulates are among the top global invasive mammals and a threat to biodiversity. Axis deer (*Axis axis*) and wild boar (*Sus scrofa*) are of increasing concern in multiple regions. A management program reduced wild boar abundance and soil damage below target levels through controlled still shooting from watchtowers and dog-hunting performed by recreational hunters at El Palmar National Park, Argentina. Here we assess program impacts on axis deer over a 10-year period in which 2380 deer were dispatched, and document two largely unexpected outcomes: increasing axis deer abundance

toward a plateau, and a strong inverse correlation between deer and wild boar numbers. Unlike the initial steep decline and subsequent stabilization of wild boar, deer abundance indexed by standardized catch-per-unit-effort increased at 37.6% per year over 0–5 years post-intervention (YPI) and stabilized from 7 YPI on when still-shooting effort averaged 948 hunting party-hours per quarter. Deer catch was non-linearly related to still-shooting effort. Timing of deer and boar catches did not differ significantly regardless of sex, season and YPI. Catch-per-unit-effort indices and nightly spotlight deer counts showed similarly increasing trends. The fraction of older adult deer declined over 0–4 YPI and remained stable thereafter. Sex ratios were consistently skewed toward males only among older adults. Failure to reduce deer abundance may be explained by several major

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processes: protracted exponential growth of the deer population after park invasion; deer regional expansion with increasing immigration; insufficient sex- and stage-biased hunting mortality, and competitor (and perhaps predator) release from wild boar.

**Keywords** Protected areas · Invasion biology · Sustainability · Ungulate · Population dynamics · Wildlife management

## Introduction

Invasive exotic species play a major role in the current biodiversity crisis (Spear and Chown 2009). Red deer (*Cervus elaphus*, Linnaeus 1758) are among the top invasive species (Lowe et al. 2004), but several other species of Cervidae have been introduced to various continents and oceanic islands for venison, game hunting and aesthetic appreciation (Dolman and Wäber 2008). Exotic ungulates are frequently viewed both as a desired game animal and an undesired pest at the same location (Choquenot et al. 1996; Davis et al. 2016). However, overabundant deer, either exotic or native, cause significant direct impacts on vegetation and indirect effects on fauna and ecosystem processes (Côté et al. 2004; Davis et al. 2016; Waller and Alverson 1997; Flueck et al. 2003; Simberloff et al. 2003).

Another example of an invasive ungulate is Chital or Indian spotted deer (*Axis axis* Erxleben 1777), a moderately large-sized deer native to the Indian subcontinent which has been introduced to Australia, New Zealand, USA, Argentina and other countries (Duckworth et al. 2015). Axis deer often form large herds that persist in defined areas and reach high annual population growth rates (range 20–30%), with densities averaging 3–50 and up to 200 per km<sup>2</sup> in its native range (Schaller 1967; Duckworth et al. 2015). Axis deer are typically associated with forest and grasslands interfaces but are highly adaptable to a wide range of habitats and changing conditions, including suburban settings (Duckworth et al. 2015). They are generalist grazers that also browse leaves, stems, fruits, seeds, flowers and bark when the preferred food items are scarce or during droughts (Elliott and Barrett 1985; Anon 2016). As in other deer species, bucks frequently cause secondary infections

and tree death through antler rubbing on the bark and thus interfere with forest regeneration (Côté et al. 2004). Trampling of native vegetation, creation of trails that may lead to increasing erosion and runoff, competition with other native grazers and livestock, crop damage, pathogen transmission (including bovine tuberculosis) and vehicle-axis deer collisions have been described both in the native and introduced range (Hess et al. 2015).

These serious impacts warranted launching eradication or control-in-perpetuity programs of axis deer in island and continental settings (e.g., Hawaii, California, New Zealand) (Gogan et al. 2001; Hess et al. 2015; Nugent and Choquenot 2004). The most successful control strategies for axis deer to date are believed to be fencing and ground shooting including commercial harvesting, state-funded culling and sport hunting or a combination thereof (Gogan et al. 2001; Nugent and Choquenot 2004; Davis et al. 2016). Deer hunting using trained dogs caused much greater mortality and was less selective than still-shooting (Novak et al. 1991), but dogs also caused greater disturbance which decreased deer sighting rates (Godwin et al. 2013). Fertility reduction (contraception) and non-lethal removal have played marginal roles (Davis et al. 2016).

In southern South America, axis deer were introduced to Argentina on multiple occasions and locations since 1906, and then largely expanded their range through sections of Patagonia, mid- and north-eastern Argentina (Novillo and Ojeda 2008, and references therein). They were introduced to Uruguay in 1930, spread widely and invaded south-western Brazil (Sponchiado et al. 2011; Pereira-Garbero et al. 2013). Axis deer currently occur in at least 13 provinces and 4 protected areas throughout Argentina (Chébez and Rodríguez 2014), including El Palmar National Park (hereafter denominated EPNP or the park) where they function as a magnet for illegal hunters, as reported by local park rangers. The park was created in 1965 to protect one of the few extant stands of the iconic yatay palm tree *Butia yatay*. The invasion of exotic wild boar (*Sus scrofa*, Linnaeus 1758) was first noticed in 1976, though recent reports by local rural residents date it back to the 1950s; axis deer (first noticed in 1988; apparently absent up to the early 1980s: Crespo 1982), and the sporadic occurrence of blackbucks *Antilope cervicapra* (rarely sighted at EPNP after the 1990s) triggered

nonsystematic control efforts by park rangers using trained dogs (only for wild boar) and firearm shooting from vehicles, starting on 1983 (wild boar) and 1996 (axis deer). Although no damage attributable to axis deer was documented at that time, their proven impacts elsewhere, threats of potential competition with or pathogen transmission to native deer, and undue occurrence in a protected area justified targeting them jointly with wild boar and blackbucks.

Because these control efforts proved insufficient to halt the notorious increase of wild boar numbers, over 2006–2015 the park implemented a new management program of exotic ungulates (mainly based on recreational hunters performing controlled still shooting from watchtowers), which rapidly reduced and then stabilized wild boar abundance at levels that caused minimal soil damage (Gürtler et al. 2017). To assess population trends we used the available records of harvest and hunting effort to estimate period- and stage-specific capture-per-unit-effort (CPUE) indices. CPUE indices have classically been used for stock assessment of fish and a few game populations under several assumptions (Clark 1985; Hilborn and Walters 1992; Skalski et al. 2005). The CPUE index (i.e., number killed per 100 hunting party-hours) for a defined hunting method, area and time period is expected to be linearly related to density through the catchability coefficient. This index, standardized by restricting hunting effort and catch to a fixed time window, was positively correlated with another index of wild boar damage (rooting area) and served well for prolonged monitoring of its abundance (Gürtler et al. 2017).

Here we assess the impacts of the 10-year management program at EPNP on axis deer population dynamics and compare its outcome with those on wild boar. Program managers expected that culling would reduce the abundance of wild boar and axis deer at rather similar rates given their proven vulnerability to still shooting and the no-selectivity policy. This prediction was supported by interim observations at the onset of the third year post-intervention (YPI), when wild boar catches plummeted and axis deer numbers were relatively low. As for other effective culling programs (e.g., Hilborn and Walters 1992) including wild boar at EPNP, we expected the deer stage distribution to shift toward younger (smaller) specimens relative to baseline levels, and overall harvest composition to be stage-biased (i.e., size-

biased). No sex differential was expected according to the policy against trophy selection. In view of increasing deer numbers, we expected that at some point their body condition would deteriorate and reflect in a time-dependent decline of log-body length modified by sex and season, both of which are known to affect individual growth rates. We fitted the observed CPUE indices to simple population viability models to estimate the growth rate of the axis deer population and detect whether it was density-independent or density-dependent. We also examined whether the catch times of deer and wild boar culled through still shooting displayed any systematic differential over time, season and sex; hypothetically, the hunting-related disturbance triggered during a given session by an earlier-appearing target species might reduce the likelihood of shooting another later-appearing target species. This is probably the first long-term study of hunted axis deer in the introduced range, but more generally, long-term studies of hunted ungulates are rare (Servanty et al. 2011).

## Materials and methods

### Study area

El Palmar National Park (31°55'S, 58°16'W, Entre Ríos, north-eastern Argentina) covers ~ 8500 ha of savannahs, grasslands, scrublands and gallery forests (Batista et al. 2014). Local climate and biota are described in online materials (Text S1).

### Program design

The management program recruited local sport and subsistence hunters to cull wild boar and exotic deer under a regulated framework compatible with park conservation goals (administrative decision no. 154 issued by Argentina's Administración de Parques Nacionales on August 1st, 2005). Details of the program and hunting efforts over January 1st, 2006 to December 31st, 2015, including a map of the study area with the location of watchtowers, were described elsewhere (Gürtler et al. 2017). No harvest quotas were set, and hunters committed to conduct non-selective hunting and comply with park regulations. Only one annual trophy was allowed to each hunter. One of the main objectives of the 2005 program,

conceived within an adaptive management framework, was to reduce the abundance of axis deer and blackbucks.

Three control techniques were implemented to cull exotic ungulates: controlled still shooting, hunting with dogs, and firearm shooting from vehicles. Controlled still shooting was conducted from 35 to 44 watchtowers (4–6 m high) distributed across the park, each of which nearly always had two shooters with their own, licensed firearms and one person in charge of illuminating the targets. Hunting occurred year round over most of the decade (see Fig. 2b in Gürtler et al. 2017). Hunters were required to bait the surroundings of watchtowers with corn or ground pet food (mainly targeting wild boar, though also consumed by axis deer and other wildlife) twice a week before hunting sessions and deploy blocks of salt (targeting deer only). Hunting sessions were conducted every 2–4 weeks, generally starting at 6 p.m. and frequently extending past midnight over 2006–2007, depending on park stipulations. Hunting with trained dogs targeted wild boar only and was mainly accomplished by using 8–9 mixed-breed dogs and hunters external to the park over the first 2 years of the program (Table 1). Dogs were especially trained to not to chase or attack deer or other wildlife. Axis deer incidentally found during dog-hunting sessions were dispatched. Most dog-hunting parties started before 9 a.m. and all used horses. For vehicle hunting, park personnel drove pick-up trucks and used spotlights to locate and shoot the targets for variable time periods (Table 1). However, fewer effort was invested in vehicle hunting because most park rangers were involved in supervising or conducting other program-related activities.

For present purposes we define a hunting party to represent a group of hunters sharing a watchtower, vehicle or pack of dogs on a given occasion regardless of whether any exotic ungulate was dispatched. For each hunting party, park staff filled in a form including date, time and type of hunt, hunter's name, each specimen's morphometric measurements and other details (Gürtler et al. 2017).

The specimens were measured at a central operating post (i.e., a check station), classified by stage and sex; butchered, and uniquely identified with a label. All body measurements were taken on intact deer with a non-stretching tape measure to the nearest cm (Text S1). We assigned the specimens qualitatively to three

stages using body length because this was the most frequent measurement available in the database: juveniles were up to 100 cm (minimum, 31.8); young adults measured between 100.1 and 130.0 cm, and older adults greater than 130 cm. Female axis deer may conceive at 9 months of age and at > 23 kg, i.e., 50% of mature liveweight, if well nourished (Chapple 1989); hence we infer that females staged as young and older adults were in reproductive age. Males reach puberty between 14 and 16 months old, and usually mate at a greater age depending on the presence of dominant stags; hence we infer that males staged as older adults would be able to reproduce. Pregnancy status and the number of embryos were not systematically recorded and therefore were excluded from further considerations. Hunters were allowed to take home 50–67% of each kill and the remainder was donated to local public schools, community shelters, retirement homes, and park personnel.

For an additional index of axis deer abundance [including other native and exotic mammals such as the brown brocket *Mazama gouazoubira* (Fisher 1814)], two people rode on the back of a vehicle circulating at 10 km/h along all park roads and trails and used spotlights to sight deer at dusk on two occasions separated by 2 or 3 days per survey (total distance, 111–124 km per survey). Sighting surveys were conducted on September 2006, April 2007, September 2007, July 2008, July and September 2011, August 2012 and 2013, January and September 2014, and February 2015, with no surveys conducted in 2009 and 2010 because of lack of personnel. Nightly spotlight surveys and vehicle hunting were conducted by different teams on different occasions.

#### Data management and analysis

The program kept records of hunting effort, catch and other attributes for interim assessment and decision making. All data recorded in each hunting form were entered in an Excel database by park personnel, and the digital database revised for consistency, completeness and potential duplicate records by the research team. The database included a total of 2380 deer specimens with date of catch, hunting method and party identification; for those culled by still shooting, at least one of the following attributes were measured: 1903 assigned to sex; 1850 measured for body length (and other attributes); 1207 for body weight, and 1803

**Table 1** Annual crude hunting effort (per 1000 hunting-party hours) and catch of axis deer by method and year post-intervention (YPI) in El Palmar, 2006–2015

YPI	Still shooting			Dog hunting <sup>a</sup>		No. of deer dispatched <sup>b</sup>			
	No. of sessions (no. of parties)	Mean duration (SD, in h)	Total crude hunting effort	No. of sessions (no. of parties)	Mean duration (SD, in h)	Still shooting	Vehicle <sup>c</sup>	Dog	Total
0	47 (264)	11.7 (2.83)	3.081	129 (161)	5.1 (1.83)	91	10	27	128
1	57 (570)	7.4 (2.99)	4.234	90 (107)	4.4 (1.45)	164	12	20	196
2	33 (517)	5.1 (1.59)	2.640	5 (5)	4.4 (0.89)	121	0	0	121
3	31 (553)	5.0 (1.57)	2.780	2 (2)	4.3 (0.35)	174	0	2	176
4	28 (560)	4.8 (1.47)	2.687	17 (25)	4.4 (1.22)	205	0	11	216
5	28 (579)	5.0 (1.13)	2.919	18 (27)	4.2 (1.28)	227	0	12	239
6	16 (407)	4.9 (2.09)	2.008	0	0	211	0	0	211
7	13 (279)	5.7 (2.66)	1.708	0	0	182	0	0	182
8	27 (780)	5.5 (1.44)	4.327	0	0	398	0	0	398
9	15 (515)	5.6 (1.27)	4.573	0	0	513	0	0	513
Total	295 (5024)	5.8 (2.46)	3.097	260 (310)	4.8 (1.67)	2286	22	72	2380

<sup>a</sup>Directed to wild boar

<sup>b</sup>Includes 16 deer reportedly wounded by still shooting and assumed as crippling losses, and 23 hunting sessions from vehicles

<sup>c</sup>The mean duration of vehicle-hunting sessions was 5.6 h (SD, 3.01). A total of 16 and 7 sessions were conducted on 0 and 1 YPI, respectively

for catch time. Missing data for these variables were assumed to occur at random since no precise reason for their missingness was apparent and it is not possible to verify the exact type of missingness (Little 2002). However, we used maximum-likelihood estimation methods, which are expected to return consistent parameter estimates when missing data occur at random (Rabe-Hesketh and Skrondal 2008, p. 207). A total of 103 unidentified specimens with complete morphometric measurements (excluding tail length) were finally assigned to axis deer through a discriminant analysis of log<sub>10</sub>-transformed measurements of 1631 identified axis deer and 1666 identified wild boar having complete data, as described in Gürtler et al. (2017).

The density of the standing axis deer population was assessed by means of period-specific CPUE indices (i.e., number culled per 100 hunting party-hours) based on aggregate (crude) catch *C* (i.e., harvest) per aggregate (crude) effort *E* for a fixed area and for each quarterly, biannual or annual period (Clark 1985; Hilborn and Walters 1992). CPUE indices were only computed for still-shooting sessions because very few deer were culled by dog- and

vehicle-hunting. Aggregate *C* was taken as the sum of all deer dispatched in a given still-shooting session (i.e., date) or time period *t* (quarter, semester or year), whereas aggregate *E* was measured as the total number of hunting party-hours in a given session at *t*, as detailed elsewhere (Gürtler et al. 2017). The total duration of a hunting session at *t* is taken as the difference between termination and initiation times of each hunting party summed over all hunting parties at *t*. To allow for the much longer duration of still-shooting sessions during 0–1 YPI we computed standardized CPUE indices by restricting crude *E* and crude *C* to the most frequent time span of sessions over the 10-year period (5 p.m. to 11 p.m.). All catches were increased by one unit to analyze the data as log-ratios between successive CPUEs (see below). Stage structures were derived from stage-specific standardized CPUEs (i.e., the ratio between the standardized CPUE for stage *i* at *t* relative to total standardized CPUE at *t*).

We investigated whether the log-ratio of deer-to-boar catches displayed a time trend using linear regression analysis as implemented in Stata 14.2 (StataCorp 2017). We used linear regression with no

intercept to test whether the catch of axis deer was linearly related to still-shooting effort, and then added a term (squared hunting effort) to examine non-linear effects. We tested whether catch times by still shooting varied with ungulate species, sex, season (i.e., quarter, with four levels) and YPI using multiple linear regression. The stability of sex ratios (i.e., proportion of males over all deer identified to stage and sex) over stages and YPI was tested by multiple logistic regression, whereas the stability of annual stage frequencies over seasons and YPI was examined with  $\chi^2$  tests. Multiple linear regression analysis was used to test whether log-body length varied with sex, season, YPI and their two-way interactions. Linear regression residuals were tested for normality using the Shapiro–Wilk test (command `swilk`); heteroskedasticity, skewness and kurtosis using the Cameron and Trivedi information matrix test (command `estat imtest`), and three versions of the Breusch–Pagan and Cook–Weisberg tests for heteroskedasticity vs homoskedasticity (command `estat hottest`, not for linear regressions with no intercept).

To assess the impact of controlled still shooting on deer population dynamics and estimate its growth rate, we fitted density-independent ( $\log(N_{t+1}/N_t) = r$ ) and density-dependent discrete population models (Morris and Doak 2002, pp. 108–118) to standardized CPUE data using maximum-likelihood nonlinear regression as implemented in package `stats` (3.4.0) and function `nls` in R software (version 3.1.0) (R Development Core Team 2014). We verified the results were robust to the initial parameter values selected. The density-dependent population models considered were the discrete logistic ( $N_{t+1} = N_t/(1 + r(1 - N_t/K))$ ), Beverton–Holt ( $N_{t+1} = \lambda N_t/(1 + (\lambda-1) N_t/K)$ ), Ricker ( $\log(N_{t+1}/N_t) = r(1 - N_t/K)$ ), and theta-logistic ( $\log(N_{t+1}/N_t) = r(1 - (N_t/K)^\theta)$ ), where  $K$  is the carrying capacity,  $r$  is the instantaneous population growth rate,  $\lambda$  is the finite population growth rate ( $= 1 + r$ ), and  $\theta$  is the parameter theta governing the type of density-dependence. We used the  $\log_e$ -transformed ratios between standardized CPUE indices on successive periods post-intervention to estimate parameter values (including residual variances); compute the corrected Akaike's Information Criterion ( $AIC_c$ ) to identify the most parsimonious model that best described the data, and compute Akaike weights to quantify the relative support of all models considered. This process was replicated for three different time

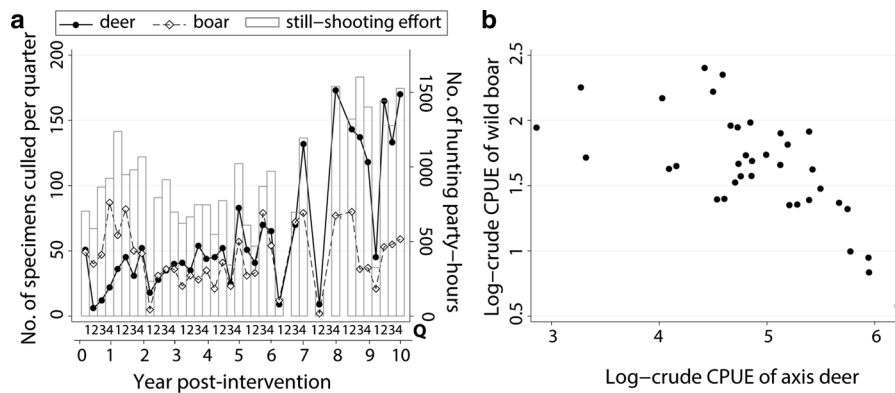
steps: quarter, semester and year (January–March 2006 taken as the first quarter and January–June 2006 as the first semester) to assess how this affected model selection. The total number of  $\log_e$ -transformed ratios between standardized CPUE indices taken on successive quarters, semesters and YPI was 36, 17 and 9, respectively. The data point for the first quarter and semester was clearly an anomalous value and was alternatively included and excluded from the calculations to assess its influence. This initial period was very unusual in several ways: initial adjustment of procedures, fewer hunters, and exceptionally long still-shooting sessions which started much earlier and finished much later than over 2–9 YPI.

## Results

### Aggregate catch and hunting effort

A total of 2380 axis deer were dispatched over 591 sessions involving 5693 hunting parties (Table 1). Culling was mostly accomplished by controlled still shooting (96.1%) and very few deer were killed by dog-hunting (3.0%) and from vehicles (0.9%). Successful hunting parties by still shooting (i.e., those who at least culled one deer in a given session) most frequently caught one (1084) and two (333) specimens over the same session; very few parties dispatched three (95), four (50), five (9) and six (1) deer. In addition to the 513 axis deer dispatched by still shooting during 2015, 16 (3.0% of the catch) reportedly escaped wounded. Annual crude still-shooting effort (per 1000 hunting party-hours) increased from nearly 3.1 to 4.2 between 0 and 1 YPI, varied little from 2.6 to 2.9 over 2–5 YPI, decreased to 1.7–2.0 over 6–7 YPI, and finally more than doubled to 4.3–4.6 over 8–9 YPI (Table 1, fourth column).

The aggregate catch of wild boar exceeded that of axis deer in still-shooting sessions over 0–1 YPI; then deer were culled slightly more frequently over 3–5 YPI, and finally twice as many deer as wild boar were culled over 8–9 YPI (Fig. 1a). Aggregate log-CPUE of deer and wild boar were negatively and significantly correlated ( $r = -0.662$ ,  $n = 36$ ,  $P < 0.001$ ) (Fig. 1b). The log-ratio of deer-to-boar catches showed a significant, positive time trend (slope  $b \pm$  standard error  $SE = 0.02197 \pm 0.00920$ ,  $F = 5.68$ ,  $df$  1 and 34,  $P = 0.023$ ,  $Adj. R^2 = 0.118$ ).



**Fig. 1** Aggregate (crude) catch of axis deer (*Axis axis*) and wild boar (*Sus scrofa*) (connected lines) and aggregate (crude) hunting effort by still shooting (bars) according to year post-

intervention and quarterly period (a), and correlation between log-transformed crude CPUE of axis deer and wild boar (b) in El Palmar, 2006–2015

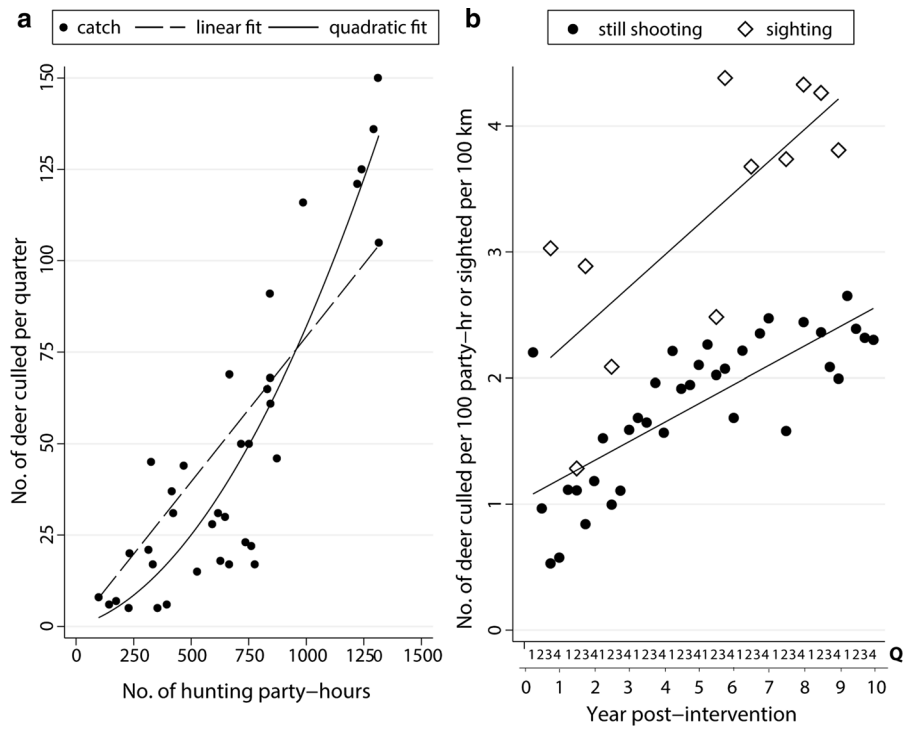
The standardized catch of axis deer  $C$  was non-linearly related to standardized hunting effort  $E$  over quarterly periods, such that high levels of effort caught proportionally more deer ( $b \pm SE = 0.0183 \pm 0.0135$ ;  $b1 = -0.000064 \pm 0.000014$ ,  $n = 36$ ,  $Adj. R^2 = 0.917$ ,  $P < 0.001$ ; Fig. 2a). Residuals for the quadratic fit were normally distributed, with no significant skewness, kurtosis and heteroskedasticity. The quadratic model was slightly better than a linear model with no intercept ( $b \pm SE = 0.0792 \pm 0.0052$ ,  $Adj. R^2 = 0.866$ ). Regression coefficients estimated for crude  $C$  on crude  $E$  were very close to those obtained for standardized  $C$  and  $E$ . Two indices of deer abundance, crude CPUE and nightly spotlight counts from a slow-moving vehicle, increased linearly over quarters post-intervention ( $r = 0.725$ ,  $n = 11$ ,  $P < 0.02$ , and  $r = 0.711$ ,  $n = 36$ ,  $P < 0.001$ , respectively), showing approximately parallel trends (Fig. 2b). Nightly spotlight counts of brown brockets per 100 km tended to remain at low values over 0–9 YPI except for a clearly anomalous observation (Fig. S2).

The mean catch time of axis deer (7.4 p.m.  $\pm$  1.80 h: mean  $\pm$  SD,  $n = 1111$ ) was nearly indistinguishable from that of wild boar (7.4 p.m.  $\pm$  1.40 h,  $n = 609$ ) over still-shooting sessions starting from 5.0 p.m. to 8.0 p.m. and ending from 8.01 p.m. to 11.0 p.m. over the 10-year period (Fig. 3). Mean catch time was not significantly ( $P > 0.3$ ) modified by ungulate species, sex, YPI and season using multiple linear regression ( $F = 3.28$ ,  $df$  14 and 1570,  $P < 0.001$ ,  $Adj R^2 = 0.020$ ). Residuals deviated highly significantly from normality, and displayed skewness and heteroskedasticity according to

Breusch-Pagan/Cook-Weisberg test. Of these, heteroskedasticity is particularly serious and implies that standard errors are no longer unbiased and hypothesis tests may be invalid. All two-way interaction terms between ungulate species and YPI, season or sex were nonsignificant.

#### Deer population growth rates

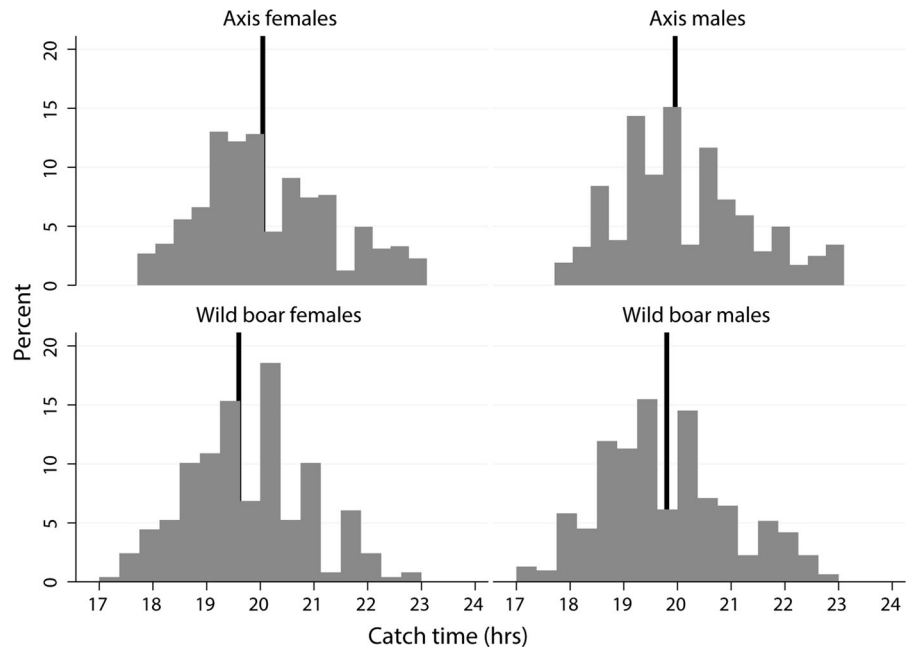
The log-standardized CPUE of axis deer by still shooting steadily increased over 0–4 YPI and then gradually slowed down until approaching a plateau over 7–9 YPI regardless of whether a biannual or annual time scale was considered (Fig. 4a). Standardized CPUEs for successive quarterly periods showed an analogous, though more noisy trend (Fig. S3). For comparison, a similar trend analysis for wild boar at EPNP displayed a steep decline over 0–1 YPI and a rather stable pattern thereafter (see Fig. 4 in Gurtler et al. 2017). The log-ratios of standardized CPUE indices of axis deer between successive time steps showed substantial evidence of negative density-dependence over biannual (Fig. 4b), annual or quarterly periods. Of the candidate models tested after excluding the data for the first semester, the discrete logistic model had most relative support (Akaike weight, 0.410) and best fitted the data relative to the Ricker, Beverton-Holt, and theta-logistic models (Table 2), but differences among them were trivial ( $\Delta AIC_c < 2$ ). The density-independent model was nearly 6 Akaike units from the best fitting model, and therefore was considered a much less plausible description of the data (Akaike weight, 0.016).



**Fig. 2** Linear and quadratic regressions (with no intercepts) of standardized catch of axis deer (*Axis axis*) on standardized still-shooting effort (a) and comparison between crude catch-per-

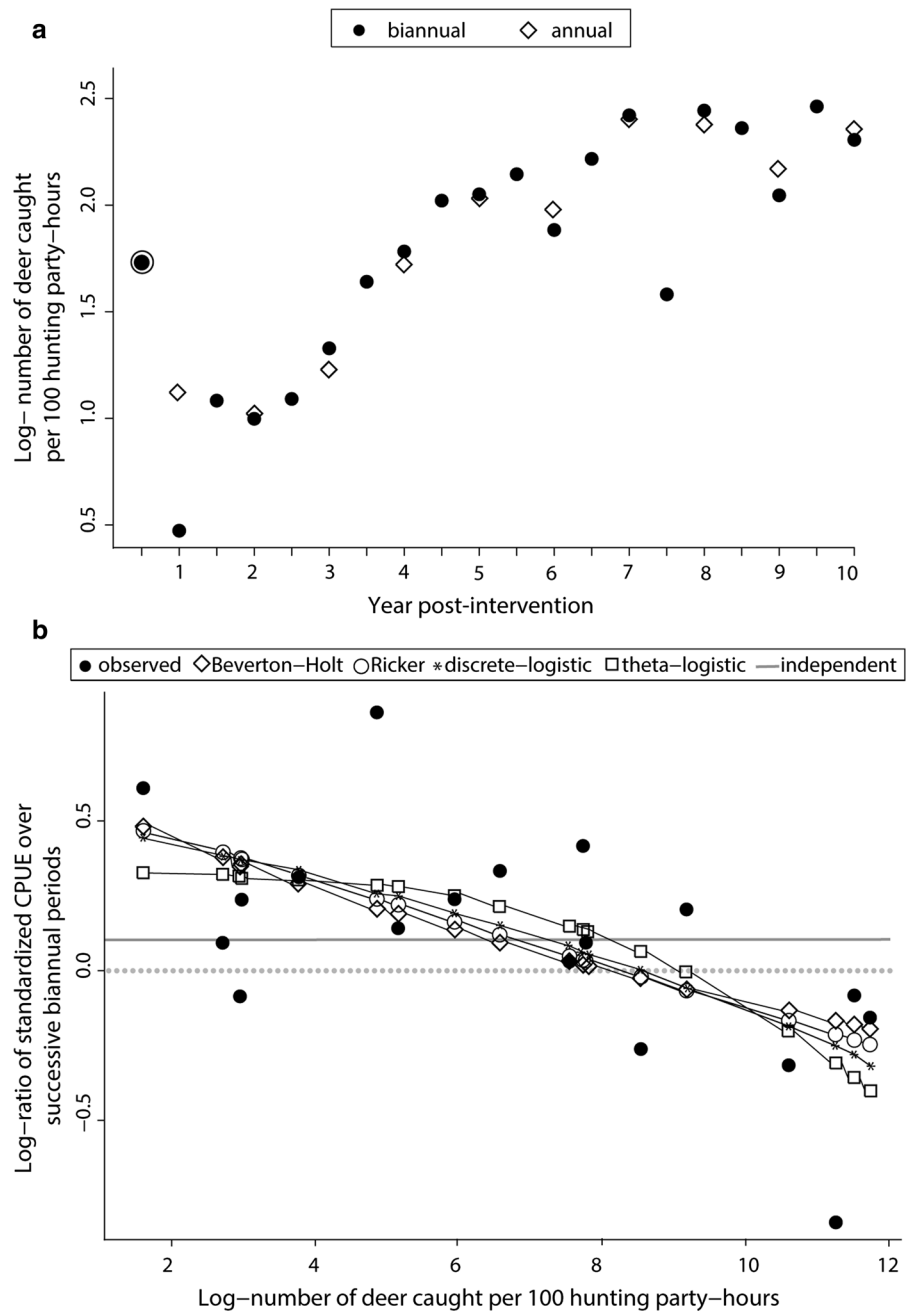
unit-effort (CPUE) by still shooting and nightly spotlight counts from a slow-moving vehicle (b) over quarterly periods in El Palmar, 2006–2015

**Fig. 3** Sex-specific catch times of axis deer (*Axis axis*) and wild boar (*Sus scrofa*) culled by still shooting in sessions spanning over 17–23 h in El Palmar, 2006–2015. Vertical lines mark the mean catch time for each species and sex





**Fig. 4** Log-standardized CPUE of axis deer (*Axis axis*) over successive biannual and annual periods (the first data point marked with a circle was excluded for parameter estimation) (a) and fit of the log-ratios of standardized CPUE indices over successive biannual periods to density-independent and density-dependent models (b) in El Palmar, 2006–2015



Including the first-semester datum strongly reduced the difference between models except for the theta-logistic (Akaike weight, 0.051) which was practically excluded (data not shown). When the data were aggregated annually, the support for virtually all models except the theta-logistic was practically identical ( $\Delta AIC_c < 1-3$ ) regardless of whether the first-year datum was included or not; however, the number

of data points was small (9 and 8, respectively). For data pooled over quarterly periods, all density-dependent models were within 2 Akaike units from the best-fitting model (discrete logistic) whereas the density-independent model had  $\Delta AIC_c < 4$ . During the initial time period (0–4 YPI), in which there was no evidence of density-dependence, the exponential population growth rate  $r$  (estimated from biannual standardized

**Table 2** Parameter estimates of five models fitted to standardized catch-per-unit-effort of axis deer culled by controlled still shooting in El Palmar over biannual periods, 2006–2015

Model	r (SE)	K (SE)	Theta (SE)	RV	No. of parameters	MLL	AIC <sub>c</sub>	Akaike weights
Discrete logistic	0.669 (0.214)	8.484 (0.896)		0.0798	3	− 2.792	13.30	0.410
Beverton–Holt	1.898 <sup>a</sup> (0.481)	8.144 (1.461)		0.0881	3	− 3.679	15.07	0.169
Ricker	0.583 (0.171)	8.243 (1.124)		0.0838	3	− 3.230	14.17	0.264
Theta logistic	0.330 (0.142)	9.134 (1.063)	3.165 (2.336)	0.0746	4	− 2.175	15.43	0.141
Density-independent	0.102 (0.089)			0.1342	2	− 7.466	19.73	0.016

The number of data points is 16 (the first semester was excluded). *RV* residual variance, *MLL* maximum log likelihood, *AIC<sub>c</sub>* corrected Akaike's information criterion

<sup>a</sup>exp(r)

CPUEs, excluding the first semester) equalled 18.6% semester<sup>−1</sup> (SE, 6.6%), i.e., 37.2% per year.

#### Stage, sex and size structure

On average, juveniles comprised 13.5%, young adults 62.6%, and older adults 23.9% among 1977 deer culled by still shooting with measured body length. The fraction of older adults gradually decreased from 43 to 19% over 0–4 YPI and then fluctuated little between 19 and 25% (Fig. 5a). The annual stage structure significantly differed among years ( $\chi^2 = 32.5$ , *df* 18,  $P = 0.019$ ) and seasons ( $\chi^2 = 35.6$ , *df* 6,  $P < 0.001$ ). Juveniles were most frequently hunted over summer (20.1%) and spring (15.7%) and then dropped to a minimum in winter (9.5%), whereas older adults increased from 20.1% (summer and fall) to 27.8% in spring. For each of these stages at EPNP, the median (first and third quartiles) body masses (in kg) were 21 (16, 28), 40 (33, 48) and 60 (50, 82), respectively. [For comparison, the body mass of axis deer raised in captivity increased logarithmically to reach higher values in stags (Chaple 1989).]

Males averaged 51.3% (Agresti-Coull 95% confidence interval, 48.9–53.6%) among 1732 deer culled by still shooting and classified by stage and sex (Fig. 5b). The overall proportion of males increased from 45.1 and 47.9% among juveniles and young adults, respectively, to 63.6% among older adults ( $\chi^2 = 33.7$ , *df* 2,  $P < 0.001$ ). Multiple logistic regression showed that sex ratios varied significantly among

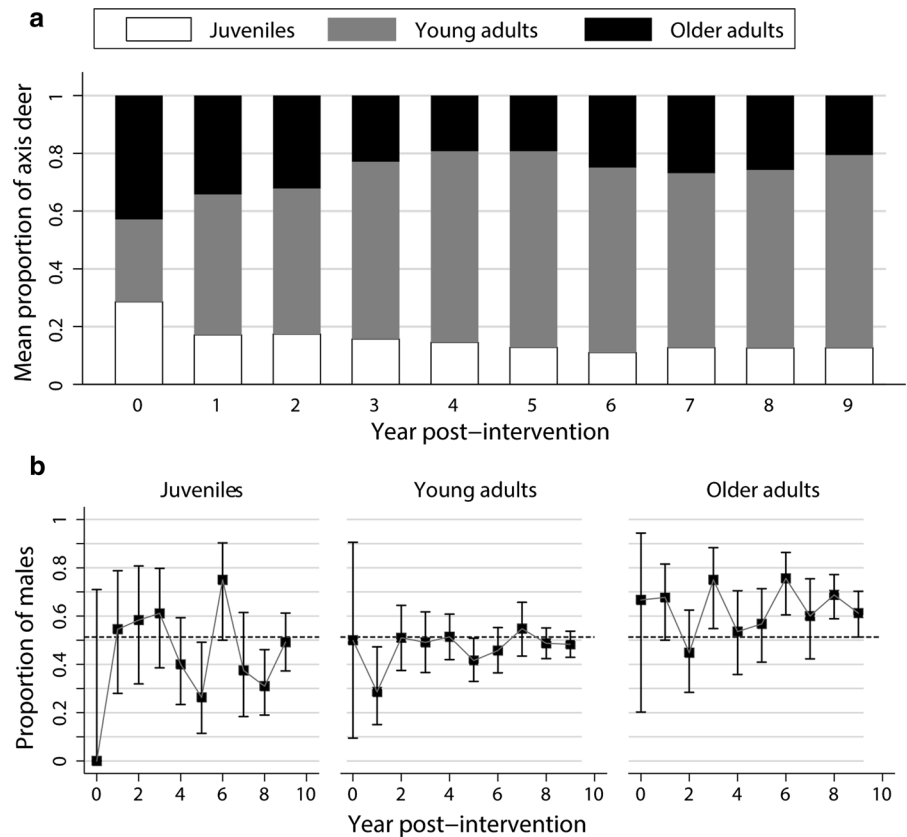
stages ( $P < 0.001$ ) but not among years ( $P > 0.4$ ), and their interaction was nonsignificant ( $\chi^2 = 42.9$ , *df* 11,  $P < 0.001$ ).

We tested whether log-body length of axis deer culled by still shooting varied with sex, season and YPI using multiple linear regression (Table S1). Log-body length was significantly greater in males and increased in fall, winter and spring relative to summer, as expected from background information and possibly increased juvenile recruitment during spring–summer, but varied little among YPI; the only significant two-way interaction term occurred between sex and season ( $F = 3.32$ , *df* 15 and 1636,  $P < 0.001$ ,  $n = 1652$ , *Adj R*<sup>2</sup> = 0.021). Residual analysis showed highly significant deviations from normality by the Swilk test; no evidence of skewness and kurtosis according to Cameron and Trivedi's test, and significant heteroskedasticity by the latter test but not by the Breusch–Pagan and Cook–Weisberg test.

#### Discussion

Our study documents two largely unexpected outcomes of the management program at El Palmar National Park: increasing abundance of axis deer toward a plateau, and a strong inverse correlation between deer and wild boar numbers. The program quickly reduced and then stabilized the relative abundance of wild boar from 2 YPI on, but contrary to park managers' expectations, the interventions failed to reduce the axis deer population over a

**Fig. 5** Annual stage distribution (a) and proportion of males (b) of axis deer (*Axis axis*) culled by still shooting in El Palmar, 2006–2015. Horizontal lines mark the mean overall proportion of males; error bars are 95% confidence intervals



10-year period despite increasing still-shooting effort and increasing deer harvest. Failure to reduce deer abundance may be explained by the combined effects of several putative processes: (1) virtually unchecked population growth of axis deer over nearly two decades; (2) deer range expansion through the region leading to increasing immigration to the park; (3) sex- and stage-biased hunting mortality of insufficient intensity, and (4) competitor (and perhaps predator) release from wild boar. We review the evidence for each of these processes first, and then discuss other demographic aspects, catch-effort curves and the management implications of our assessment.

First, the process of axis deer invasion of EPNP, gradual establishment in new terrain (typically slow in deer), and virtually unchecked increase in numbers over at least two decades before the program, suggest the deer population size continued growing (the eruptive phase of Caughley 1976) at the lower rates imposed by culling until reaching a plateau by 7 YPI (Fig. 4a). The park provides plenty of suitable habitats

for deer, wild boar and other herbivores including unrestricted access to water, forage and cover, absence of large predators, and appropriate regional context (i.e., marginal axis deer hunting outside of the park, maize or soybean crops, expansion of tree plantations, and unusual dry periods such as the one that occurred at 2 YPI). Habitat restoration measures (i.e., prescribed burns and opening of fire breakers offering permanent pastures) may have benefited axis deer as they prefer burned rather than cut plots (by 7.5–1) to consume ashes, sprouts and better-quality forage (Moe and Wegge 1997). Conversely, supplemental feeding provided as hunting bait at EPNP was unlikely to translate into improved ungulate vital rates (Milner et al. 2014) inasmuch as most of the bait-attracted individuals were dispatched at a subsequent hunting session as local diet studies suggest (Ballari et al. 2015). On the flip side, wild boar and foxes may kill neonates and fawns (e.g., Chapple 1989; Jedrzejewski et al. 2011), and fox density at EPNP substantially increased after the 2006–2007 outbreak of canine

distemper (Gürtler et al. 2017). Most of these factors accompanied or followed, rather than preceded, the steady increasing trend in deer numbers, and therefore are unlikely to explain such variations.

Second, part of the deer population increase may be related to immigration from neighboring farms and across the Uruguay River as part of its perceived range expansion through the region. The latter is supported by: (1) the substantial increase of deer-vehicle collisions along the fast highway running by the western park limits, as reported by local park rangers and newspapers, and (2) new regulations recently issued by Entre Rios Province (home to EPNP) extending the annual hunting season of wild boar and axis deer from 6 to 12 months and increasing hunt quotas, in response to growing trends in exotic ungulates and subsistence hunters combined with declining numbers of sport hunters.

Third, the intensity and stage/sex distribution of still-shooting mortality may not compensate for deer productivity and immigration. Older adult females (reproductive) were relatively less represented than older adult males (see below) although ungulate females live longer than males (Gaillard et al. 2003). Furthermore, two facts suggest juveniles were less exposed to, sighted or targeted by hunters and thus suffered lower hunting mortality: (1) juveniles were greatly underrepresented throughout the study despite being a large fraction of a growing population, and (2) axis deer do not have a well-defined reproductive season (i.e., estrous cycles and rutting are not synchronised: Duckworth et al. 2015) and continue to produce offspring throughout the year, albeit at variable rates depending on a race/environment interaction (Lincoln 1992). Thus, sex- and stage-biased hunting mortality may lead to compensatory, density-dependent increases in reproduction and survival that alleviate the effects of culling. In general, reductions in deer density enhance juvenile survival and lower the age at first reproduction in long-lived ungulates (Eberhardt 2002; Coulson et al. 2004), whereas temporal variations in juvenile survival greatly affect population growth rates in harsh environments (Gaillard et al. 2000). The sex- and stage-biased harvest obtained through moderate-to-intense still-shooting efforts at EPNP probably kept per capita deer recruitment rates at sub-maximal levels for most of the decade. For example, our estimated exponential population growth rate under still-shooting efforts

over 0–4 YPI ( $37.2\% \text{ year}^{-1}$ ) is slightly greater than the upper range reported for axis deer elsewhere (Duckworth et al. 2015), and notably exceeds the zero population growth rate of wild boar recorded at EPNP over 2–9 YPI.

Four, in the absence of harvest quotas, the strong inverse correlation between wild boar and axis deer numbers suggests competitor, and perhaps predator, release of deer from the detrimental effects of high-density wild boar as the program progressed. Wild boar invaded the park at least 12 years before axis deer and reached much greater apparent densities than them by the time the program started. Evidence for exploitative and interference competition and predator–prey interactions between various deer species and wild boar abound in the literature, as the following account shows. Dietary overlap between axis or other deer species and wild boar would be especially intense in non-mast seasons when herbage (including grasses) would represent the main food item available for wild boar in other locations (Wood and Roark 1980; Kuiters et al. 2005; Groot Bruinderink et al. 1994). In contrast, grasses, forbs and acorns (preferred by wild boar) were a large part of the diet of axis and other deer species depending on their (seasonal or annual) availability elsewhere (Everitt and Alaniz 1980; Wood and Roark 1980; Elliott and Barrett 1985; Rollins 1999 and several references therein). We found no information on axis deer diet in Argentina and elsewhere in the region. A recent review concluded that wild boar diet comprised  $\sim 90\%$  of plant material including mast crops, forbs and graminoids (Ballari and Barrios-Garcia 2014). Specifically at EPNP, wild boar stomachs largely contained corn provided as bait (mean volume, 41.4%) and monocotyledonous plants (i.e., grasses in the local context), especially when one of its apparently preferred food items (yatay fruit) was not available (Ballari et al. 2015).

Signs of interference competition between foraging deer species and wild boar have been frequently recorded (Latham 1999; Ferretti et al. 2008). For example, black-tailed deer usually withdrew when confronted by wild boar, and both species were inversely associated in buckbrush habitats (Barrett 1982), whereas white-tailed deer avoided feeders and foraging areas used by wild boar (Tolleson et al. 1995). Axis deer displayed aggressive behavior and modified the habitat selection and feeding patterns of white-tailed deer (Faas and Weckerly 2010) and out-

competed the latter in experimental exclosures over an eight-year follow-up in Texas (Anon 2016). There is a broad consensus that various deer species may be affected by competition with wild boar at times of resource constraints (Barrios-García and Ballari 2012, p. 2290).

Predation of deer neonates and fawns (rather than scavenging) has also been recorded: wild boar stomachs contained fawns, juvenile pigs, newborn lambs and kids, ground-nesting birds, eared doves (*Zenaida auriculata*), among others (reviewed in Rollins 1999; Tolleson et al. 1995; Ballari and Barrios-Garcia 2014). Similarly, axis deer remains were found in a wild boar stomach at EPNP over 3–5 YPI (Ballari et al. 2015), though here predation and scavenging could not be distinguished. Moreover, a search of public media sources documents that overabundant wild boar frequently killed calves, lambs and kids in various areas through Argentina, including Patagonia and north-eastern wetlands (<http://www.lanacion.com.ar/2046330-en-carmen-de-patagones-autorizan-cazar-jabalies-porque-son-una-plaga>, accessed 23 July 2017; <http://www.ellitoral.com.ar/232418/Productores-preocupados-por-los-cerdos-salvajes>, accessed 28 October 2017). Wild boar is well known for killing lambs and kids in Patagonia (Flueck 2010), and there were controversial reports in Texas (Rollins 1999, p. 48 and p. 63). Whether wild boar predation on axis deer fawns or juveniles is additive or compensatory remains to be established.

Although dietary overlap between two ungulate species is weak evidence of competition (Spear and Chown 2009), behavioral intolerance, fawn predation and inverse population trends add more support to the hypothesis that the rise of axis deer was at least partially related to declining wild boar numbers. Exclosure experiments are required for a definitive appraisal. In the absence of historical data on local deer abundance and given its long-standing invasion of EPNP, we hypothesize that the steep decline in wild boar abundance brought about by the program expanded the herbivores' carrying capacity and allowed further increases in deer population size boosted by immigration. Several examples attest that a management intervention on a given target species embedded in a poorly known, complex food web may have unintended consequences (Bull and Courchamp 2009). In this regard, the park has suffered the expansion of multiple exotic woody plants which

increased forest cover and possibly facilitated the persistence of axis deer.

### Population growth and structure

Unlike the exponential drop of wild boar numbers over 0–1 YPI followed by long-term stabilization, the time series of CPUE indices for axis deer was best described by density-dependent population growth models, with greater relative support for the discrete logistic than for other candidates. However, all but the density-independent model were appropriate descriptions of the current data because  $\Delta AIC_c$  values were within 2.5 Akaike units of the best model (Burnham and Anderson 2002). Model selection was sensitive to the temporal resolution of the data; using biannual indices struck a balance between sample size and noisy data including gaps in the time series. Sigmoidal deer population growth toward the plateau reached by 7 YPI may be partly associated with two processes: growing resource competition with other grazers (including the large, rapidly increasing capybara population, A. Maranta, unpublished observations) during the dry season, and increased hunting pressure over 7–9 YPI. Although we cannot partition the effects of these processes, deer body length (related to body condition status) displayed very little variations over 1–9 YPI despite increasing deer densities, suggesting no obvious competition-related effects on a proxy for body condition. In addition, increased deer avoidance behavior (including eventual emigration from the park) as a consequence of increased hunting pressure is unlikely to explain the CPUE plateau: casual sightings by park rangers and hunters suggested deer were little disturbed by still-shooting sessions held approximately every 2 weeks.

The annual population structure of axis deer culled by still shooting revealed two distinct patterns: (1) a steady decline in the fraction of older adults over 0–4 YPI and a concomitant increase in younger adults, in agreement with the predicted effects of culling on the stage and body-size distribution of exploited resources (e.g., Hilborn and Walters 1992), and (2) a strongly biased sex ratio toward older adult males combined with stable stage-specific sex ratios. In the absence of deer culling restrictions and sex-related asymmetries in catch times, the consistent skew toward males among older adults may be explained by hunter selectivity for antler or larger males (thus rejecting the

hypothesis of no selectivity); males' greater exposure and mobility, and male-biased deer dispersal leading to differential immigration rates. In consequence, the deer population apparently harbored relatively more reproductive adult females as the management program progressed, which likely lead to compensatory recruitment rates and fast recovery from hunting-related losses.

### Catch-effort relationship

Our study documents a non-linear (concave upward) relation between standardized deer catch and standardized still-shooting effort, mainly derived from a more-than-proportional catch at very large levels of standardized  $E$  ( $> 1000$  hunting party-hours per quarter) from late 7 YPI on, when the log CPUE-YPI curve was concave downward (Fig. 4a). Allowing for the non-linear relation between  $C$  and  $E$  would accentuate the decrease in underlying deer density.

The equal-catchability assumption is crucial for CPUE-based assessments (Hilborn and Walters 1992), and entails homogeneous catchability across park sections (compatible with the notion that axis deer are a diffusive resource stock with a sizable home range, regardless of vegetation cover and visibility), seasons, years and hunters (but see deCalesta 2017). This strong assumption cannot be verified with the available data, and the exact details of how hunting with firearms is conducted may modify the linear relationship. For example, using ground shooting assisted with dogs to flush out the deer, CPUE indices plateaued at large levels of sika deer density (Iijima 2017). We standardized still-shooting efforts and catches over YPI by restricting hunting sessions to a common, more effective time window matching the mainly crepuscular foraging behavior of axis deer and wild boar. However, using crude CPUE indices did not affect the conclusions. Two pieces of evidence suggest that culling both exotic ungulates were independent events: the catch times of axis deer and wild boar were nearly identical and unaffected by other factors, and the mean and variance of still-shooting catches over quarterly periods were linearly related, with slope values compatible with a random (Poisson) process (R.E.G., unpublished results).

CPUE indices and nightly spotlight counts displayed approximately consistent time trends, as did CPUE indices determined by still-shooting and dog-

hunting for wild boar (Gürtler et al. 2017) and white-tailed deer (Novak et al. 1991). Spotlight counts suffer from many shortcomings, even after being corrected for detection error, because of inconsistencies between and among observers and the inherent non-random nature of road-based sampling (Collier et al. 2013). In our study, spotlight surveys were not always performed at the same season and detection error was not assessed. Here our goal was to confirm whether the time trend displayed by standardized CPUE indices was supported by spotlight counts, rather than obtaining precise deer density estimates.

### Limitations

Our analyses of axis deer and wild boar population dynamics under control efforts share similar limitations (Gürtler et al. 2017) related to lack of information on: rates of in- and out-migration of deer through the park's wired fences, which allow the passage of wildlife; individual age determination, pregnancy and survival rates for age-classified population analysis; forage availability and quality, and estimates of deer population size for using more realistic harvest models (Skalski et al. 2005). Lack of complete information on each specimen's physical attributes during the early years of the program precluded a more thorough analysis of body size and condition. Measurement errors in physical attributes were not assessed and may bias regression coefficients. Poachers' offtake was assumed to be relatively marginal (as suggested by the rare finding of deer remains in an intensely patrolled park), whereas the occurrence of wounded deer was frequently reported by the hunters and may represent crippling losses. The assumption of a constant catchability coefficient  $q$  merits further research: if  $q$  decreases or increases with hunting-related disturbance at large shooting efforts, the true abundance of deer may be substantially under- or overestimated.

### Management implications

The EPNP management program halted deer population growth using an average of 948 standardized hunting party-hours per quarter over 7–9 YPI, and failed to reduce deer density. Although sport hunting usually proved inadequate in preventing deer from overpopulating broad areas (Côté et al. 2004; Simard et al. 2013), success cases are not rare (e.g., deCalesta

2017). Possible solutions, including prolonged hunting seasons, liberalization of harvest quotas and increasing hunter motivation and participation, were not sufficient to reduce local deer density at EPNP despite conducting long-term hunting efforts that proved effective for wild boar. A key difference between the control interventions on both exotic ungulates is related to intense dog-hunting over 0–1 YPI targeting wild boar only. Intensive culling will be needed to bring down deer abundance at current levels. Deer management focused at the level of individual areas (as EPNP) was found to be ineffective for achieving ecological objectives (Austin et al. 2013). Conversely, long-term success in deer reduction within protected areas and islands has been linked to control operations covering open terrain with no forested areas (Gogan et al. 2001; Nugent and Choquenot 2004). Thus, the gradual expansion of forest cover at EPNP may have favored the persistence of exotic ungulates.

A better understanding of axis deer population ecology, diet and damage in the introduced range is required to guide management (Davis et al. 2016). The adverse impacts of overabundant axis deer at EPNP remain unknown and may affect the smaller native deer *M. gouazoubira*, although no sign of apparent damage has been detected so far (Fig. S2). Lack of a full understanding of and consensus on the effects of overabundant deer conspires against adopting more effective policies (Diefenbach et al. 1997; Nugent et al. 2011). A precautionary approach is in point because overabundant deer cause severe, long-term impacts that are difficult to reverse (Côté et al. 2004). On a positive note, the persisting axis deer population partly sustained hunters' motivation and efforts to control wild boar and therefore contributed to program sustainability.

Optimal allocation of the intensity of hunting effort over space and time (Gamelon et al. 2012), rather than simply increasing total effort, may contribute to further reductions of deer and wild boar abundance without creating undesired disturbance and enhanced avoidance behavior. Program effectiveness may be improved by identifying and targeting park sections including high-quality ungulate habitat under lower hunting coverage, and by increasing hunting pressure on juvenile and adult females at appropriate times, on a species-specific basis. More generally, the program should develop quantitative management goals based on the functional relationship between damage

attributable to axis deer (yet to be gauged) and deer density (Hone 2007).

Likewise for wild boar at the park (Gürtler et al. 2017) and in other protected areas, cessation of culling may lead to rapid deer population recovery, which emphasizes the need for more effective, sustainable control of exotic ungulates. Collaborative management with local land owners and expanding efforts to a regional scale may be crucial to keep damage at acceptable levels. Current hunting policies of exotic ungulates need to be revised in the light of their current range expansion and presumed impacts in the region. Controlling axis deer may be problematic because it is a charismatic species, and there is a growing conflict of interest between sectors obtaining recreational or economic gains from the exploitation of exotic wildlife and sectors promoting the conservation of biodiversity. Reliable quantitative data on axis deer occurrence, density and damage at a broader scale are needed to gauge the magnitude of what appears to be a growing regional problem.

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#### Compliance with ethical standards

**Conflict of interest** The authors declare no conflict of interest.

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