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RESEARCH PAPER
https://doi.org/10.1071/WR23127

WILDLIFE RESEARCH

Taylor's law and quasi-experimental hunting of invasive wild boar and axis deer in a protected area of north-eastern Argentina

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Handling Editor:
Peter Brown

Received: 10 October 2023
Accepted: 1 May 2024
Published: 23 May 2024

Cite this: Gürtler RE *et al*. (2024) Taylor's law and quasi-experimental hunting of invasive wild boar and axis deer in a protected area of north-eastern Argentina. *Wildlife Research* **51**, WR23127. doi:10.1071/WR23127

ABSTRACT

Context. Overabundant ungulate populations frequently cause ecological and economic damage and are difficult to control. Sustained culling efforts at El Palmar National Park have largely reduced wild boar (*Sus scrofa*) numbers and damage but have failed to halt the ever-increasing abundance of axis deer (*Axis axis*) for undefined reasons. Multi-year camera-trap surveys indicated a mismatch between deer core activity and the usual timing of hunting sessions. **Aim.** We used the spatial and temporal forms of Taylor's law (TL, a power relationship between the sample mean and sample variance) to test whether overnight hunting sessions are more effective for culling axis deer and wild boar than are daytime sessions, and assessed whether they modify ungulate harvest composition. **Methods.** We implemented a quasi-experimental trial (i.e. 'experiments in which units are not assigned to conditions randomly'), including nine alternating blocks of four to seven hunting sessions each (overnight or daytime) in which an average of 42 hunter groups performed controlled shooting over bait from fixed elevated blinds, retrieved, sexed, weighed and measured all quarry. **Key results.** The relationship between the mean and variance of ungulate crude catch per hunting-party session and crude catch per unit effort (CPUE, where effort is measured in hunting-party hours) by hunting shift satisfied the spatial and temporal TL. On average, axis deer catch was 2.39–2.61 times greater in overnight than in daytime sessions, whereas CPUE indices were 1.54–1.73 times greater. For wild boar, overnight sessions returned catches similar to (0.94–1.03×), and a significantly lower CPUE (0.63–0.67×) than for daytime sessions. The harvest indices were substantially aggregated in daytime sessions only, and were consistently skewed towards yearlings or subadults and males, especially among adult deer. Overnight sessions culled proportionally more adults and more pregnant hinds and sows than did daytime sessions, and significantly heavier deer and wild boar males. **Conclusions.** Overnight sessions were substantially more effective for culling deer than were daytime sessions, and selected for individuals with greater fitness. Stage- and male-skewed harvest most likely explains the steady population growth of axis deer despite increasing hunting pressure over a decade. **Implications.** Adjusting the schedule of hunting sessions to time intervals of peak ungulate activity substantially increased the efficiency of management efforts in terms of removal rates and reproductive value of the culled specimens.

Keywords: abundance, *Axis axis*, controlled shooting, invasive exotic species, population dynamics, *Sus scrofa*, Taylor's law, ungulates, wildlife management.

Introduction

Several ungulate species have become overabundant (relative to human preferences) in their native and introduced ranges and cause economic and ecological damage (Nugent *et al*. 2011; McShea 2012; Davis *et al*. 2016; Carpio *et al*. 2021). Top in the list features wild boar, its hybrids with domestic pigs (*Sus scrofa*) and several deer species, including axis deer (*Axis axis*, chital or Indian spotted deer). Both ungulates affect plant community structure and dynamics, raid crops, transmit several zoonotic pathogens of global concern, cause traffic accidents and pose other threats that warrant management efforts (Hone 2002; Campbell and Long 2009; Hess *et al*. 2015).

Management of wild boar and deer populations has been conducted through shooting with firearms from the ground, vehicles, and helicopters; hunting with trained dogs; poisoned baits; walk-in baited traps and snares, and fencing (Choquenot *et al.* 1996; Campbell and Long 2009; Massei *et al.* 2011; Bengsen *et al.* 2020). Hunting usually imposes some selective pressure on individuals of specific sex, age or size class, regardless of whether selectivity is intentional or derives from the relative vulnerability of some individuals or stages to specific hunting methods. Therefore, hunting affects the population structure and growth rate of target populations (Festa-Bianchet 2003; Milner *et al.* 2007). In theory, for polygamous mammalian wildlife, the most productive populations are those with a female-skewed sex ratio above a threshold of male breeders (Milner *et al.* 2007; Fryxell *et al.* 2014, p. 379).

Ungulates may react to hunting pressure, depending on its type and intensity, by modifying their diel activity and habitat-selection patterns, as they do with other sources of anthropogenic disturbance (Lewis *et al.* 2021; Tucker *et al.* 2023). Wild boar in undisturbed areas are apparently active in daytime, and under intense hunting pressure adopt more nocturnal habits, shift home-range location and size or even remain within the same area of cover despite intense disturbance by hunting dogs; however, such patterns vary widely among locations (Mcilroy and Saillard 1989; Mayer 2009*a*; Johann *et al.* 2020). A recent review of the effects of recreational hunting on wild boar behaviour concluded that the results in the literature were mixed and often contradictory, with the impact of hunting possibly depending on the past intensity of disturbance that the animals had faced (Keuling and Massei 2021). Axis deer are most active at dawn and dusk in their native range in India (Rajawat and Chandra 2020), and more nocturnal during spring and summer under year-round hunting pressure in Croatia (Centore *et al.* 2018). The activity patterns of wild boar and sika deer (*Cervus nippon*) shifted towards daytime during the non-hunting season and became more nocturnal as non-hunting human disturbance increased, after the onset of the hunting season, and with high-intensity culling efforts during daytime (van Doormaal *et al.* 2015; Ikeda *et al.* 2019).

Introduced to the Southern Cone countries (Argentina, Bolivia, Brazil, Chile, Paraguay and Uruguay) of South America over the late 19th and early 20th Centuries, wild boar of Eurasian lineage and axis deer have expanded their range and thrive in many protected areas (Ballari *et al.* 2019; Tellarini *et al.* 2019; Cuevas *et al.* 2021; Hegel *et al.* 2022). In north-eastern Argentina, wild boar largely affected the recruitment of *Butia yatay* palm trees, the main conservation value at El Palmar National Park (hereafter, the park). The managers of the park appealed to local recreational hunters to launch intensified control efforts via hunting with dogs and controlled shooting over bait from elevated blinds distributed throughout the protected area (Gürtler *et al.* 2023). These efforts quickly dropped the relative abundance of wild boar, the intensity of soil damage (rooting) and mortality of palm-tree seedlings (Gürtler *et al.* 2023), but failed to reduce the relative abundance of axis deer over a 10-year period, despite substantial increases in shooting effort (Gürtler *et al.* 2018). Adjacent forest plantations were excluded as a deer refuge (Burgueño *et al.* 2022). One potential explanation for the failure to reduce axis deer abundance was that it may have developed an evasive behaviour in response to the fixed type of culling method employed for more than a decade (i.e. daytime shooting starting in the evening vs occasional overnight sessions). Extensive camera-trap surveys over a 4-year time period showed a mismatch between daytime hunting efforts and the two main bouts of axis deer activity, which occurred after midnight (Nicosia *et al.* 2021, 2023). This suggested the testable hypothesis that overnight hunting would augment the efficiency of culling efforts relative to daytime sessions.

Testing this hypothesis in the field is not straightforward. Wildlife management studies are usually observational and offer few opportunities for conducting replicated manipulative experiments (Morrison *et al.* 2008, but see Hone *et al.* 2017). In practice, randomisation may be operationally unfeasible, unaffordable or unethical. For example, a systematic review of ground-based shooting of overabundant mammal populations identified very few studies that randomised treatments (Bengsen *et al.* 2020). Quasi-experimental studies (i.e. 'experiments in which units are not assigned to conditions randomly', according to Shadish and Cook (2002), p. 12) offer the next-best possible solution. Among them, interrupted time-series analysis is especially valuable for evaluating the effectiveness of population-level interventions implemented over a clearly defined time period (Bernal *et al.* 2017).

A second challenge faced by wildlife management trials is analytical. The large spatial and temporal variability in the population abundance of the target species, especially when these are invasive organisms under control pressures promoting evasive responses, frequently makes it more difficult to assess the impact of alternative tactics. Hunting, in particular, is affected by weather variations (Baur *et al.* 2021; Elliott and Harms 2023), which tend to occur at random. In hundreds of species (Taylor 2019), variability in population density tends to increase with an increasing mean density according to Taylor's law (TL) (Taylor 1961). TL relates the sample variance v to the sample mean m of population density or abundance through a power law $v \asymp 10^a m^b$, or equivalently, a linear relationship on log–log coordinates, $\log_{10} v \asymp a + b \times \log_{10} m$. In most organisms, the slope b ranges between 1 and 2, but, in general, b values depend on the mechanisms generating variability in population density. In the temporal form of TL, n populations (labelled i) followed over time provide an estimate of the sample mean and the sample variance of population size averaged over time for each individual population i (Cohen *et al.* 2017*a*). The temporal TL describes the sample mean and sample variance if $\log_{10} v_i \asymp a + b \times \log_{10} m_i$ for all populations i. In the spatial TL, different populations occurring in specific sites are grouped by distinct time periods (labelled t) and the mean and variance of population size in these sites at time t provide one pair of data (spatial mean m_t, spatial variance v_t) for each time t. The spatial TL describes these paired data if they are well approximated by a least-square linear regression of $\log_{10} v_t$ as a function of $\log_{10} m_t$ for all times t.

Empirical examples of TL include parasites (Cohen *et al.* 2017*b*), human population densities (Cohen *et al.* 2013*a*), forest trees (Cohen *et al.* 2016), and crop yields (Döring *et al.* 2015), among many others. Taylor's law can be generated by many different models, including the Cohen–Lewontin stochastic population growth model (Cohen *et al.* 2013*b*). TL described well the relationship between the temporal and spatial mean and variance of the relative abundance of wild boar and axis deer by controlled shooting over a 10-year period at the park (Gürtler and Cohen 2022). This analysis (1) showed no significant effects of hunting shift (daytime vs overnight) on the parameter values of the spatial TL for either species, and (2) overnight sessions yielded 36–39% greater mean crude catches of both ungulates than did daytime sessions, although these were not significantly greater. These comparisons, based on an imbalanced data set collected for other purposes, suggested an effect but did not provide conclusive evidence on the relative effectiveness of hunting shifts.

Here, we report the outcomes of a quasi-experimental trial designed to test whether overnight sessions of controlled shooting over bait were more effective for culling axis deer, and similarly effective for wild boar, than were the routine daytime sessions. The trial involved successive blocks of four to seven hunting sessions, each being held park-wide, over 18 months. The response variables were crude catch per hunting-party session and crude catch per unit effort (CPUE, where effort is measured in hunting-party hours) for each ungulate species. A 'hunting party' represents a group of hunters hunting together (using the same blind) on a particular occasion (session), regardless of whether they shot and dispatched any exotic ungulates. A 'hunting session' is the activity of a hunting party on a given day over one continuous time interval. We also tested whether overnight and daytime sessions affected the harvest composition of both ungulate species by selecting for individual attributes (stage, sex, pregnancy status and body mass) closely linked to fitness.

Materials and methods

Study area

El Palmar National Park (31°55′S, 58°16′W), in Entre Ríos, north-eastern Argentina, is the last relict of a severely threatened ecosystem, the palm-tree savanna of *B. yatay*. It has 8200 ha of savannas, grasslands, scrublands and gallery forests surrounded by forest plantations, sometimes mixed with small cattle ranches, with patches devoted to agriculture, a fast highway corridor, and the Uruguay River (Gürtler and Cohen 2022). The increasing expansion of several exotic trees and shrubs in the park, closely linked to the suppression of spontaneous fires and exclusion of cattle in 1970, has provided a good cover for exotic ungulates to hide.

The park is traversed by a permanent stream, which divides it into a public (northern) zone open to park visitors and a restricted (southern) zone closed to tourists, and several secondary streams. The mean annual temperature over 2006–2015 was 19.8°C, and the annual mean rainfall was 1389 mm at the closest weather station in Concordia. Although the regional climate lacks a distinctive dry season, rainfall varies widely from year to year and severe droughts used to occur approximately once in a decade, but they did not occur over 2018–2019. Dry periods mainly span from the late austral fall through the austral winter. Although some degree of poaching targeting deer and capybaras occurs in some park sections, it is unlikely to affect deer and wild boar culling rates.

Management program of exotic mammals

The program launched in 2006 aimed to reduce ground rooting area, mortality of yatay palm-tree seedlings and the abundance of axis deer by using operating procedures that changed little since its inception (Gürtler and Cohen 2022; Gürtler *et al.* 2023). The park recruited local recreational or subsistence hunters to cull wild boar and axis deer by using dogs (mainly over 2006–2007) and controlled shooting over bait from elevated blinds built in designated places from 2006 on. Program-affiliated hunters were required to comply with regulations and typically developed a long-term relationship with the park that was renewed every year through signed agreements; hunter turnover rates were low. The dates and duration of hunting sessions were stipulated by park management in consultation with the two hunter associations 'Club de Caza Mayor, Menor y Tiro Conservación Tierra de Palmares' and 'Asociación Reguladores de Mamíferos Exóticos Invasores'. Hunters possessed valid firearm and game licences, insurance coverage, and a clean medical bill. In practice, weather conditions determined whether a session was conducted as scheduled; the number of parties that participated in a session was defined by the choices of individual hunting parties. Hunters were allowed to take home 50–75% of each kill and the remainder was donated to local public schools, community shelters, and retirement homes.

Ethics approval

The trial was conducted as part of an ongoing management program of exotic ungulates in a protected area under federal jurisdiction, sanctioned in 2005, in compliance with Ley 22351 ('Parques Nacionales, Monumentos Naturales y Reservas Nacionales'); Ley 24375, adhering to the Convention on Biological Diversity, and Resolution HD 172/2007 on 'Lineamientos estratégicos para el manejo de especies exóticas en la APN'. Shooting operations did not require additional Animal Ethics approval.

Study design

We conducted a quasi-experimental trial involving nine alternating blocks of four to seven hunting sessions each, where each block included only daytime or only overnight sessions. Treatments were assigned systematically, starting with the traditional daytime hunting shifts, to ensure that both treatment arms were as much interspersed as possible while providing a fair number of repeat sessions within each block to allow for the natural variability in the relative abundance and harvest of wild boar and axis deer. The trial was run over 18 months to cover all seasons and inherent variations in the reproductive biology of both ungulate species.

Preparatory meetings were held to promote stakeholder participation in the trial. First, the results of camera-trap surveys and the status of axis deer and wild boar control were reviewed jointly by park management and researchers. A second meeting assessed the design, implementation and feasibility of the trial described below. Third, program hunters were convened to a large meeting with park management and researchers, to further discuss the rationale of the trial and provide feedback on all aspects. The trial proposal was well received, in part because it entailed additional hunting opportunities and promise of increased harvest, and sanctioned for implementation. Daytime (or diurnal) sessions were conducted usually on Wednesday or Friday evenings between 1600–1800 hours and 2200–2400 hours. Overnight sessions nearly always started slightly before or after Saturday midnight and lasted until Sunday morning, from 2300–2400 hours up to 0700–0800 hours. On average, overnight sessions were 2 h longer than daytime sessions to extend to a few hours after dawn when both ungulates are active.

The first block started in early winter and involved five daytime hunting sessions every 7–14 days (13, 23 and 30 June, 4 and 18 July 2018) to provide baseline (reference) values of relative abundance by using the standard schedule and procedures. The second block (i.e. first perturbation pulse) comprised five successive overnight sessions every 7–14 days (29 July, 5, 12 and 27 August, 9 September 2018) by using the same procedures as in the daytime sessions. The third block covered four daytime hunting sessions (12, 15 and 26 September, 3 October); one planned session was cancelled because of a sudden storm and persistent bad weather. The fourth block included five overnight sessions as in Block 2 (20 and 27 October, 4, 11 and 17 November 2018). The fifth block included five daytime sessions (28 November, 1 and 19 December 2018, and 6 and 16 February 2019), interrupted by the summer vacation period involving a large influx of park visitors and campers. The sixth block included five overnight sessions (24 February, 9, 16 and 24 March, 6 April 2019). The seventh block comprised five daytime sessions (12 and 24 April and 11, 18 and 25 May 2019). Hunting sessions were halted during winter holidays; spotlight hunting from vehicles removed 180 axis deer over 18 sessions conducted over 1 July–5 August 2019. The eighth block involved seven daytime (rather than overnight) sessions (7 and 28 August, 7, 14, 18, 21 and 25 September 2019), on the basis of a joint decision of park management and hunter associations. The ninth block included seven overnight sessions (28 September, 5 and 25 October, 9 and 23 November, and 1 and 8 December 2019).

Weather conditions during the trial were recorded by the park weather station (Davis, Vantage VUE Model 6351) up to 25 May 2019. Temperature varied similarly between daytime (mean 16.0°C, s.e. 1.1°C, min 7.8°C, max 24.1°C) and overnight (mean 14.4°C, s.e. 1.4°C, min 2.0°C, max 25.0°C) sessions, as did wind speed in daytime (mean 3.2 km/h, s.e. 0.7 km/h, min 0 km/h, max 10.4 km/h) and overnight sessions (mean 3.9 km/h, s.e. 0.8 km/h, min 0 km/h, max 8.2 km/h). Two overnight sessions displayed extreme weather conditions; one (5 August 2018) was held at an average of 2°C (range, 1–4°C); the other (24 February 2019), affected by a sudden summer storm with strong winds and heavy rainfall (34 mm/h), was held despite conditions that would normally lead to cancelling activities.

Hunting procedures

For controlled shooting, hunters were required to deploy bait (corn, soybean and blocks of salt) once or twice during the week before the scheduled hunting sessions, and were allowed to shoot along 5–20 shooting lanes (200–300 m long and 3–5 m wide) cleared of vegetation around each blind. Hunters were requested to cull as many exotic ungulates as possible regardless of sex or condition and to immediately report any shot, successful or not. All hunting parties had to communicate with the supervising park ranger through a VHF radio to announce when they would descend from the blind to retrieve the quarry, when they returned to duty, and when they reached and left the premises. There were no catch quotas, and park hunters have always been required to conduct non-selective culling. Trophy hunting was discouraged (only one annual trophy was allowed to each party), and no incentives were provided to increase culling rates.

All 51 blinds existing over 2018–2019 remained at fixed positions and were operated by the same hunting parties. Each hunting party was required to register two authorised shooters and one assistant, who aided in spotting, retrieving and processing the quarry. In practice, program regulations did not require that both shooters should occur together. Hunters used high-powered rifles with designated calibres (usually 0.270, 0.300, 0.308 and 0.30-06 loaded with moderate to heavy-weight, lead-based, soft- or hollow-point bullets, i.e. 150–180 grains), night vision equipment and no muzzle blast suppressor. Follow-up shots were applied if required. Active hunting parties are those who participated in a hunting session, regardless of whether they culled any specimens or not and of how long they hunted.

All hunters registered at a central operating post an hour before starting a scheduled session and returned to this post at its completion to process the quarry, collect data of every individual specimen, and obtain transport permits before leaving park premises. Every specimen was weighed, measured, sexed, butchered, and uniquely identified with a pre-marked plastic tag. Body mass was measured with a spring scale. Other body measurements (body length, measured from tip of snout to base of the tail; height at withers; thorax diameter; tail, ear and metatarsus length) were taken on intact quarry with a non-stretching tape to the nearest centimetre. Apparent pregnancy status and the number of embryos were assessed visually and recorded systematically; failure to detect small embryos by visual assessment is expected to occur at a constant rate regardless of hunting shift and occasion. Park staff recorded the information in an individual form for every hunting party attending a session; records included date, hunters' names, hunting method, initiation and termination times of the session, firearms and calibres, reported time at culling, and whether any boar or deer was wounded and escaped (i.e. incapacitated). In 2019, park staff registered the approximate shooting distance to a culled specimen as reported by hunters, on the basis of the relative distance to bait sites deployed on each shooting lane.

In the absence of age data, we used body length as a state variable to approximate the population stage structure. In hunted wild boar, log-transformed body length was strongly and linearly related to log-body mass in each sex, and both traits showed a logarithmic relationship with age approximately up to 36–39 months (Dzięciołowski *et al.* 1990; Markina *et al.* 2004; Cellina 2008, figs 3.2, 3.9, 3.24). In captive axis deer, body mass also increased with log-transformed age (Chapple 1989, fig. 2.2.1); we are unaware of any data connecting log-body length and age for axis deer. For simplicity, we assigned all ungulate specimens to the following four stages on the basis of Moretti (1995) for wild boar: juveniles, <100 cm (aged ~4–8 months); yearlings, 100–120 cm (aged ~8–12 months); subadults, 121–135 cm (aged ~13–18 months); and adults (i.e. full-grown), ≥136 cm (aged >19 months, combining Moretti's Classes 4 and 5). On the basis of tooth eruption, Mayer (2009*b*, p. 35) denominated the following five stages: piglets (approximately <9 months), juveniles (9–12 months), yearlings (13–19 months), subadults (20–35 months) and adults (≥36 months). The age at first breeding among female wild boar averaged 6 months and was widely variable (up to 18 months) depending on food quality and genetic makeup; the threshold female body mass for reproduction ranged from 20 to 35 kg (Comer and Mayer 2009, p. 53). Axis deer hinds may conceive at 9 months of age and at about 23 kg if well nourished (Chapple 1989). For 25 ungulates with data for bodyweight but not for body length, we classified them to stage on the basis of the species- and sex-specific allometric equations between log-bodyweight and log-body length estimated from the trial data. Sex information was not recorded for 39 deer and 9 wild boar, stage for two deer and one wild boar, and body mass for 14 deer and 3 wild boar.

Data analysis

All data used in this study are included in this published article and its supplementary information files (Table S1). The code used for TL analysis has been included as supplementary files elsewhere (Gürtler and Cohen 2022, appendix S1).

We tested the adequacy of Taylor's law as a description of the data in three steps following the account in Cohen *et al.* (2017*a*). We adhere to our previous definitions for harvest indices as metrics of ungulate relative abundance (Gürtler and Cohen 2022). Catch is the number of specimens culled by a hunting party j during a fraction or the whole of a hunting session by using a given hunting method, and includes a few discarded specimens in a poor body condition. Wounded specimens that escaped (as reported by hunters) were excluded from catch estimates. Hunting effort is the sum of hunting-party hours for a given hunting party and session, regardless of whether the party caught any boar or deer, and regardless of whether there was one shooter or there were two shooters on a hunting blind in a given session (see Fig. S1). Hunting success was measured as the proportion of active hunting parties that culled at least one quarry over a defined time period (e.g. session).

All statistical procedures used Stata (ver. 15.1, Stata Corporation, College Station, TX, USA). First, for each ungulate species separately, for each session separately, we computed the sample mean, m_t, and the sample variance, v_t, of the crude catch and (separately) the crude CPUE across every active hunting party. Then, we performed an ordinary least-squares linear regression of $\log_{10} v_t$ on $\log_{10} m_t$, across all trial sessions conducted from June 2018 to December 2019, for each ungulate species and hunting shift. Analyses always complied with the requirements that the mean abundance at each session was greater than 0, and at least 15 observations (i.e. hunting parties) for each session were used to calculate each mean and variance, and that the linear regression for a given species and hunting shift should include at least five paired data of v_t and m_t (Taylor *et al.* 1988, p. 721). All data were included in the calculations, including the two outliers occurring in overnight sessions.

Second, we tested for curvature in the relation of $\log_{10} v_t$ to $\log_{10} m_t$, by fitting a quadratic regression $\log_{10} v_t = a + b \times \log_{10} m_t + c \times (\log_{10} m_t)^2$ by least squares. We examined the residuals of the linear regression models for heteroscedasticity, normality, skewness and kurtosis by using the commands swilk, estat hottest and estat imtest.

Third, when the analyses in steps 1 and 2 did not reject TL, we used analysis of covariance (ANCOVA) to test for differences in the slope and intercept of the species-specific TLs fitted to different subsets of the data (i.e. hunting shifts). For example, one ANCOVA treated 'hunting shift' as a categorical variable and asked whether 'hunting shift' and the interaction term 'hunting shift × log-sample mean' significantly influenced log-sample variance. If 'hunting shift' influenced log-sample variance but not the interaction term, then the intercept of TL differed between hunting shifts. If the interaction term influenced log-sample variance, then 'hunting shift' affected the slope. If both 'hunting shift' and the interaction term influenced log-sample variance, then both the intercept and the slope of TL depended on the hunting shift. We used Welch's *t*-test for two quantities with unequal variances to compare slope estimates between hunting shifts. We also used Student's *t*-tests to examine whether the slope b differs significantly from the value 1 expected from a Poisson distribution (i.e. to determine whether the variance responds to any source of variation other than pure random fluctuations).

A helpful reviewer asked whether seasonal differences in target species behaviour would influence harvest susceptibility and lead to bias. We investigated the potential effects of time of year on harvest metrics in the following two ways: (1) by extending a spatial TL with separate terms for selected weather variables (i.e. mean temperature, mean wind speed, and the mean of their product, taken as continuous variables) in separate regressions for daytime versus overnight sessions. The weather variables were averaged over the half-hours of weather data included within the maximum time span of each hunting session; and (2) by means of a linear mixed regression model of log-crude catch per hunting party as a function of hunting shift, mean temperature, mean wind speed and the mean of their product (computed as above) for each exotic ungulate. We ran the same models for log-CPUE as the response variable. These analyses of weather effects included fewer data than the key comparison between daytime and overnight trial sessions because the local weather station stopped working by the end of the first year of the trial.

To address the potential occurrence of a confounding effect of uncontrolled variation in the average number of shooters per hunting party at an identified blind i across all trial sessions (mn_shooters_i, ranging from 1 to 2), we used a temporal TL to test for hunting-shift effects on the log-variance of ungulate harvest indices. The regression model was as follows:

$$\log_{10} v_i = a + b \times \log_{10} m_i + c \times \log_{10} m_i \times \text{shift} + d \times \text{shift} + e \times \text{mn\_shooters}_i + f \times \text{shift} \times \text{mn\_shooters}_i$$

In a related question, we tested whether one versus two hunters influenced the log-transformed harvest indices + 1 (y, standing for 'yield') of each ungulate species at each hunting blind and session. To answer this question, we used a linear mixed regression model separately for each harvest metric, separating wild boar from deer, as follows:

$$y \sim a + b \times \text{shift} + c \times \text{shooters} + d \times \text{shift} \times \text{shooters},$$

where shooters and hunting shift are binary predictors.

The time trend of log-transformed harvest indices as a function of time elapsed since trial initiation (in days) was examined by ordinary least-squares regression. The equality of proportions of males in consecutive stages (yearling to subadult, subadult to adult) was tested separately for each ungulate species by using the prtest command in Stata, with data being clustered by hunting block and an intraclass correlation coefficient of 0.2. We examined the association between stage (outcome variable with four levels, with juveniles as the reference base) and hunting shift (two levels: daytime and overnight sessions) by using multinomial logistic regression with robust standard errors. Similarly, we tested the effects of stage, hunting shift and their interaction on sex and pregnancy status (outcome binary variables) by using multiple logistic regression.

Results

Aggregate findings

The trial included 2033 hunting parties attending 48 sessions grouped into nine blocks (Table 1). The number of hunting parties per session averaged 43 (daytime) and 41 (overnight) and displayed no significant time trend. On average, daytime sessions lasted 4.7–6.0 h and overnight sessions lasted 7.2–8.4 h. In total, 1626 axis deer, 361 wild boar and two exotic ungulates not identified to species level were culled over 12,702 hunting-party hours. The overall mean ratio of deer-to-wild boar culled was 4.5 and varied from 1.5 to 4.2 among blocks of daytime sessions to 5.7–8.8 in overnight sessions. The number of deer culled per hunting party in overnight sessions (mean ± s.e., 1.21 ± 0.046, range 0–9) and daytime sessions (0.47 ± 0.023, range 0–5) were 7.0 and 2.6 times greater than the corresponding figures for wild boar (overnight: 0.17 ± 0.016, range 0–3; daytime: 0.18 ± 0.015, range 0–4).

Hunters reported the frequency of wounded-and-escaped (incapacitated) ungulates after each session, totaling 338 deer and 42 wild boar (plus 6 unidentified quarry) across the trial. These figures represented 17.2 and 10.4% of all (culled or incapacitated) quarry of each ungulate species respectively. The mean number of incapacitated deer per hunting party in overnight sessions (0.24 ± 0.021) doubled that in daytime sessions (0.11 ± 0.012), whereas for wild boar, overnight and daytime sessions returned the same figures (0.02 ± 0.005).

Table 1. Number of hunting sessions and participating parties, session duration, hunting effort and number of wild boar and axis deer culled according to daytime versus overnight hunting shift at El Palmar National Park, 2018–2019.

Block	Hunting shift	Number of sessions	Number of parties	Session duration (h)		Number of hunting-party hours	Wild boar	Axis deer	Deer-to-boar ratio
				Mean	s.e.				
1	Daytime	5	220	5.2	0.04	1144	27	93	3.4
2	Overnight	5	204	7.8	0.04	1583	31	194	6.3
3	Daytime	4	178	6.0	0.03	1061	28	43	1.5
4	Overnight	5	206	8.4	0.03	1736	35	245	7.0
5	Daytime	5	209	5.2	0.06	1079	62	100	1.6
6	Overnight	5	207	7.5	0.07	1551	47	269	5.7
7	Daytime	5	224	4.7	0.06	1043	46	122	2.7
8	Daytime	7	298	4.8	0.04	1437	41	173	4.2
9	Overnight	7	287	7.2	0.04	2067	44	387	8.8
Total	Daytime	26	904	5.1	0.02	7046	204	531	2.6
	Overnight	22	1129	7.7	0.02	12,048	157	1095	7.0
Grand total		48	2033	6.2	0.03	12,702	361	1626	4.5

When two hunters occupied a hunting site for 1 h within the allowed hunting interval, that counts as one hunting-party hour.
s.e., standard error.

The mean approximate shooting distance to a culled deer reported by park hunters in 2019 averaged 160 m (±2.7, range 20–290, n = 308) in daytime sessions and 163 m (±2.0, range 9–300, n = 587) in overnight sessions. For wild boar, these distances were on average 69% of those for deer (daytime: 115 ± 4.2 m, range 50–230, n = 114; overnight: mean 105 ± 4.2 m, range 60–220, n = 79). Shooting distances highly significantly differed between ungulate species in daytime (Welch's t = 9.2, d.f. = 213.9, $P < 0.001$) and overnight sessions (Welch's t = 12.3, d.f. = 116.0, $P < 0.001$).

The mean catch of axis deer per hunting party in overnight sessions nearly always exceeded the number removed in daytime sessions, with clear-cut differences between successive blocks (Fig. 1*a*). The two overnight sessions with extreme weather events displayed the lowest deer catches and similar numbers of wild boar as did other sessions; the maximum deer catch occurred right after one of the overnight sessions with extreme weather. A similar, though weaker, trend was recorded for crude CPUE (Fig. 1*b*). Unlike for deer, wild boar catch or CPUE showed no marked contrasts between shifts (Fig. 1*c*, *d*). One extreme data point (maximal for wild boar and submaximal for axis deer in daytime shifts) corresponded to the first annual hunting session after the 50-day summer break. The $\log_{10}$-transformed crude catch of axis deer significantly increased over time (measured in days, not in the number of the hunting sessions) across daytime sessions (slope ± s.e. = 0.00059 ± 0.00020, P = 0.007), and marginally increased across overnight sessions (0.00032 ± 0.00018, P = 0.08); the $\log_{10}$-transformed CPUE of axis deer significantly ($P < 0.001$) increased across daytime (0.00077 ± 0.00024) and overnight (0.00045 ± 0.00017) sessions. None of the time trends for wild boar indices was significant.

The log-mean crude catch of wild boar was not related to the log-mean crude catch of axis deer at each hunting session (Fig. 2). This independence was verified at the level of individual hunting parties across daytime (χ^2 = 2.72, d.f. = 6, P = 0.84) and overnight (χ^2 = 3.75, d.f. = 6, P = 0.71) sessions (Table S2). Overall hunting success during overnight sessions (65.7% = (904–310)/904) substantially exceeded the success achieved during daytime sessions (43.1% = (1129–642)/1129); these overnight and daytime figures were 60.4% (546/904) versus 33.7% (380/1129) for axis deer, and 13.5% (122/904) and 14.4% (162/1129) for wild boar respectively.

Spatial Taylor's law

The spatial TL was not rejected for crude catch per hunting-party session and crude CPUE of wild boar and axis deer in either hunting shift (Table S3), except for weak curvature effects on crude CPUE of wild boar in daytime shifts. Residuals were always normally distributed according to the Shapiro–Wilk test and showed no significant deviations from homoscedasticity. Hence, it was valid to compare hunting-shift effects by using ANCOVA.

For axis deer, ANCOVA showed significant (P = 0.021) effects of hunting shift on the slope of crude catch and strong effects on the slope (P = 0.005) and intercept ($P < 0.001$) of crude CPUE (Fig. 3*a*, *b*). TL fitted the data better in daytime sessions, with adj. R^2 ranging from 0.841 to 0.901, and displayed looser fits (adj. R^2 = 0.617 and 0.638) in

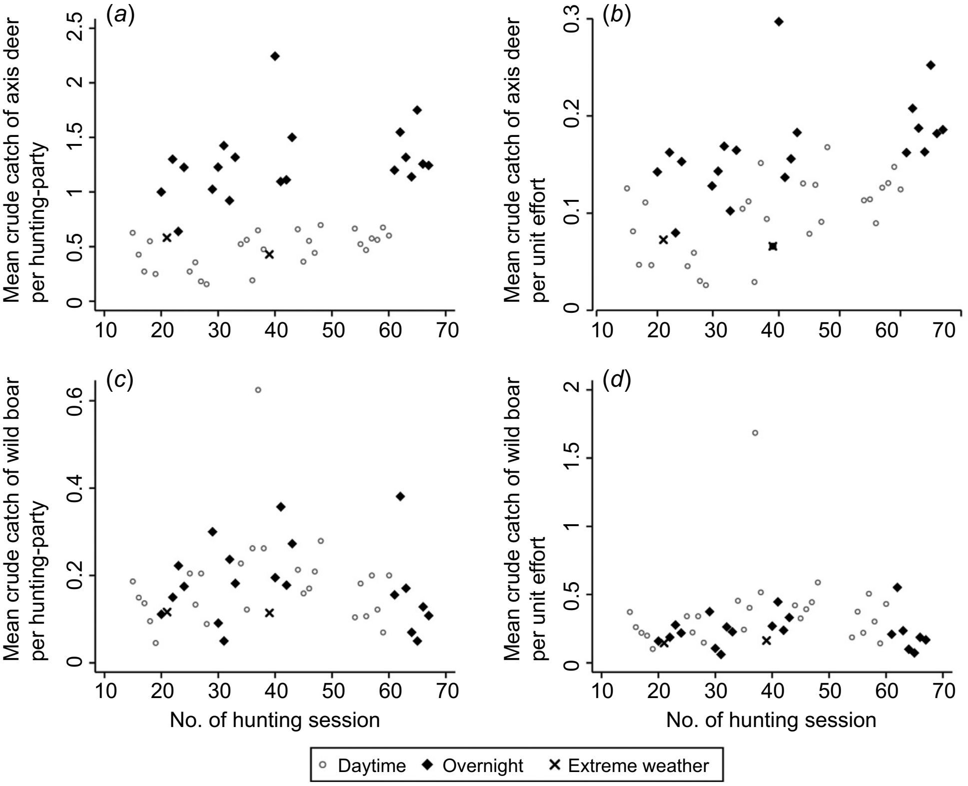

Fig. 1. (*a*, *c*) Mean crude catch per hunting-party session and (*b*, *d*) crude catch per hunting-party hour of (*a*, *b*) axis deer and (*c*, *d*) wild boar under conditions of controlled shooting from a fixed elevated blind according to daytime versus overnight hunting shift at El Palmar National Park, 2018–2019. x, an overnight session with extreme weather conditions.

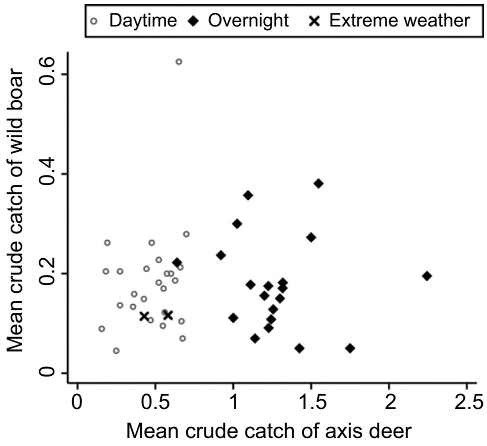

Fig. 2. Mean crude catch per hunting-party session of wild boar and axis deer under conditions of controlled shooting from a fixed elevated blind according to daytime versus overnight hunting shift at El Palmar National Park, 2018–2019. x, an overnight session with extreme weather conditions.

overnight sessions. The slopes of TL for crude catch in daytime (1.217 ± 0.105) and overnight (0.809 ± 0.131) shifts differed widely, and so did the slopes of TL for crude CPUE (1.463 ± 0.097 and 0.921 ± 0.156 respectively) (Table S3, Fig. 3*a*, *b*). Intercept estimates differed strongly from and were greater than 0 for crude catch only. Excluding the two outlier data points for overnight sessions with extreme weather conditions rendered the hunting-shift effects on slope and intercept not significant ($P > 0.10$) and aligned the regression lines of crude catch for both hunting shifts (not shown).

For wild boar, no significant ($P > 0.10$) effects of hunting shift on the slopes and intercepts of the spatial TL for crude catch and crude CPUE were detected by ANCOVA (Fig. 3*c*, *d*). The fit of TL was better than for axis deer (range of adj. $R^2 = 0.809–0.878$). The slopes of TL for crude catch varied little, from 1.241 (±0.092) to 1.133 (±0.100), in daytime and overnight shifts respectively, and likewise for crude CPUE, from 1.360 (±0.103) to 1.164 (±0.123) respectively (Table S3, Fig. 3*c*, *d*). Intercepts were significantly different from 0 for both metrics and shifts except for crude CPUE in daytime sessions.

We tested whether the slope coefficients *b* differed significantly from the value 1 expected from a Poisson distribution expressing pure random fluctuations. All *b* coefficients for daytime sessions in Table S3 were higher than 1; they differed significantly (crude catch) or highly significantly

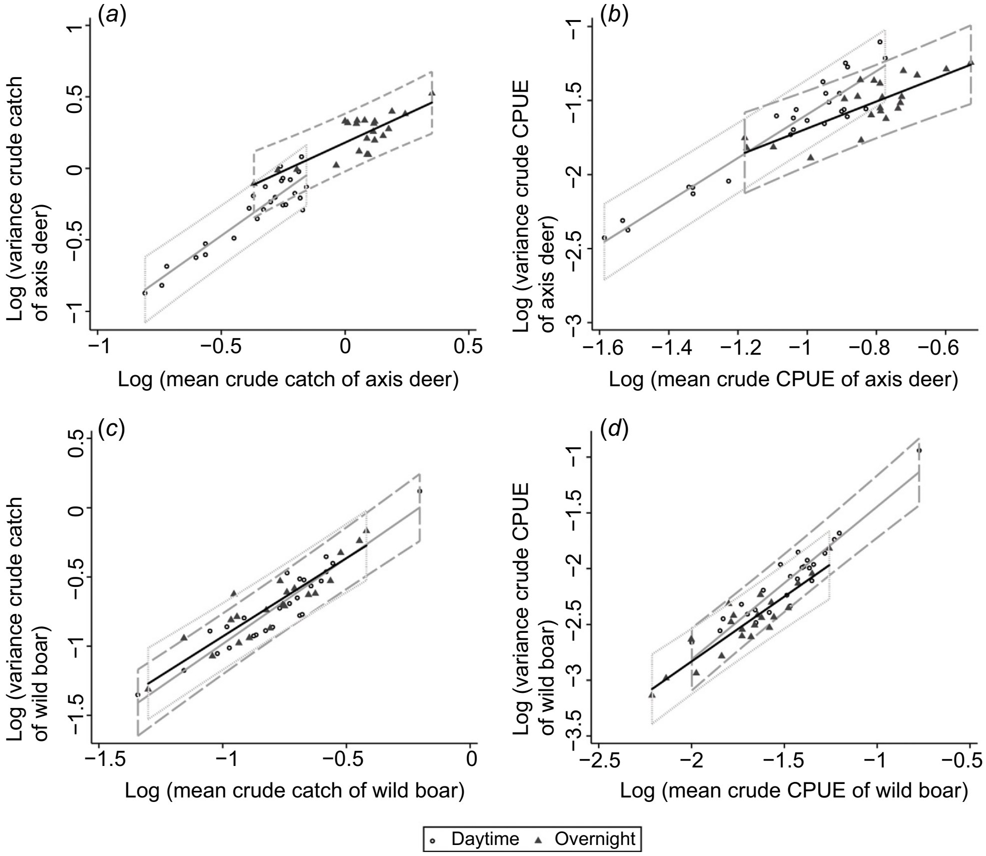

Fig. 3. The spatial TL described the relationship between $y = \log_{10} v_t$ and $x = \log_{10} m_t$ of the crude catch per hunting-party session and crude CPUE of exotic ungulates, under conditions of controlled shooting from a fixed elevated blind, according to daytime versus overnight hunting shift. Each point represents, on $\log_{10}$ axes, the spatial mean m_t and spatial variance v_t of (*a*, *c*) crude catch and (*b*, *d*) crude CPUE for (*a*, *b*) axis deer and (*c*, *d*) wild boar across El Palmar National Park over 2018–2019. The solid straight lines are fitted by least-squares regression to the data from each hunting shift separately. The dashed belt above and below each solid regression line represents a 95% confidence interval for individual residuals.

(CPUE) from 1 using Welch's *t*-tests. By contrast, none of the *b* coefficients for overnight sessions was significantly different from 1.

On average, across the trial, the back-transformed mean crude catch of axis deer per hunting-party session was 2.61 times greater in overnight than daytime sessions (Welch's $t = -8.3$, d.f. = 47.95, $P < 0.001$), and 1.73 times greater according to crude CPUE (Welch's $t = -4.2$, d.f. = 45.66, $P < 0.001$). For wild boar, overnight sessions displayed non-significant differences (0.94×) from daytime sessions for crude catch (Welch's $t = 0.4$, d.f. = 45.11, $P = 0.69$) and significantly lower crude CPUE (0.62×) than for daytime sessions (Welch's $t = 3.0$, d.f. = 46.92, $P = 0.005$).

Temporal Taylor's law

Both hunting metrics for axis deer and wild boar culled at identified blinds failed to reject TL, i.e. there was no significant evidence of curvature (Table S4). Adjusted R^2 ranged from 0.774 to 0.895. Only the slope $b = 1.206$ for daytime crude CPUE of wild boar differed significantly ($P < 0.01$) from 1 (Fig. 4, Table S4). Intercepts for crude catch were all but one significantly different from and greater than 0, whereas those for CPUE were all negative. Residuals for wild boar crude catch and crude CPUE in both shifts deviated highly significantly from normality and homoscedasticity.

ANCOVA of TL parameters yielded no significant differences between hunting shifts for both metrics and ungulate species. Axis deer crude catch ($t = -6.6$, d.f. = 99.69, $P < 0.001$) and crude CPUE ($t = -3.2$, d.f. = 99.76, $P = 0.002$) differed highly significantly between shifts; on average, across the trial, both metrics favoured overnight to daytime shifts by 2.39× and 1.54× respectively (Fig. 4). For wild boar, mean crude catch did not differ significantly between daytime and overnight sessions (1.03×) across the trial ($t = -0.2$, d.f. = 80.74, $P > 0.8$), whereas mean crude CPUE significantly disfavored overnight sessions (0.67×, $t = 2.3$, d.f. = 80.40, $P = 0.02$).

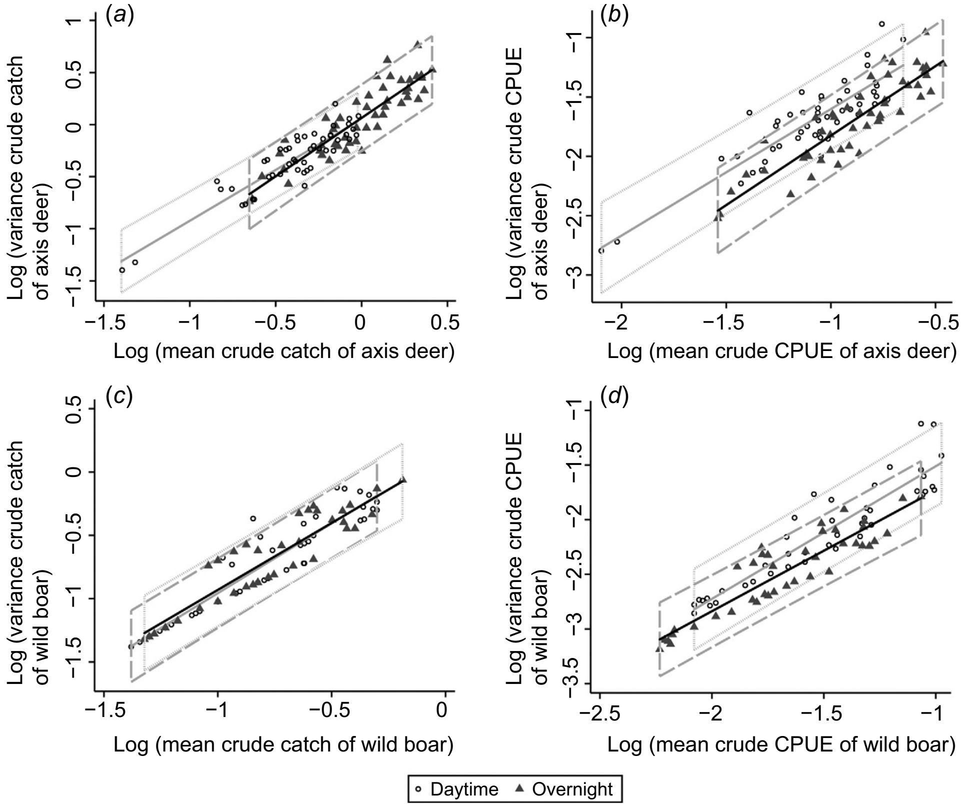

Fig. 4. The temporal TL described the relationship between $y = \log_{10} v_i$ and $x = \log_{10} m_i$ of the crude catch per hunting-party session and crude CPUE of exotic ungulates, under conditions of controlled shooting from a fixed elevated blind, according to daytime versus overnight hunting shift. Each point represents the temporal mean and temporal variance of (*a*, *c*) crude catch and (*b*, *d*) crude CPUE for (*a*, *b*) axis deer and (*c*, *d*) wild boar across El Palmar National Park at one hunting blind over 2018–2019. Key as in Fig. 3.

Weather and shooter effects

The outcomes of the extended spatial TL, including selected weather variables recorded during the hunting sessions, are shown in Table S5. For axis deer and both harvest metrics, we found weakly significant ($0.01 < P < 0.05$) effects of wind speed and its interaction with temperature only in overnight sessions. For wild boar, none of the metrics was significantly associated with any weather variable in either hunting shift. Similarly, using a linear mixed regression model of log-crude catch per hunting-party session (or CPUE) as a function of hunting shift and the mentioned weather variables, we found weakly significant ($0.01 < P < 0.05$) effects of mean wind speed and its interaction with mean temperature. Wild boar crude catch was not significantly related to any weather variable, whereas crude CPUE was weakly significantly ($0.01 < P < 0.05$) related to mean temperature and its interaction with mean wind speed. None of the interaction terms between hunting shift and each weather variable was significant.

We tested whether variation in the mean number of shooters at an identified hunting blind across sessions modified the relation between log-crude catch (or log-crude CPUE) and hunting shift using an extended temporal TL. For both harvest metrics and for both exotic ungulates, each taken separately, the mean number of shooters alone or in interaction with hunting shift exerted insignificant ($P > 0.3$) effects on the log-variance of catch or CPUE. To illustrate this, the scatterplots of log-mean and log-variance of ungulate crude catch by the mean number of shooters according to hunting shift are shown in Supplementary Fig. S1. The mean number of shooters at each hunting blind in daytime and overnight sessions was highly significantly correlated ($r = 0.986$, $n = 51$, $P < 0.001$), implying that each hunter group tended to keep a similar number of shooters across the trial, regardless of whether the session was in daytime or overnight. A spatial TL and a linear mixed regression model yielded the same qualitative results (not shown); neither the number of shooters nor its interaction with hunting shift was significant.

Harvest composition

The stage distribution of axis deer consistently displayed a relative excess of yearlings (44.5–52.8%, the modal class across every hunting block) and few juveniles (11.0–14.0%), regardless of whether the sessions were daytime or overnight (Fig. 5*a*). Overnight sessions returned a significantly greater mean fraction of subadult (25.5%) and adult (19.4%) deer than did daytime sessions (19.4% and 13.8% respectively) according to a multinomial logistic regression model (Wald $\chi^2 = 19.2$, d.f. = 3, $P < 0.001$, $n = 1625$ observations). The relative-risk ratio (RRR) of culling subadult deer was 1.67 times greater (95% confidence interval, 95% CI, 1.16–2.41, $P = 0.006$) during overnight versus daytime sessions relative to juveniles (the reference level), whereas for adult deer, the RRR was 1.77 times greater (95% CI, 1.19–2.62, $P = 0.005$) in overnight sessions, with no differences for yearlings (RRR = 1.07, 95% CI, 0.77–1.48, $P = 0.7$). For wild boar, juveniles fluctuated between 12.1% and 19.2% and adults increased from 15.8 (daytime) to 24.2% (overnight) (Fig. 5*b*). The stage distribution and modal class varied widely among blocks. Multinomial logistic regression showed no significant effect of hunting shift on the stage distribution (Wald $\chi^2 = 5.9$, d.f. = 3, $P = 0.12$, $n = 360$).

Overall sex ratios slightly favoured males in both axis deer (53.1–54.0%) and wild boar (55.2–56.6%) and did not differ significantly between hunting shifts in either species ($\chi^2 < 0.1$, d.f. = 1, $P > 0.7$) (Table 2). The stage–sex distribution by hunting shift differed between ungulate species (Fig. 5*c*, *d*). For axis deer, both in daytime and overnight sessions, the mean percentages of males were nearly balanced among juveniles (51.3 and 54.9%) and yearlings (52.0 and 51.4%) respectively, then fell to 35.2 and 42.7% among subadults, and were strongly skewed toward males (77.5 and 82.0%) among adults (Fig. 5*c*). The large skew among adult males was verified in eight of the nine hunting blocks across both shifts. Hence, the mean fraction of males across shifts *decreased* from yearlings to subadults by 14.3% (from 51.6% to 37.3%), and then the trend was reversed to a large mean *increase* of males (43.5%, from 37.3% to 80.8%) between the subadult and adult stages. A test of proportions showed that the differences between yearlings and subadults were not significant ($z = 1.1$, $n_1 = 752$, $n_2 = 373$, nine clusters, $P = 0.3$) and those between subadults and adults were significantly different ($z = -3.2$, $n_1 = 373$, $n_2 = 276$, nine clusters, $P = 0.002$). Multiple logistic regression confirmed the significant effects of subadult (OR = 0.54, 95% CI 0.38–0.77, $P = 0.001$) and adult (OR = 3.81, 95% CI 2.51–5.79, $P < 0.001$) stage on the proportion of males, and the lack of significance of hunting shift (OR = 0.93, 95% CI 0.74–1.16,

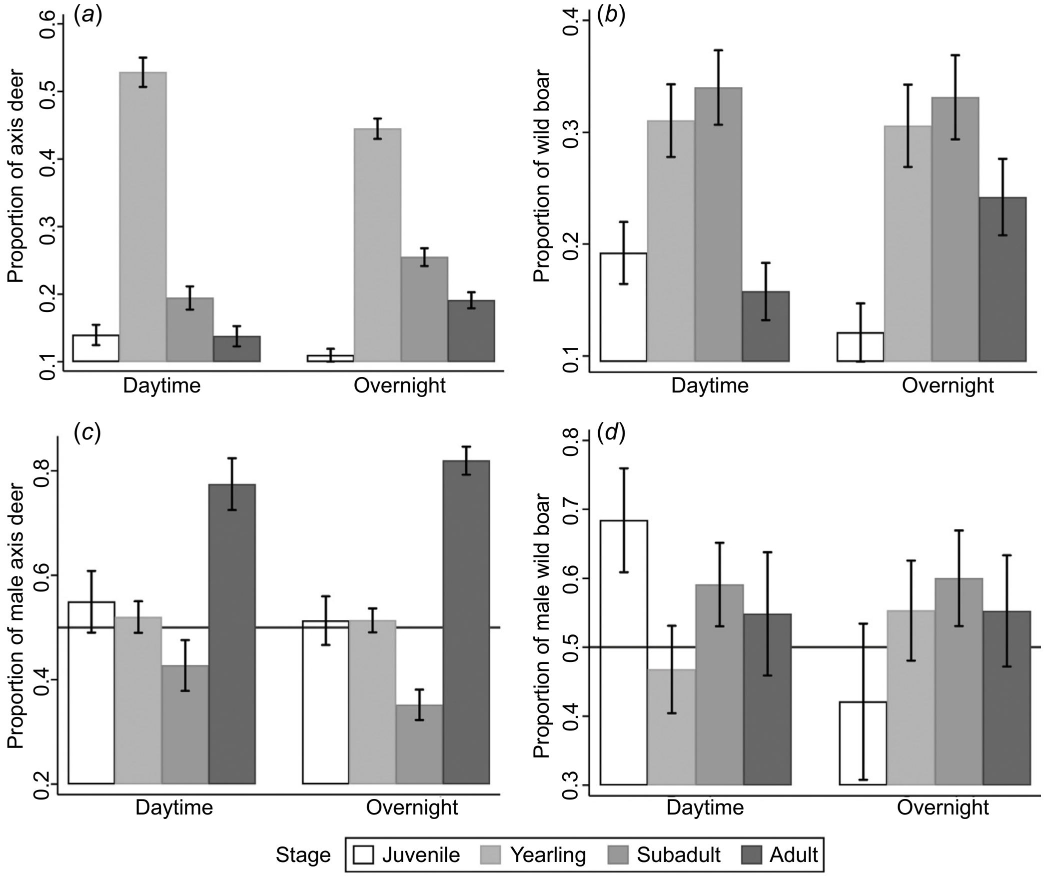

Fig. 5. (*a*, *b*) Stage and (*c*, *d*) sex distribution of axis deer and wild boar in daytime and overnight sessions at El Palmar National Park, 2018–2019. The horizontal lines represent 50% males. Bars represent the mean ± s.e.

Table 2. Distribution of sex ratio, apparent pregnancy status and sex-specific body mass and body length of wild boar and axis deer according to daytime versus overnight hunting shift at El Palmar National Park, 2018–2019.

Attribute	Statistic	Wild boar		Axis deer	
		Daytime	Overnight	Daytime	Overnight
Male sex (%)	Mean	56.6	55.2	54.0	53.1
	s.e.	3.5	4.0	2.2	1.5
	n	198	154	520	1067
Apparent pregnancy (%)	Mean	4.7	8.7	8.4	15.4
	s.e.	2.3	3.4	1.8	1.6
	n	86	69	239	500
Female body mass (kg)	Mean	52.4	54.9	37.9	41.9
	s.e.	2.3	2.7	0.9	0.6
	n	85	69	235	499
Male body mass (kg)	Mean	50.6	60.5	44.4	51.1
	s.e.	2.4	3.0	1.4	1.1
	n	111	84	279	564
Female body length (cm)	Mean	119.5	120.4	113.3	116.8
	s.e.	1.9	2.9	1.0	0.7
	n	83	69	231	500
Male body length (cm)	Mean	117.5	125.1	118.1	122.4
	s.e.	2.0	2.1	1.2	0.9
	n	107	84	272	566

s.e., standard error; *n*, number examined.

$P = 0.51$) (Wald $\chi^2 = 110.4$, d.f. $= 5$, $P < 0.001$, $n = 1587$). The interaction between stage and shift ($P = 0.5$) was not retained in the model.

For wild boar sex ratios, the fraction of males among juveniles varied widely between daytime (68.4%) and overnight (42.1%) sessions, but differences between hunting shifts were slight for yearlings (46.8% and 55.3%), subadults (59.1 and 60.0%) and adults (54.8% and 55.3%) respectively (Fig. 5*d*). Most hunting blocks displayed adult sex ratios slightly skewed to males. Unlike the deer, the mean fraction of male wild boar did not show any significant upswing between consecutive stage transitions from yearlings to subadults ($z = -0.7$, $n_1 = 109$, $n_2 = 116$, nine clusters, $P = 0.5$) and from subadults to adults ($z = 0.3$, $n_1 = 116$, $n_2 = 69$, nine clusters, $P = 0.7$). Multiple logistic regression confirmed the lack of effects of stage, hunting shift and their interaction ($P = 0.2$) on the fraction of male wild boar (Wald $\chi^2 = 6.5$, d.f. $= 4$, $P = 0.49$, $n = 351$).

The overall prevalence of apparent pregnancy among females of all stages was nearly two-fold greater in overnight than in daytime sessions in both axis deer (15.4% vs 8.4%) and wild boar (8.7% vs 4.7%) (Table 2). For axis deer, pregnancy rose steeply whenever the sessions shifted from daytime to overnight (Fig. 6*a*) and also increased with an increasing stage, ranging from 1.8 (juveniles, only one pregnant juvenile detected) to 40.5% (adults, with two peaks >60%) in overnight sessions and from 0% to 20.3% in daytime ones (Fig. 7*a*). Two of 97 pregnant hinds bore twins; the remainder had singletons. Multiple logistic regression of pregnancy status showed significant effects of overnight shift (OR = 1.77, 95% CI 1.03–3.05, $P = 0.04$), subadult (OR = 23.15, 95% CI 3.14–170.66, $P = 0.002$) and adult (OR = 40.53, 95% CI 5.21–315.13, $P < 0.001$) stage relative to juveniles (Wald $\chi^2 = 46.2$, d.f. $= 4$, $P < 0.001$, $n = 739$). For wild boar, most pregnancies were detected in hunting blocks conducted over winter and spring and none was detected in Blocks 1, 5 and 7 (Fig. 6*b*). Overall pregnancy increased with stage from 0% to 7.4% (daytime) and from 0 to 11.8–15.0% (overnight) (Fig. 7*b*). To allow model convergence, we classified stage in two levels (yearlings and later stages) and excluded

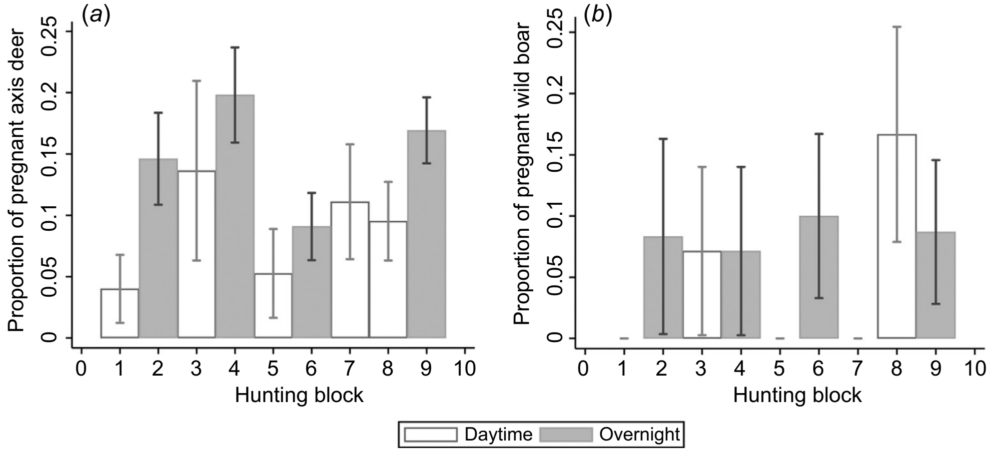

Fig. 6. Distribution of apparent pregnancy status over hunting blocks in (*a*) axis deer and (*b*) wild boar according to daytime versus overnight hunting shift at El Palmar National Park, 2018–2019. Bars represent the mean ± s.e.

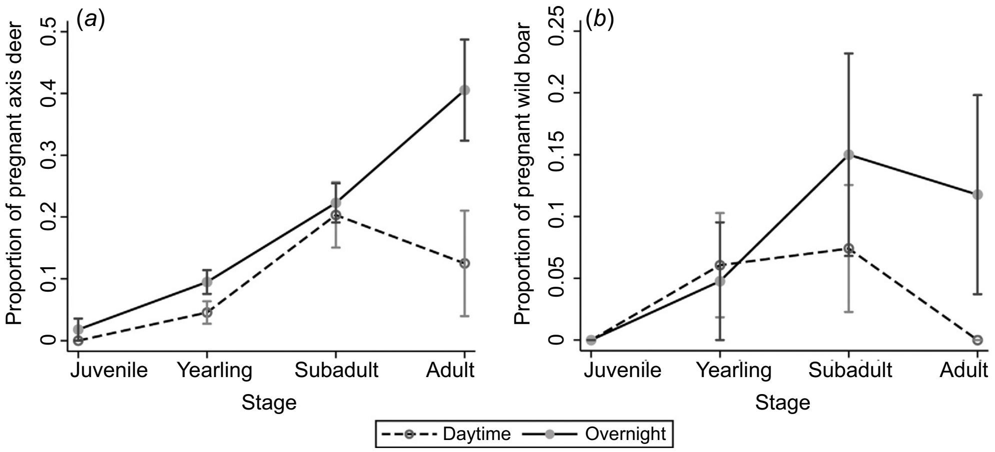

Fig. 7. Stage-specific prevalence of apparent pregnancy among females of all stages in (*a*) axis deer and (*b*) wild boar culled by controlled shooting according to daytime versus overnight hunting shift, 2018–2019. Bars represent the mean ± s.e.

juveniles and hunting blocks with no pregnant female. No significant effects of hunting shift, stage and their interaction on the relative odds of apparent pregnancy were detected (Wald $\chi^2 = 2.2$, d.f. = 3, $P = 0.52$, $n = 86$).

The distribution of axis deer body mass by sex is shown in Fig. 8*a*, *b*. Mean body mass was larger in overnight sessions than in daytime sessions by 4.0 kg (females) and 6.7 kg (males) respectively. The mean of log-transformed body mass

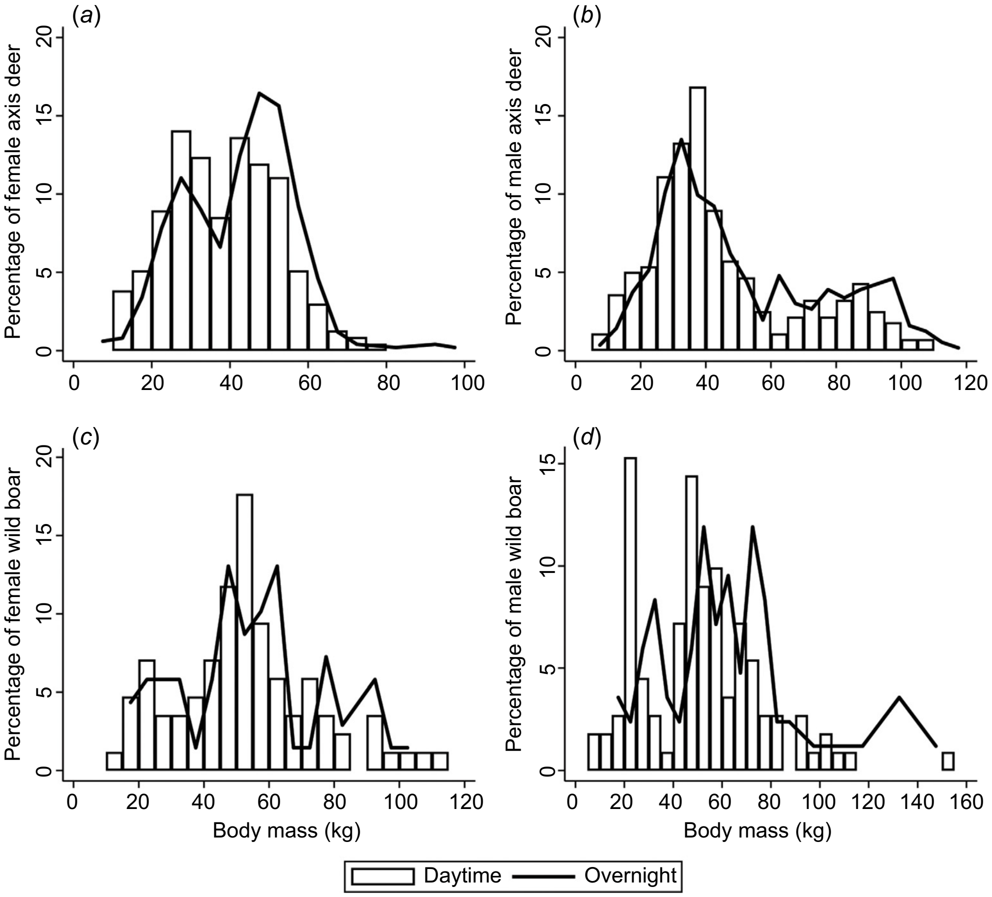

Fig. 8. Distribution of body mass in (*a*) female and (*b*) male axis deer and (*c*) female and (*d*) male wild boar according to daytime versus overnight hunting shift at El Palmar National Park, 2018–2019.

was significantly greater in overnight than daytime sessions in both female (Welch's $t = -3.5$, d.f. = 430.4, $P < 0.001$) and male (Welch's $t = -3.8$, d.f. = 544, $P < 0.001$) deer. For wild boar, the mean of log-transformed body mass was 10 kg greater in overnight than daytime sessions among males (Welch's $t = -2.8$, d.f. = 192.6, $P = 0.005$), and 2.5 kg heavier in overnight sessions among females (Welch's $t = -0.6$, d.f. = 147.0, $P > 0.5$) (Fig. 8*c*, *d*).

Discussion

Our longitudinal trial demonstrated that controlled shooting over bait during overnight sessions was much more effective for culling axis deer than was that over the routine daytime sessions, as determined by crude catch and CPUE at a park-wide scale. Whenever a hunting block switched from daytime to overnight sessions, the crude catch of deer jumped to much higher levels and remained approximately at such high levels until falling steeply when hunting switched back to daytime sessions (i.e. fully reversible effects). Using the temporal and spatial forms of TL to allow for increasing variability with increasing harvest in both hunting shifts, on average, axis deer were culled 2.39–2.61 times more often in overnight than in daytime sessions; in terms of CPUE, the differential was 1.54–1.73 times greater for overnight sessions. Conversely, wild boar were culled less often in overnight sessions when measured by CPUE, and were removed at similar rates in both shifts as determined by crude catch. Although overnight sessions were 51% longer than daytime sessions, the former culled 106% more deer and 23% less wild boar. Overall hunting success (a fundamental measure of hunter satisfaction related to program sustainability) was 50% greater in overnight sessions. Culling of axis deer increased around and after midnight, with a secondary peak around dawn in some spring–summer hunting blocks, closely matching the outcomes of camera-trap surveys (Nicosia *et al.* 2023). To our knowledge, this may be the first trial that has quantified the relative effectiveness of shooting time schedules for deer and wild boar by using a quasi-experimental study design, showing distinctive effects on harvest size and composition of both ungulate species.

The trial confirmed that the spatial and temporal TLs adequately describe the linear relationship of the log-sample variance to the log-sample mean of the harvest of wild boar and axis deer over two contrasting hunting schedules (Gürtler and Cohen 2022), with weak evidence of curvature recorded in 1 of 16 cases. We also corroborated that wild boar and deer catches were not Poisson distributed, suggesting that there were sources of variation other than purely random fluctuations, which especially affected daytime catches. Finding an intercept a significantly different from 0 or a slope b significantly different from 1 rejects the Poisson distribution as a sufficient model of pure randomness for harvest variability. The tests rejected the null hypothesis that the intercept $a = 0$ in six of the eight cases for the spatial TL and in seven of the eight cases for the temporal TL. The four b coefficients for daytime sessions in the spatial TL (range, 1.217–1.463) differed significantly from 1, being consistent with substantial aggregation of the crude catch and CPUE of both ungulate species. For comparison, in the alpine woodlands of south-eastern Australia, b coefficients for the density of fresh dung pellets of feral pigs displayed aggregated temporal and spatial patterns, with mean estimates of b ranging from 1.7 to 2.1 (Hone 2012), tending to be greater than our hunting-based estimates of relative abundance. When b is significantly greater than 1, the variance in crude catch or CPUE increases faster than in proportion to the mean catch or CPUE. A tentative interpretation of $b > 1$, as in the spatial TL, is that hunters sighting more prey, deploying more bait regularly or having better gear or skills would tend to depart more from their average performance than do other less experienced or poorly equipped hunters in less suitable habitats attracting fewer ungulates. Conversely, for the temporal TL, none of the four b slopes for overnight sessions (range, 1.057–1.114) and only one of the eight slopes b (range, 0.981–1.206) differed significantly from 1, suggesting lack of aggregation. Overnight sessions would allow more opportunities for improved performance of hunter parties that usually harvest well below average.

The time schedule of hunting sessions (shift) did not induce a statistically significant change in the slopes of TL in six of the eight comparisons across species and indices in Tables S3 and S4. The two exceptions (for deer crude catch and crude CPUE, Fig. 3*a*, *b*) were related to extreme weather conditions during two overnight sessions that would not have been held under routine (no trial) operations. Excluding both outliers aligned the regression lines for crude catch, but not completely for CPUE. Thus, extreme variations in weather conditions may strongly affect hunter effectiveness and related indices of abundance, and consequently modify TL parameters. For example, low temperatures and precipitation reduced the speed of movement of adult female wild boar during winter, and a similar response was expected for adult males (Thurfjell *et al.* 2014). Similarly, white-tailed deer harvest was negatively correlated with average minimum temperature and number of rainfall and snowfall days in Iowa over 2006–2021 (Elliott and Harms 2023).

Unlike in roe deer (Baur *et al.* 2021), for example, variations in mean temperature and wind speed exerted weak effects on deer harvest indices and weak or no effects on wild boar indices within the slightly restricted range of weather conditions in which the hunting sessions were conducted. These results were based on an extended spatial TL and a linear mixed regression model. Therefore, our key conclusions related to the effects of daytime versus overnight hunting sessions on ungulate harvest were robust to weather-related variations. However, the trial was not designed to assess weather-related effects on harvest indices, and therefore, it cannot rule out whether a wider range of weather conditions with a larger number of sessions, other variables (e.g. precipitation, length of the day, moon phase), and time lags would show weather effects on harvest indices.

In the same vein as for weather variables, using an extended TL and linear mixed models, we verified that having one or two shooters at the same hunting blind did not modify, to any significant extent, the effects of hunting shift on the log-variance and log-mean of ungulate harvest indices. These results were expected on the basis of hunters' accounts of the shooting process and the broad scope of their practices; while some highly skilled hunters monopolised the shooting within a party, others took turns to shoot, or one of the hunters had the rifle scope adjusted for long-distance shots. In very rare cases did both hunters shoot at the same prey in quick succession. Although the occurrence of two shooters would imply an advantage in some hunting blinds (those with several windows overlooking multiple shooting lanes), in practice they may not shoot independently; hence, hunting effort may become loosely or not related to the number of shooters.

Both indices of relative abundance provided consistent inferences for axis deer but not for wild boar. From the perspective of reducing ungulate population size, the catch per hunting-party session rather than the catch per hunting-party hour (CPUE) over the usual timing of a hunting session would better represent what hunters can achieve in practice. Although the amount of time a hunting party may be effectively engaged in a shooting operation under defined conditions is limited (e.g. by fatigue or arduous weather), two main reasons justified the timing and longer duration of overnight sessions running over the weekends. First, overnight sessions should include the midnight and early morning hours when core deer activity occur, and second, for safety reasons, overnight sessions should allow enough time for the hunters to process the quarry and return home in daylight. The pay-off for the extended effort was the much-improved overall hunting success of most parties during overnight sessions and the substantially larger harvest for the same cost of transportation, as most hunters resided within 50–120 km from the park. Beyond the unpaid labour contributed by hunters, another significant cost component that scaled proportionally with harvest and, hence, differed between hunting shifts was the total expense in ammunition. The operating costs to hunters were partially offset by access to wild-game meat and recreation. The stable participation of hunters in both types of sessions across the 18-month period points to enduring motivation and reward, two pillars underlying program sustainability.

The harvest of wild boar and axis deer at the level of individual hunting parties and sessions did not reject the hypothesis of independence at both hunting shifts, i.e. culling specimens from one species did not affect the chance of culling specimens from the second species. However, further work is needed to determine whether the catch of both ungulate species was spatially autocorrelated, and whether the time sequence of culls between ungulate species would affect the subsequent chance of culling the other species.

The harvest composition by stage and sex of exotic ungulates in the park, as shown by controlled shooting, reflected a selective regime modified by the timing of hunting sessions (shift) and ungulate species. The management program traditionally culled more yearlings or subadults than adult hinds (Gürtler *et al.* 2018), as in the current trial and in other heavily hunted populations. Despite long-standing program regulations intended to discourage trophy hunting and other types of selectivity (e.g. for antlered males, sparing adult females), controlled shooting apparently selected for mid-sized individuals (yearlings and subadults) with lower reproductive values than for the full-grown adults of both ungulate species, which were approximately aged 2–3 years (on the basis of tooth-eruption patterns of a sample of the deer and boar culled; authors G. N., unpubl. data). Juveniles were proportionally much fewer than expected for a steadily growing population of axis deer with no defined birth pulse, and for wild boar populations with a stable stage structure (Bieber and Ruf 2005). These patterns were recorded in both hunting shifts and may be partly related to hunter preferences for larger targets and meat yield (Fryxell *et al.* 1988; Solberg *et al.* 2000). As the underlying stage- and sex-structures of both ungulate populations remain unknown, the stage-specific selectivity or vulnerability ratios associated with controlled shooting cannot be estimated. More generally, data on the effects of selective harvesting on population structure are lacking for both wild boar (Vetter *et al.* 2020) and axis deer.

Comparison between the outcomes of hunting shifts operated by the same groups of hunters at the same blinds provided insights on how the time schedule of sessions created a *relative* selection bias. Overnight sessions culled proportionally more individuals with greater fitness than did daytime sessions, including more adults from both species and more pregnant hinds, 4.0–6.7 kg heavier female and male deer, and 10 kg heavier wild boar males. Overnight sessions also harvested more pregnant subadult or adult sows, but the small samples sizes preclude any definitive conclusion on this respect. Pregnancies occurred year-round among axis deer and increased with stage, especially in overnight sessions, whereas adult pregnancies dropped in daytime sessions in both ungulates, a largely unexpected outcome. Among several candidate mechanisms underlying selective harvesting (Mysterud 2011), the trial outcomes are more likely to be related to ungulate behaviour than to hypothetical hunter preferences for specific phenotypes (size, sex, pregnancy status) varying between hunting shifts operated by the same hunters.

Several examples illustrate the effects of ungulate behaviour as a plausible underlying mechanism. Ungulates from hunted populations display greater flight responses than do those from non-hunted populations, as do females or groups with young offspring (Stankowich 2008). For

Mediterranean mouflon, hunting exerts both immediate and delayed responses in terms of decreased daytime activities compensated by the increasing use of unsafe/foraging areas and activity levels during night-time, with sex-specific differences in the response to hunting (Marchand *et al.* 2014). Female wild boar typically display a risk-aversive behaviour during reproductive bouts, with pregnancy and lactation being low-mobility periods with a reduced exposure to death risks (Comer and Mayer 2009; Saïd *et al.* 2012). Sows with offspring respond faster to hunting-related disturbance than do males, shifting between habitats toward safer conditions (Tolon *et al.* 2009; Saïd *et al.* 2012). Moreover, adult sows display much lower hunting-related mortality than do adult male boar and subadults of both sexes (Merli *et al.* 2017). Similarly, female axis deer equipped with radio-collars display greater activity in high-quality habitats during the night-time than in daytime over the hot-dry season in Nepal (Moe and Wegge 1994). In Hawaii, Graf and Nichols (1966, pp. 662–664) qualified axis deer as 'extremely alert and wary, particularly the females,' with alertness and panic increasing as the distance from the shelter increased; the deer were much less responsive during the night. Schaller (1967) made a similar assessment of axis deer behaviour in a protected area of India. For wild boar, the frequent finding of male-skewed sex ratios in juveniles or yearlings was partly attributed to male lack of experience in evading hunters, greater male dispersal and home range (increasing exposure), and hunter preferences for males (Hanson *et al.* 2009; Mayer 2009*c*, p. 319; Keuling *et al.* 2013). Because wild boar adult males are typically solitary and have a larger home-range size and mobility than do adult females (Mayer 2009*a*, pp. 77–80), as do adult male deer, they may display distinctive activity patterns and include in-migrants to the park.

Sex ratios consistently favour males in both ungulate species, as was recorded in the park over 2006–2015 (Gürtler *et al.* 2017, 2018), when the mean percentage of males increased from 45% among juveniles to 64% among the full-grown ('older') adult deer. For the culled deer in the current trial (2018–2019), the mean percentage of males was nearly balanced among juveniles and yearlings, then decreased 14.3% among subadults, followed by a much larger absolute *increase* in the fraction of males (43.5%) between the subadult and adult stages across hunting blocks. This increase overcompensated the slight decrease in the fraction of males among subadult deer. In polygynous ungulates and in unhunted populations, sex ratios at birth are nearly always indistinguishable from 1:1 and become female-skewed with an increasing age (Festa-Bianchet 2003, 2007; Gaillard *et al.* 2003). For intensively surveyed populations of axis deer inhabiting protected areas, the standing sex ratios strongly favour females across most study locations (Schaller 1967; Chapple 1989, with additional examples and references therein; Gogan *et al.* 2001; Dave 2008; Ramesh *et al.* 2012; Duckworth *et al.* 2015; Pople *et al.* 2023); sometimes the female skew tended to increase with an increasing stage. These generalised empirical patterns are exactly the reverse of those returned by controlled shooting at the park. The hypothesis that a 'missing' or 'hidden' fraction of reproductive adult hinds may have moved to, or remain secluded in, safer habitats in response to hunting-related disturbance (and would likely return when it suits them) can sufficiently explain the steady population growth of axis deer despite increasing hunting effort and harvest across more than a decade. An alternative hypothetical mechanism that would account for male-skewed adult sex ratios would require an excess in-migration rate of adult males into the park consistently for more than a decade. This is less plausible because the dispersal of male deer from the natal home range occurs at the yearling stage.

The detailed records of hunting-related events allowed the estimation of incapacitated ungulates by hunting shift. Overnight sessions yielded twice as many incapacitated deer per hunting party as did daytime sessions and very few incapacitated wild boar in both shifts. The overall proportion of incapacitated deer (17.2%) exceeded that of wild boar (10.4%), lying in the range of historically observed or guessed values for crippling losses of other Cervidae (e.g. van Etten *et al.* 1965; Fryxell *et al.* 1988; Riley *et al.* 2003) and exceeding the rates achieved by professional contractors operating from a helicopter or a slowly moving vehicle in night-time (Hampton *et al.* 2022, 2023). Consistent with the patterns recorded in the park, (1) average shooting distances to the culled deer were nearly 50% greater than those for the culled wild boar, and (2) hunter-based sighting surveys conducted at the park in 2017 showed that, on average, 57.1% of the deer and 85.5% of the wild boar sighted during a session were immediately dispatched (Nicosia *et al.* 2021). A common theme in the narrative of park hunters was that the axis deer were more wary than wild boar and stood in the shooting lanes for a few seconds; the deer were less attracted by the bait than were wild boar and, hence, were much less prone to offer a clean shot. Park hunters also reported that the preferred target surface to shoot a wild boar was larger than that on an axis deer. Similarly, helicopter-based culling efforts suggested greater ease of culling wild boar than axis or fallow deer (Hampton *et al.* 2022; Cox *et al.* 2023). Although the incapacitated quarry most likely represented a secondary source of mortality, the reported data were not subject to further validation procedures. Under-reporting or over-reporting of crippling losses was inconsequential in terms of potentially adverse repercussions to the hunters beyond the cultural pressure exerted by their colleagues. How to increase the efficiency of culling efforts and reduce wounding rates to improve animal-welfare outcomes is a matter of current elaboration with park hunters.

Using the relationship between the maximum annual population growth rate and the female age at first reproduction, Hone *et al.* (2010) estimated that a mean annual reduction greater than 49% (95% CI, 19–86%) would stop the population growth of axis deer. To reach such goal in the dry tropics of Australia affected by a multi-year drought, an annual removal of ~30–35% would be needed (Pople *et al.* 2023). Hess and Judge (2021) estimated that an annual removal rate of 30% over 10 years would be needed to eliminate axis deer from the island of Maui. In the park, the rather stable indices of axis deer abundance over 2017–2019 suggest that the intensified culling efforts over 18 months were unable to halt deer population growth but kept wild boar numbers at bay. Camera-trap and hunter-based sighting surveys over 2018–2019 corroborated such trends (Nicosia 2024). The emergence of COVID-19 in late March 2020 stopped program operations for almost a year and impeded a short-term assessment of intensified culling efforts on subsequent ungulate indices.

Implications for management of invasive ungulates

What were the benefits for conservation derived from management efforts directed to removing exotic wild boar and axis deer from the protected area? The biodiversity benefits of pest control, rather than simply the number killed, should be the end outcome to measure the success of conservation projects (Hone *et al.* 2017). Depressing the relative abundance of wild boar caused a large drop in ground rooting and the mortality rate of palm-tree seedlings at the park over 2004–2015 (Gürtler *et al.* 2023). Because the damage caused by axis deer within park premises has not been assessed, we resorted to estimates produced elsewhere. On average, four 55-kg (non-lactating, non-pregnant) axis deer on maintenance rations consumed the amount of grass equivalent to that consumed by one 450-kg cow in a similar state during the wet season in northern Queensland, Australia (Watter *et al.* 2020). Preliminary observations in a cattle farm near General Lavalle (Argentina) yielded an approximate equivalence ratio of five axis deer to one cow measured in terms of the daily consumption of dry grass (axis deer, 2.1 kg/day; cattle, 10 kg/day) (P. Preliasco, unpubl. data, 2017). Such weather conditions would be roughly similar to those at the park. Therefore, the annual culling of 2000 axis deer at the park over 2019 would be equivalent to removing 400–500 cattle and boosting the availability of pasture for other native herbivores and of dry grass for prescribed fires to curb the encroachment of woody species.

This trial has confirmed that adjusting the schedule of hunting sessions to time intervals of peak ungulate activity substantially increases the efficiency of management efforts in terms of removal rates and reproductive value of the culled deer. However, controlled shooting led to male-biased harvesting (intentional or not), which would alleviate any density-dependent constraints and increase deer population growth rates and abundance over the equilibrium levels achieved by non-selective harvesting across both sexes, as recorded for white-tailed deer in the USA (McShea 2012; Fryxell *et al.* 2014, pp. 335–339). Conversely, harvesting adult females (but not yearlings) decreased the inter-annual harvest growth rate of red deer (*Cervus elaphus*) in a coarse-scale comparison across seven European countries (Milner *et al.* 2011). In the park, sustained yearling- and male-skewed harvesting most is most likely to explain, at least in part, the steady population growth of axis deer despite increasing hunting pressure, as the adult hinds with greater reproductive value were less exposed to hunting mortality. Other management tactics are needed to reduce the population size of female axis deer to acceptable levels in terms of ecological and economic damage.

Historically banned on safety grounds, night hunting has been allowed under licence in England and Wales for preserving public health or public safety, conserving the natural heritage, and preventing serious damage to public property such as crops (The Deer Initiative 2010). Night hunting has been prescribed as a special management action for wild boar and other wildlife in multiple states of the USA and in designated areas of central Japan, to cope with overabundant populations of sika deer and wild boar (van Doormaal *et al.* 2015; Ikeda *et al.* 2019). Similarly, a trial comparing the cost-effectiveness of contract and volunteer shooters to cull sambar deer in Alpine National Park (Victoria, Australia) determined that shooting at night yielded a greater CPUE than did other methods (Comte *et al.* 2023). Safety issues and settings are of primary concern. In the park, safety considerations determined the spatial distribution and distance between blinds allowing for terrain slope and access trails; stationary shooting from the elevated blinds over the shooting lanes provided adequate angles and distances to prevent the occurrence of long-distance shots outside of the designated ranges. As in New Zealand forests (Forsyth *et al.* 2013), reducing the abundance of axis deer in the mosaic of woodlands, grasslands and gallery forest along riverine areas may require substantially more control efforts and improved tactics than those in use. A new management model may be needed to curb the ever-increasing abundance of axis deer and its current range expansion, jointly with that of wild boar, throughout north-eastern Argentina and the neighbouring countries.

Supplementary material

Supplementary material is available online.

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Data availability. All data generated or analysed during this study are included in this published article as a supplementary table.

Conflicts of interest. The authors declare that they have no conflicts of interest.

Declaration of funding. The participation of R. E. Gürtler was supported by Secretaría de Ciencia y Técnica de la Universidad de Buenos Aires (UBACYT 20020170100779BA and UBANEX 2017) and Agencia Nacional de Promoción Científica y Técnica of Argentina (PICT 2018-4193). The funders had no role in study design, data collection and analysis, decision to publish and preparation of the paper.

Acknowledgements. We thank park personnel for their valuable assistance: R. Achilli, J. Ballay, M. Cravea, C. Croci, A. Luggren, D. Lozano, E. Munich, E. Ochoa, C. Sosa, and J. Zermathen; members of the UBA-sponsored volunteer program: L. I. Rodríguez-Planes, M. Bongianino, A. A. Astorga, S. Szpilbarg and A. Gaspe; and members of hunter associations: R. Bourband, J. Fabre, C. Gómez, H. and S. Larrachao, M. Morend, E. Portillo, and M. Sabaño. J. E. Cohen thanks Roseanne Benjamin for assistance during this work.

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