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RESEARCH

Controlling the abundance of invasive exotic wild boar (*Sus scrofa*) improves palm-tree conservation in north-eastern Argentina

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Abstract
Linking management of invasive species to conservation outcomes is key to assessing program success. Wild boar (*Sus scrofa*) severely reduced the recruitment of *Butia yatay* palm trees, the main conservation value at El Palmar National Park, and was targeted for long-term control efforts. We integrated scattered and unpublished information to model the quantitative relationships among culling efforts (inputs), wild boar relative abundance (outputs), and damage extent (outcomes), indexed by ground rooting surface and yatay seedling mortality, and assessed how much cumulative effort was needed to achieve program targets. Park rangers culled wild boar by hunting with dogs and shooting rifles from stationary vehicles over 2004–2005. Local hunters hunted with dogs (2006–2011) and shot with rifles from elevated blinds (2006–2015). Linear regression of log-transformed variables showed that yatay seedling annual mortality and ground rooting declined exponentially over time as did wild boar abundance measured by hunting-based indices, which were significantly correlated. Limited ranger-led hunting efforts substantially reduced seedling mortality over < 2 year. Minimal seedling mortality (2.8%) and target levels of ground rooting (1.3%) were reached within 5 year of combined operations. When control efforts were interrupted for 6 months, ground rooting resurged while wild boar numbers increased. These results support the effort-outcomes principle and demonstrate the success of the management program in achieving conservation targets related to wild boar damage. Carefully structured and managed (*organized*) sport hunting of invasive wildlife may contribute to the sustainability of conservation programs.

Keywords Palm-tree conservation · Damage control · Wildlife management · Exotic ungulates · Hunting · Sustainability · Wild boar

Introduction

Invasive species frequently have adverse economic and ecologic impacts that warrant management efforts. How much effort is needed to achieve defined outcomes, and what are the benefits for conservation derived from management efforts, are key issues that deserve more research (Hone 2002, 2012; Tear et al. 2005; Walsh et al. 2012; García-Díaz et al. 2021). Measures of the degree of implementation of management efforts were poor predictors of

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success (outcomes) in numerous conservation projects (Kapos et al. 2009). For invasive exotic species regarded as pests, the biodiversity benefits of pest control, rather than simply the number killed, should be the end outcome (Hone 2012; Hone et al. 2017). Unfortunately, the effects of management efforts are most frequently assessed based on reduced pest abundance or increased pest mortality rather than damage reduction or conservation benefits, if they are assessed at all (Pullin and Knight 2005; Hone 2007).

The effort–outcomes principle (a.k.a. the action-response curve, input–output or investment-outcome relationship, among others) addresses this linkage by positing a "cause-and-effect relationship between the desired outcomes of management and the effort applied (the inputs) but with diminishing returns" (Hone et al. 2017 and references therein). The relationship between effort and outcome(s) may adopt different functional forms and parameters and can be used to compare the cost-effectiveness of alternative actions. When the relationship between effort and damage (or pest abundance) is strongly non-linear (concave-down) and pest abundance is large, substantial reductions in pest abundance may hardly reduce the damage extent. The relationship between damage and vertebrate pest abundance was linear, curvilinear (mainly concave-down) or none (Hone 2007, p. 18–20), and sigmoidal or concave-down with a threshold level of effort (Choquenot and Parkes 2001). Examples of conservation programs measuring the effort-outcomes relation are rare.

A case in point is wild boar (*Sus scrofa*) and their hybrids with domestic pigs, also called feral hogs, pigs, or swine (hereafter referred to as "wild boar"). Wild boar are among the top invasive species (Lowe et al. 2004), with much greater fertility (Drimaj et al. 2020) and population growth rates than other ungulates of similar body mass, adapting easily to diverse habitats (Comer and Mayer 2009; Hone 2012). They have expanded rapidly across Europe (Carpio et al. 2021) and North America (e.g., Snow et al. 2017) fueled by illegal introductions and environmental changes affecting fitness traits (Gamelon et al. 2012; Massei et al. 2015; Vetter et al. 2015; Drimaj et al. 2019). The dual nature of wild boar, as a valued food or trophy and as a pest, frequently generates conflicts (Choquenot et al. 1996). Overabundant wild boar populations compete with and prey on native vertebrate species and livestock (Campbell and Long 2009; Barrios-García and Ballari 2012; Hone 2012; McDonough et al. 2022). Wild boar affected arable and livestock farming in Europe (Carpio et al. 2021) and contributed to the extinction of 14 taxa (Risch et al. 2021). Wild boar are important reservoir hosts of multiple pathogens affecting humans (Meng et al. 2009; Miller et al. 2017) and fueled the propagation of African swine fever in Europe (European Food Safety Authority et al. 2017).

Wild boar typically use their snout to root up the ground in search of food. Ground rooting affected plant diversity and growth (Engeman et al. 2007; Campbell and Long 2009; Hone 2002, 2012) and caused substantial emissions of CO_2 (O'Bryan et al. 2022). Wild boar soil disturbance also exerted positive long-term effects on plant richness and alpha or beta diversity (Cuevas et al. 2020) and may be used for woodland restoration (Sandom et al. 2013) and to benefit some bird species (Natusch et al. 2017). Rooting forms and extent varied with wild boar age, seasonality, above-ground food availability, elevation, landscape, soil compaction, and texture (Adams et al. 2019; Elledge et al. 2013; Mayer 2009a). The linkages between wild boar abundance and rooting (or crop damage and lamb predation) ranged from none to linear, power, and positive exponential (Hone 2007, p. 18; Krull et al. 2016).

Wild boar have expanded across the Southern Cone countries of South America (Pedrosa et al. 2015; Cuevas et al. 2021) and thrive in many protected areas throughout Argentina (Perez Carusi et al. 2017; Panebianco et al. 2019; Ballari et al. 2019). One of them is El Palmar National Park (hereafter, the park), created in 1965 to protect the largest remnant of the yatay palm-tree (*Butia yatay*) savannah. This severely threatened ecosystem extends over southern Brazil, northeastern Argentina, and Uruguay (Sosinski et al. 2019). Local peasants noticed the occurrence of wild boar around 1950. By the late 1990s, the large abundance of wild boar was linked to large mortality of yatay palm-tree seedlings; consumption of its fruits and seeds, and extensive ground rooting (Goveto 1999). Following unsuccessful culling efforts, the park launched in 2006 a long-term control program of exotic ungulates based on local sport hunters. These interventions mostly kept wild boar abundance low over 2006–2015 while ground rooting gradually declined to below the target level (Gürtler et al. 2017). Several hunting-related indices of wild boar abundance fluctuated spatially and temporally in accordance with Taylor's law, showing consistently higher numbers in the restricted-use zone of greater conservation value (Gürtler and Cohen 2022). Yatay seedling mortality was estimated independently (Lunazzi 2009; Pignataro 2010; Ballari 2014), and the outcomes were considered favorable in interim reports to the National Parks Administration. Previous research did not examine the linkages among culling effort, wild boar abundance, and damage extent.

Here, we integrate scattered information to model the quantitative relationships among culling efforts (inputs), wild boar relative abundance (outputs) and damage extent (outcomes), indexed by ground rooting and yatay seedling mortality, over 2004–2015. We estimate how much cumulative culling effort was used to achieve program targets and review the underlying rationale. As wild boar population size estimates in forest landscapes or protected areas are hard to obtain or impractical for management purposes, we examine the relationship between several indices of relative abundance based on hunting with dogs and controlled shooting. To achieve these aims, we searched park archival records for historical catch-and-effort data preceding the 2006 program to prolong the observation timeline back to 2004–2005 and link wild boar abundance to prior and subsequent measures of damage extent. These analyses mitigate the use of inappropriate baselines for management purposes due to lack of or limited access to past information, which is closely related to the broader issue of the shifting baseline syndrome (Pauly 1995; Soga and Gaston 2018).

Methods

Study area

El Palmar National Park (31° 55′ S, 58° 16′W), located in Entre Ríos Province (north-eastern Argentina), covers approximately 8500 ha of savannahs with high-density stands of yatay palm trees, scrublands, and gallery forests (Suppl. Fig. 1). It is limited by the Uruguay River on the east and a fast highway (Route 14) on the west. The nearest village (Ubajay, 3500 people) is 5 km distant from the nearest park border. The main features of the park and surrounding landscape have been described (Gürtler and Cohen 2022). A permanent water course divides the park in two zones, one open to public use (to the north) and one of restricted use and greater conservation value (to the south). Although the regional climate lacks a distinctive dry season (mean annual rainfall over 2006–2015, 1389 mm at a weather station in Concordia), rainfall varies widely from year to year (Ramos et al. 2018). Droughts mainly span from late austral fall through the austral winter. Long droughts (≥ 3 months) occurred from the 2005 spring–summer to the 2006 winter and over the same period in 2008–2009; from summer 2011 to winter 2012; over the 2013 fall–winter, and from summer 2014 to fall 2015 (Bongianino 2019, Table 1A). Wild boar within the park lack natural predators other than program hunters, poachers and perhaps foxes preying upon piglets.

Management of invasive ungulates

Efforts to cull wild boar and axis deer, initiated in 1983, achieved little apparent success despite intensive, undocumented operations over 1988–1991. In the 1995–1996 control plan, park rangers shot wild boar and axis deer with rifles from stationary pick-up vehicles and from a few elevated blinds. They estimated removing roughly 60–100 wild boar per year over 1990–2003, as did poachers. Poaching apparently shifted to capybaras and axis deer after 2008 when they became relatively more abundant than wild boar.

In 2004, park rangers established two packs of mixed-breed dogs trained to trail, bay and catch wild boar; conducted regular hunting sessions involving a mean of 8.6 (SD, standard deviation, 3.2) dogs and two or three people on horseback; killed the quarry with a knife (rarely with a pistol); and recorded the outcomes on paper regardless of whether a quarry was obtained or not (see below). Hunts were conducted during daylight hours early in the morning (especially during the hot season) or late in the afternoon. In parallel, park rangers culled wild boar using rifles from stationary vehicles during nocturnal routine rounds and generally recorded only successful sessions. Both methods occasionally removed axis deer.

Using this trial experience, park personnel designed a new control program of wild boar and axis deer based on experienced, unpaid hunters residing within 120 km of the park, who would operate under close supervision. The program was implemented from 2006 onwards; 2006 is taken as 0 years postintervention (YPI), with January–March 2006 as trimester 1 (covering most of the austral summer). General program descriptions given elsewhere (Gürtler et al. 2017; Gürtler and Cohen 2022) are supplemented here with relevant details. The main objectives related to wild boar were: "(i) to reduce the ground rooting area to less than a third of the existing one at the beginning of the plan and to maintain or reduce the amount over time, and (ii) to reduce the negative impacts of wild boar on the recruitment of yatay palms and maintain this trend over time".

Under the new framework, the local hunters culled wild boar using trained dogs (over 2006–2011) and both wild boar and axis deer by controlled shooting over bait from elevated blinds (from 2006 onwards). Hunting with firearms from stationary vehicles was rarely conducted over 2006–2015. Spotlight counts from vehicles, conducted on 11 occasions over 2006–2015 (Gürtler et al. 2018), yielded only six wild boar in 2006; this method was deemed inappropriate for park habitats. We use the terms "controlled shooting or hunting" to reflect that culling efforts were restricted to times and zones with designated shooting lanes, and operations were governed by the park rangers in charge of each session. Our prior usage of "still shooting" referred to the fixed position of blinds and to shooters not being allowed to chase the specimens, but this term has other meanings in the hunting literature.

Hunting with dogs since 2006 proceeded as before across six major operation sectors, but the local hunters usually brought their own dogs and horses and every hunting party was headed by a park ranger. The dog pack size averaged 9.5 (SD, 2.67, range 5–18) mixed-breed dogs vaccinated against canine pathogens and kept under veterinary supervision. An active "hunting party" represents a group of hunters on a particular occasion (i.e., hunting session), using the same blind or pack of dogs, regardless of whether they culled any specimen or not and of how long they hunted. A "hunting session" is the activity of a hunting party on a given day over one continuous time interval.

Controlled shooting from fixed blinds used high-powered rifles with designated calibers (usually 0.270, 0.300, 0.308 and 0.30–06 loaded with moderate to heavy weight bullets, i.e., 150–180 grains) and no muzzle blast suppressor. This method was sometimes included under ground-based shooting and the sit-and-wait (*espera*) method (Braga et al. 2010). Up to 100–150 hunters were involved in shooting operations. The active blinds were rather uniformly distributed across the park and increased from 35 in 2006 to 44 in 2015 (Suppl. Fig. 1). Each blind had 5–20 shooting lanes cleared of vegetation where bait (fermented corn or ground pet food and blocks of salt) was deployed before each session. Each hunting party generally had one (rarely two) shooters and an assistant and was allowed to cull as many exotic ungulates as possible, with no restriction on age, sex, or pregnancy status. Each party could take up to one annual trophy, and no incentives were given. Hunters' decision to participate or not in a session determined the realized levels of hunting effort. Most hunting sessions were generally conducted between 16–18 h and 22–24 h (diurnal or short sessions) every 1 or 2 weeks over most of the year. Overnight (or long) sessions started between 16–19 or 22 h and ran up to 6–8 h; they were common over 2006–2007 and in 2015. Although the mean crude catch of wild boar in overnight shifts was 39% greater than that in diurnal shifts, the difference was not statistically significant (Gürtler and Cohen 2022). Hunting sessions were stopped every summer for an average of 20 days over 0–5 YPI and 90 days over 6–9 YPI.

The hunters brought every culled specimen to a central processing facility in the park where they were classified by species and sex, measured, butchered, and identified with a pre-marked plastic tag for transportation (Gürtler et al. 2017). Park staff recorded this information in a numbered form for every attending hunting party, including those that culled no specimen, and issued transport permits. Hunters took half of each piece (67% since 2012), and the remainder was mainly donated to local schools, community shelters, and retirement homes.

Ground rooting

For monitoring ground rooting extent, nine fixed-strip transects were designated in palm-tree stands across both park zones based on an extensive survey that recorded 5–7 times greater densities of wild boar dung in palm-tree habitats (which had plentiful yatay fruit on the soil) than in other habitats in April 1997 (Goveto 1999). Each transect measured 12 by 1000 m and was georeferenced with a GPS (Garmin). Strip transects sometimes traversed a dirt road or firebreak and were not intentionally set on open terrain. Transect 7 was measured at the initial survey only and thereafter was replaced by transect 10 (Suppl. Fig. 1). A two-person team riding horses separated by > 6 m inspected the strip transects for evidence of rooting in September 2006, April 2007, September–December 2007, July 2008, July and September 2011, August 2012 and 2013, January and September 2014, and March 2015. Ground rooting surveys were conducted in winter (on 6 occasions), spring (4 occasions), fall (3 occasions), and summer (1 occasion). Each horse rider screened 3 m-wide strips on each side and measured the width and length of the soil removed or covered attributable to wild boar (i.e., based on its general aspect and whether the excavations were continuous, shallow, with soil pushed forward, and occurrence of wild boar tracks). Follow-up surveys recorded only fresh rootings (i.e., with no emerging seedling). The area inspected by survey totaled 108,000 m^2, except in January 2014 (48,000 m^2) due to logistic constraints. Ballari (2014) partially surveyed these strip transects using the same methods over October 2009 (54,000 m^2 inspected); June–September–December 2010, and February–May 2011 (60,000 m^2 inspected in each period).

Seedling mortality

Lunazzi (2009) delineated two large plots (measuring 3.3 and 4.0 ha) in a semi-dense (167 adult palm trees per ha) and dense (313 adult palms per ha) stand of *B. yatay* located in the public-use zone in 2003 and 2004, respectively; identified, mapped, and marked all palm trees at the outset; measured the annual survival of seedlings with pinnately compound leaves ("hoja compuesta o dividida") and their transitions to the next stage over four- (2002–2006) and three-year (2004–2007) periods in each plot, and established the putative cause of seedling death through characteristic signs (i.e., shape, length and depth of digging and occurrence of wild boar tracks) that left no doubt about the agent that caused them. Diggings by big hairy armadillos (*Chaetophractus villosus*) to uproot yatay seedlings had a characteristic conical shape. In total, 362 seedlings with pinnately compound leaves were followed up in the dense plot and 60 in the semi-dense plot. Lunazzi (2009, Fig. 2.15, p. 61) reported the annual mortality of seedlings over 2002–2003, 2003–2004, and 2005–2006 for the semi-dense stand, and over 2005–2006 and 2006–2007 for the dense stand. Annual mortality is defined here as the fraction of seedlings alive on a given date that were dead 1 year later; this fraction is expressed as a percentage. We took the average of both plots for 2005–2006 and time-specific data for the remaining years.

Pignataro (2010) conducted an exclosure experiment to assess the mortality of seedlings with pinnately compound leaves by wild boar or armadillos in the semi-dense stand mentioned above between June 2006 and December 2007, with no spatiotemporal overlap between both studies; identified and marked 90 seedlings with pinnately compound leaves; randomly allocated them to treatment (within a chicken-wire fence excluding wild boar but not armadillos) and control (no exclosure) arms, and measured individual survival over nearly 3-month periods and the cause of death. Pignataro (2010, p. 38, Cuadro 5) reported the proportion of dead seedlings (predated) over the 18-month period in each treatment arm according to the cause of death. In the control arm with no exclosures, 14 (31.1%) of 45 seedlings were eaten by wild boar across the 18-month follow-up, with mortality peaking during September–November (16.3%) and November–January (11.1%). We transformed the 18-month mortality (31.1%) to an annual rate (*m*, 22.0%) using $m = 1–(1–0.311)^{12/18}$. In the treatment arm excluding wild boar predation (not used in current analyses), 1 (2.2%) of 45 seedlings were preyed on by armadillos, and 1 (2.2%) death was attributed to unidentified causes other than predation.

Ballari (2014) designated 120 plots (each measuring 20 m^2) in five grassland patches and six palm-tree stands located in both park zones; identified all *B. yatay* seedlings with pinnately compound leaves (118 in palm-tree stands and 24 in grasslands); surveyed them on five occasions between June 2010 and May 2011, and assessed whether they were preyed on and the putative cause of death (wild boar or armadillos) using the same criteria as Lunazzi (2009) and Pignataro (2010). Ballari (2014, p. 76) reported the number and percentage of compound-leaved seedlings dead by predation (2.8%) over a year; mortality was much greater in grassland habitats than in palm-tree stands. In the three studies, annual mortality estimates were assigned to the midpoint date of each observation period.

Data management

Our current analyses include recently retrieved paper records for hunting with dogs and from vehicles over 2004–2005 and a comparison of the digital database (2006–2015) with the original paper forms (mid 2006–2015) and other sources; this led to slight changes in catch, effort, and rooting numbers. Data for the 10-year study period are included as Online Resource 1. All data management and statistical procedures were run in Stata 15.1 (Stata Corp 2018).

Definitions and data management procedures were described elsewhere (Gürtler and Cohen 2022). Crude catch (C_j) is the number of specimens culled by a hunting party (j) during a fraction or the whole of a hunting session using a defined method. C_j includes a few culled specimens in poor body condition that were discarded and not measured; wounded specimens that escaped were excluded from current analyses. For a given hunting party, session and method, crude hunting effort (E_j) is the sum of hunting party hours regardless of whether the party caught any specimen or not, and regardless of whether one or two shooters were on a hunting blind in a given session. Standardized indices and standardized hunting effort are constrained to hunting activity over 17–23 h (i.e., the most typical time interval and session duration across the decade). Annual occupancy was calculated as the percentage of all possible sessions in which an active blind was used by any hunting party across all active blinds and sessions in a given year.

Catch indices were calculated as the unweighted mean of local values (i.e., at the hunting blind level), as recommended for large, heterogeneous areas (Walters 2003). All four metrics for log mean wild boar abundance, collapsed by trimester and computed over a decade, were highly significantly correlated (range of *r*, 0.909–0.988) across active hunting blinds (Gürtler and Cohen 2022). To simplify the exposition, we mainly refer to mean crude catch per hunting party session using a given method. This metric also includes effort (i.e., a hunting party session); session duration varied little over time within each type of hunting shift. Hunting success was measured as the proportion of active hunting parties that culled at least one wild boar over a session. Throughout $\log = \log_{10}$. Although vehicle-hunting parties removed as many wild boar as hunting with dogs over 2004–2005, lack of information on unsuccessful parties prevented calculating an analogous index of abundance.

We used ordinary linear regression of log-transformed response variables measuring damage extent (seedling mortality and ground rooting) and mean crude catch of wild boar per hunting party session using a defined method. Our independent variable was time postintervention (measured in trimester numbers). We also used linear regression to describe the relation between the log-mean crude catch of wild boar using dogs versus controlled shooting. We forced the regression line to pass through the origin to relate ground rooting to mean crude catch using each hunting method. To compare estimates of slope under two conditions, we used Welch's t-test for two quantities with unequal variances.

For ground rooting, the outlier recorded in March 2015 (3.2 m^2 per ha, trimester 37) was excluded from the analyses because (i) it was far above the range of previous and subsequent observations, with 52% of all rooting surface recorded occurring in one of the nine transects; (ii) this was the only summer estimate of rooting recorded by the same skilled team that conducted previous surveys, thus ruling out poor method standardization as a possible explanation (most apparent rooting activity in the park was believed to occur during winter-spring); (iii) occurred in the context of an unusually intense 4-month drought (summer 2014–fall 2015) during which controlled shooting stopped over a 3-month summer break, and (iv) wild boar numbers fluctuated around the low-density equilibrium.

Results

Hunting effort and wild boar abundance

Hunting with dogs was limited over 2004–2005, peaked in 2006–2007 (trimesters 1–8) boosted by local dog hunters, gradually declined as hunting success plummeted, and was phased out by trimester 25 (Fig. 1a). In total, 314 parties hunting with dogs culled 476 wild boar throughout this period (Suppl. Table 1). Mean crude catch per hunting party session fell from a maximum of 2.9 wild boar at the outset to 0–0.7 during trimesters 20–24 (Fig. 1b). Mean hunting success (for semesters [6-month intervals] that included at least 9 parties hunting with dogs) declined linearly from 100 to 50% across the follow-up (Fig. 2a). In the regression equation, proportion of parties that culled wild boar $= a + b*$(time postintervention [semester number], the least-squares estimates of the coefficients were $a = 0.8832 \pm 0.030$; $b = -0.033 \pm 0.006$, *adj.* $R^2 = 0.820$, $n = 9$. Vehicle hunting and a few opportunistic hunts conducted by park rangers removed 80 wild boar over 2004–2005 (plus 6 axis deer) and 22 wild boar over 2006.

Controlled shooting over 2006–2015 totaled 470 sessions including 6015 parties and nearly 35,000 hunting party hours. Hunting effort remained roughly stable up to a trough at trimesters 25–26 (6 YPI), when operations were virtually halted for 6 months after the park's top management changed, and then gradually increased, though with diminished or nil activity over most (austral) summer periods (Fig. 1c). The frequency of participating hunting parties closely approximated the amount of hunting party-hours by trimester except for the first year. Controlled-shooting sessions removed 1716 wild boar across the follow-up (Suppl. Table 1). Mean crude catch plummeted over trimesters 1–8, then surged during trimesters 24–31 (5–6 YPI) to fall again and oscillate around the long-term average (Fig. 1d). Although the relative surge during trimesters 24–31 occurred in both zones, it was more pronounced in the restricted-use zone than in the public-use zone (Fig. 2b).

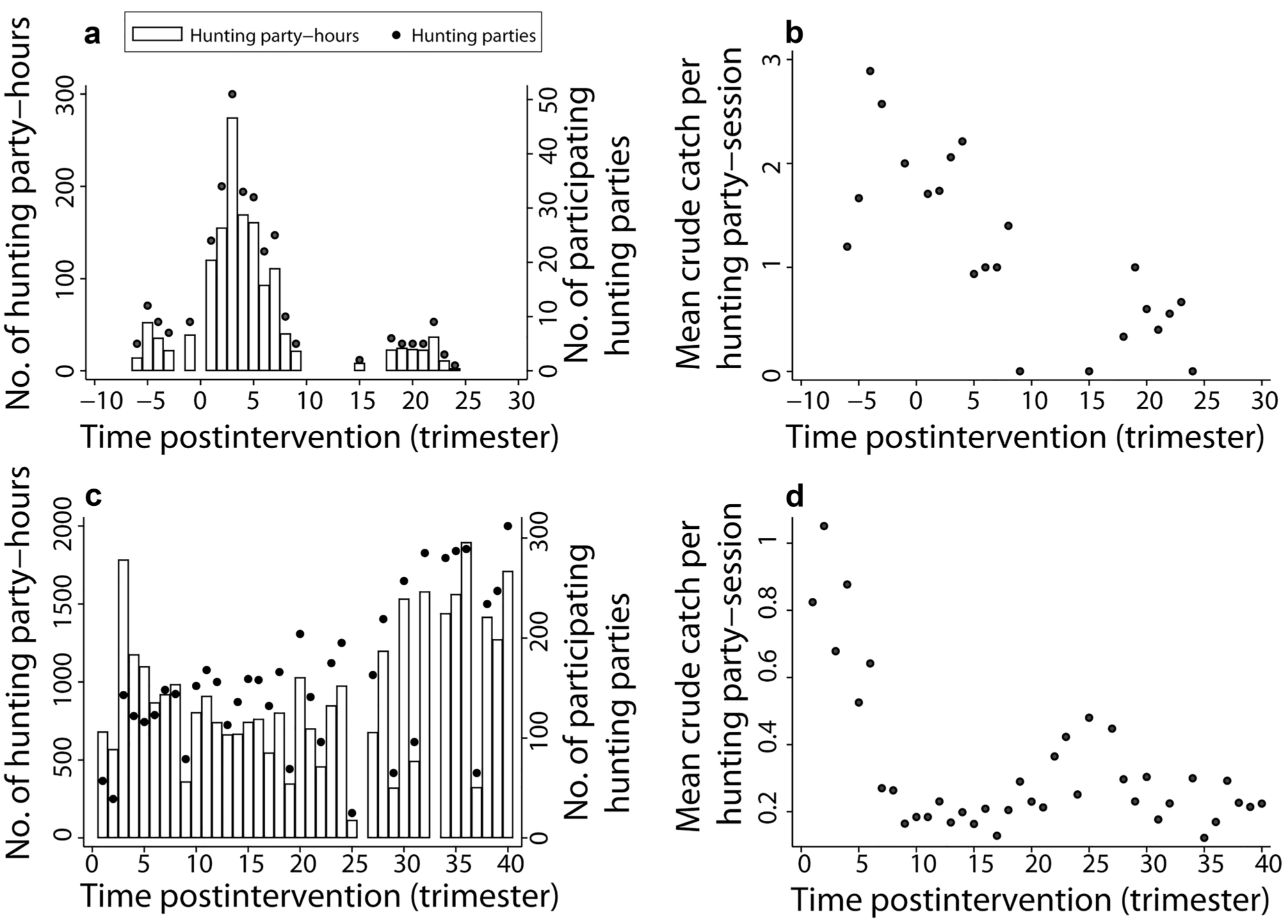

Fig. 1 Crude hunting effort (measured by the number of hunting party hours, shown by bars) and the number of participating parties (black dots) (**a**, **c**) and mean crude catch of wild boar per hunting party session (**b**, **d**) using dogs (**a**, **b**) and controlled shooting (**c**, **d**) over time. Trimester 1 was January–March 2006

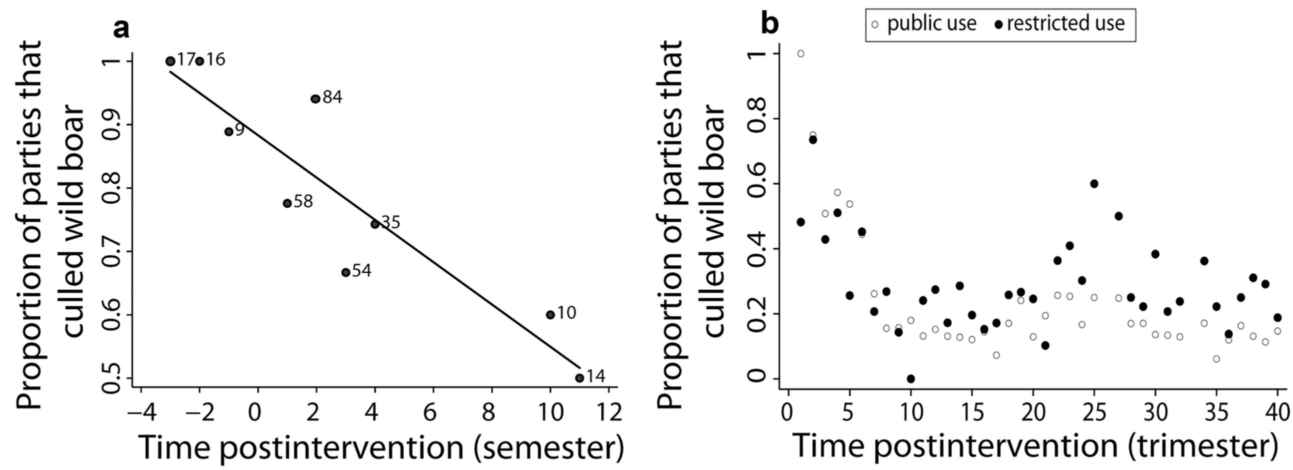

Fig. 2 Proportion of hunting parties that culled wild boar in a session over time using dogs (**a**, averaged by semester [six-month interval]) and controlled shooting (**b**, averaged by trimester) in the public- and restricted-use zones of the park. In **a**, numbers next to the circles represent the number of parties hunting with dogs; semester 1 was January–June 2006. In **b**, trimester 1 was January–March 2006

The log-transformed mean crude catches of wild boar by hunting with dogs and shooting were highly significantly correlated ($r=0.735$, $P<0.001$) (Fig. 3). When the comparison was restricted to trimesters 1–8 (i.e., when both hunting methods coexisted and sample sizes were more balanced), the slope coefficient of log mean crude catch on log hunting effort using dogs ($b=0.7572$, s.e. $=0.02556$, *adj.* $R^2=0.991$) was much greater than for controlled shooting ($b=0.5947$, s.e. $=0.01624$, *adj.* $R^2=0.994$) at widely different levels of effort.

Damage

Both the annual mortality of yatay seedlings and ground rooting surface declined exponentially ($P<0.005$) over time (Fig. 4). Regression coefficients for the model Log-seedling mortality $= a + b$*(trimester number) were: $a=1.438\pm0.070$; $b=-0.042\pm0.006$, *adj.* $R^2=0.897$, $n=6$; and for log-ground rooting: $a=0.455\pm0.102$; $b=-0.017\pm0.005$, *adj.* $R^2=0.512$, $n=13$. According to the Welch *t*-test, the slopes differed significantly (Welch's $df=14.17$, $P=0.006$). Seedling mortality peaked (80–81%) at trimesters –10 and –14, decreased to 25–32% around program onset in 2006, and reached the all-time minimum value (2.8%) at trimester 20. The rooting surface was maximal (3.9 m^2 per ha) in trimester 3 (late winter), after a severe 10-month draught followed by a 7-month long soil saturation period (Bongianino 2019, Table A1). Rooting surged in trimester 23 (winter).

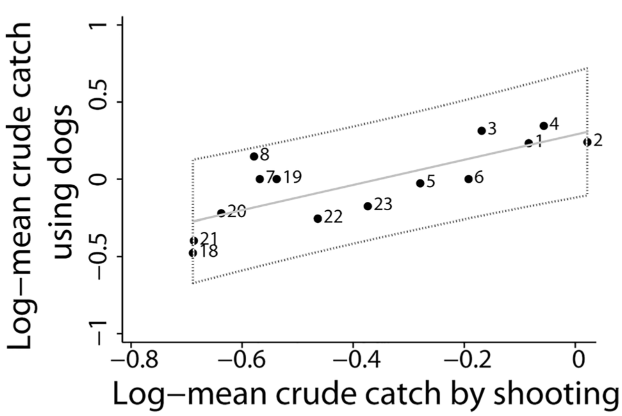

Fig. 3 Log–log regression of mean crude catch of wild boar per hunting party session using dogs and controlled shooting over trimesters 1–23. The belt above and below the regression line represents a 95% confidence interval for individual residuals. Numbers next to the circles represent trimesters. Trimester 1 was January–March 2006

Mean log-crude catch of wild boar using dogs declined highly significantly ($P<0.001$) over time ($a=0.230\pm0.045$; $b=-0.023\pm0.004$, *adj.* $R^2=0.674$, $n=19$) in parallel to palm-tree seedling mortality (Fig. 5). These slopes differed significantly though weakly by the Welch *t*-test (Welch's $df=11.63$, $P=0.022$).

Ground rooting declined exponentially over time at a slower pace than the mean crude catch of wild boar by controlled shooting, which reached minimal abundance by trimester 18 (Fig. 6). Following the upward trend in wild boar numbers during trimesters 22–26, rooting further declined to lower levels while mean catch fluctuated around the lower-density average.

Ground rooting surface increased linearly and significantly with increasing mean crude catch of wild boar by hunting with dogs and separately by controlled shooting (Fig. 7). Slope coefficients for the linear regression with no intercept ($a=0$) of ground rooting surface on mean crude catch using dogs were: $b=1.814\pm0.326$, $P=0.001$, *adj.* $R^2=0.810$, $n=7$; for shooting: $b=4.330\pm0.621$,

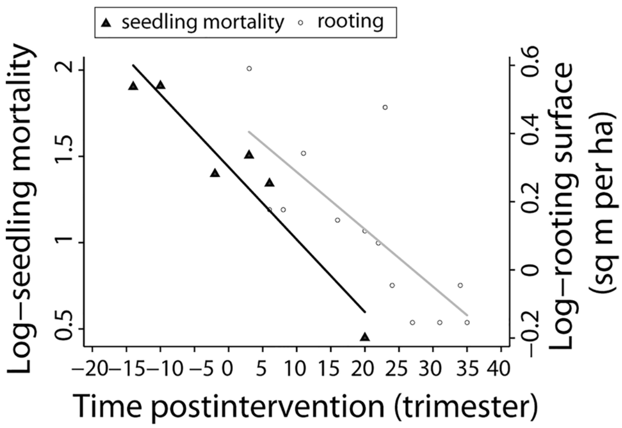

Fig. 4 Log-transformed ground rooting surface (m^2 per ha) and log-annual mortality of *Butia yatay* palm-tree seedlings over time. Seedling mortality data from Lunazzi (2009), Pignataro (2010) and Ballari (2014). We excluded one outlier value for rooting from the regression calculation and omitted it from the graph. Trimester 1 was January–March 2006

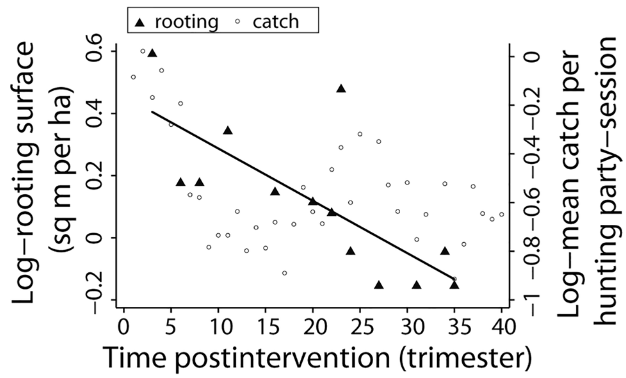

Fig. 6 Log-transformed ground rooting surface (m^2 per ha) and log-mean crude catch of wild boar by controlled shooting over time. We excluded one outlier value for rooting from the regression calculation and omitted it from the graph. Trimester 1 was January–March 2006

$P=0.043$, *adj.* $R^2=0.785$, $n=13$. The slope for shooting (4.330 ± 0.621) is significantly greater than the slope for hunting with dogs (1.814 ± 0.326) (Welch *t*-test, Welch's $df=18.11$, $P=0.002$), indicating that small changes in the scale of mean crude catch per hunting party-session using controlled shooting imply larger variation in rooting surface than small changes of the same magnitude in mean catch using dogs.

The initial decline in yatay seedling mortality (from 80–81% to 25–32%) was preceded by ranger-led hunting efforts with dogs and firearms from vehicles (Fig. 8a). Seedling mortality decreased slightly to 22% by trimester 8 (i.e., end of combined hunting efforts using dogs and shooting on 1 YPI) and reached the all-time minimum value (2.8%) at trimester 20 when cumulative hunting party-hours were 1390 (hunting with dogs) and 16,466 (shooting).

Ground rooting surface declined following substantial increases in cumulative hunting effort over time (Fig. 8b). The pre-defined target level was met at trimester 20. Ground rooting continued to decline further as shooting effort increased. Log-ground rooting declined linearly with increasing log-cumulative effort by controlled shooting (Suppl. Fig. 2, $a=2.753 \pm 0.714$; $b=-0.635 \pm 0.172$, *adj.* $R^2=0.513$, $n=13$).

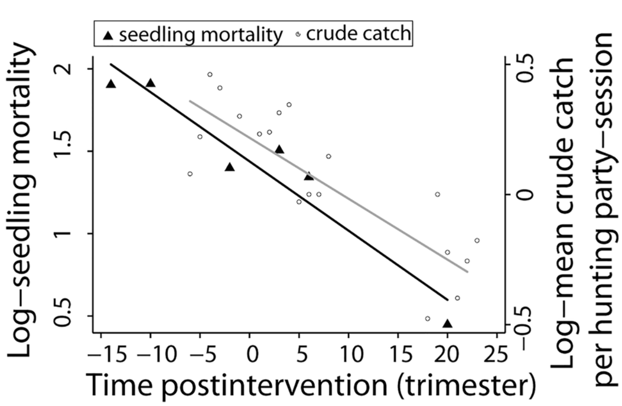

Fig. 5 Log-transformed annual mortality of *Butia yatay* palm-tree seedlings (2002–2010) and log-mean crude catch of wild boar using dogs (2004–2011) over time. Seedling mortality data from Lunazzi (2009), Pignataro (2010) and Ballari (2014). Trimester 1 was January–March 2006

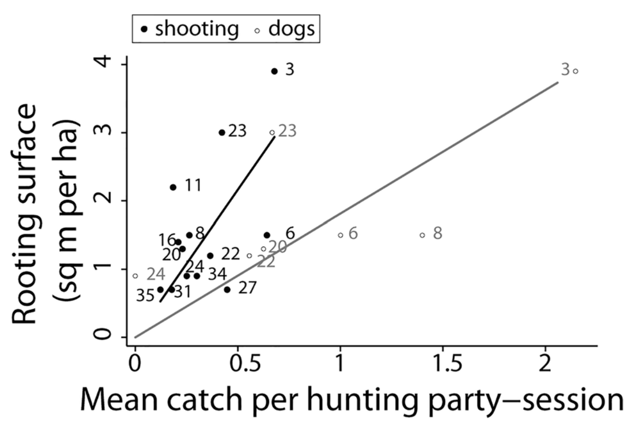

Fig. 7 Linear regression through the origin of ground rooting surface (m^2 per ha) on the mean crude catch of wild boar by hunting with dogs and controlled shooting over 0–8 YPI. We excluded one outlier value for rooting from the regression calculation and omitted it from the graph. Numbers next to the circles represent trimesters. Trimester 1 was January–March 2006

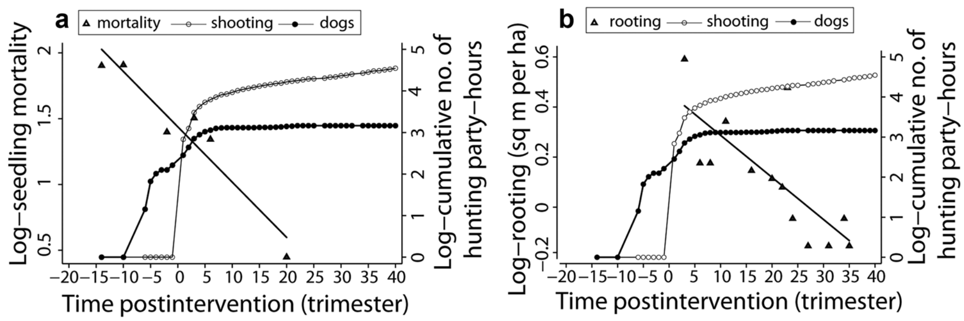

Fig. 8 Log-annual seedling mortality of *B. yatay* palm trees (**a**) and log-ground rooting surface (**b**, m^2 per ha) together with log-cumulative hunting effort using dogs and controlled shooting over time. We excluded one outlier value for rooting from the regression calculation and omitted it from the graph. Trimester 1 was January–March 2006

Discussion

Damage

We found congruent relationships between culling effort using two methods (inputs), wild boar abundance using several indices (outputs), and damage extent indexed by ground rooting and palm-tree seedling mortality (outcomes). The exponential decline in damage meant that most of the conservation benefits were derived early, and it took longer and longer to decrease the damage extent by any fixed amount because the fraction reduced per unit of time was constant. These results support the effort-outcomes principle and the success of the management program in achieving the targets related to wild boar damage.

The 2004–2005 data allowed linking peak values of seedling mortality to peak wild boar numbers before the program onset in 2006. The cumulative effort-seedling mortality curve shows that the large, initial decline in mortality was preceded by ranger-led culling efforts using dogs and vehicle hunting, and occurred over a short time despite a severe drought. Intense hunter-led efforts over 0–1 YPI further reduced seedling mortality towards the all-time minimum value (2.8%) recorded by late 4 YPI, when cumulative hunting efforts were 16,466 (shooting) and 1390 (hunting with dogs) party hours. These efforts also met the goal of reducing rooting to one-third of its baseline value.

The intensity of culling efforts determined wild boar abundance and program success in the park. However, in the absence of well-known functional relationships among culling effort, wild boar abundance and damage extent, measures of effort are not sufficient for decision making because they are affected by multiple factors (see next section) and the immediate effects of effort are hard to anticipate. For example, although the culling efforts over 2004–2005 were limited, they substantially reduced wild boar numbers and cause-specific seedling mortality. Similarly, all wild boar indices fell to near-minimum values by early 2 YPI while ground rooting was well above target levels, perhaps because the vegetation in damaged ground recovered slowly. A similar pattern was recorded in Namadgi National Park in eastern Australia, where a 2-year lag occurred between minimal values in the fraction of plots containing wild boar dung and the rate of the monthly change in the frequency of rooting after lethal control efforts (Hone 1995, p. 315–316). Setting target levels of effort or wild boar abundance implies defining how much yatay seedling mortality and ground rooting would be acceptable (and the rationale on which these damage limits are based) and having a comprehensive understanding of the damage functions. The literature offers no guidance.

Ground rooting surface declined exponentially over time as did yatay palm-tree seedling mortality and wild boar mean catch per session using dogs and controlled shooting. Hone (2007, p. 18) reported linear relationships between ground rooting measures and wild boar indices based on sighting individuals, dung, or tracks. Here, we show that ground rooting was linearly related to the hunting catch of wild boar and that the mean catch using controlled shooting was more sensitive to reveal ground rooting variation than mean catch using dogs.

Both ground rooting and wild boar indices surged during trimesters 23–26 (5–6 YPI) as the shooting was interrupted for 6 months and the soil was saturated for 10 months (Bongianino 2019), favoring rooting. The upsurge in wild boar was more pronounced and lasted longer in the restricted-use zone than in the public-use zone; the former displayed consistently greater wild boar numbers, most likely related to the proximity of crop fields (Gürtler and Cohen 2022). The outlier rooting value in trimester 37 is most likely explained by the joint action of several factors (see Data management) affecting the rooting activity of wild boar, which varied 6- to sevenfold across a 24-year period (Hone 2012). Rooting may occur in both dry and wet seasons depending on soil characteristics, location, and the relative availability of above- and below-ground food items (Welander 2000; Mayer 2009a; Elledge et al. 2013). A few wild boar in a group may inflict a large amount of soil damage in a short time (Sandom et al. 2013). Therefore, ground rooting extent may be less valid and precise as an index of wild boar abundance than other metrics.

The data on wild boar damage analyzed here mostly came from several studies with heterogeneous study designs, spatiotemporal coverage and sample sizes, with no control or comparison zone. This heterogeneity limits the strength of the evidence related to wild boar damage. Seedling mortality observations were not designed to monitor park-wide responses to management efforts. Hence, the paucity of data points that support the effort-outcome relationship impede a more accurate assessment of exactly when mortality reached target values and at what levels of cumulative effort. By contrast, the minimum value of annual seedling mortality ever recorded (2.8%) was well-supported, based on 120 plots deployed across main habitats and park zones (Ballari 2014). Ground rooting estimates came from convenience sampling of palm tree stands and excluded other habitats. Although the time to the disappearance of fresh rootings was not measured, the average time separation between successive surveys allowed a clear distinction between fresh and residual ground rooting, barring July and September 2011 surveys when rooting dropped by 69%.

This case study provides an opportunity to evaluate the potential implications of setting inappropriate baselines for impact assessment, either because prior data are lacking or because past records are not considered. For ground rooting, the program used the mid-2006 estimate (3.9%) as the baseline to define the target value (1.3%). However, the greater wild boar abundance in 2004 suggests that ground rooting at that time was most likely greater than in mid-2006, and if known, it would have led to a higher target value than that selected. Similarly, had the 2006 seedling mortality (32%) been taken as the "preintervention" baseline (instead of using 80–81%, as measured in 2002–2003), the prior effects of abundant wild boar on seedling mortality would have been severely underestimated and control efforts would have been stopped when seedling mortality fell to the putative "preintervention" baseline, prompted by the lack of a pre-defined acceptable damage threshold. The long-standing occurrence of wild boar under limited control, coupled with boar's large impacts on yatay seedling recruitment, are consistent with matrix projections showing that the asymptotic population growth rate of yatay palm trees was well below replacement levels by 2006 (Lunazzi 2009). In 2017, the density of compound-leaved seedlings in semi-dense and dense stands increased by 60% and 633%, respectively, with remarkable concomitant increases in the juvenile stage (Bongianino 2019).

The rooting extent at the park was quite limited over 2006–2015, and peak values (3.9 m^2 per ha) were qualitatively lower than in other protected areas. In the northern jarrah forest in western Australia, ground digging averaged 18.3 m^2 per ha-yr (Adams et al. 2019). In the Great Smoky Mountains National Park (USA), rooting averaged 8000 m^2 per ha in northern hardwoods and 30–3000 m^2 per ha in cove forest and oak types (Singer 1981). In Kampanios National Park (Poland), rooting in the most intensely impacted forest was 100–1000 m^2 per ha in any season (Jezierski and Myrcha 1975). Inside the Kilauea Forest Reserve (Hawaii), wild boar ground rooting covered 1132 m^2 per ha (Ralph and Maxwell 1984).

Wild boar abundance and culling efforts

Intensified hunting over 2004–2007 steadily reduced wild boar abundance to nearly minimal values by early 2008 (2 YPI), and then controlled shooting kept it within a low-density fluctuation band. Several hunting-based indices showed consistent trends, as did measures of wild boar-inflicted damage. Moreover, wild boar indices derived from sighting and camera-trapping surveys over 11 YPI largely agreed with hunting-based indices (Nicosia et al. 2021). Hence, mean crude catch and related metrics were appropriate for monitoring wild boar population trends.

The overall stability of wild boar numbers over 2–5 YPI was disrupted by the 6-month paralysis of control actions, while the 3-month summer breaks were compensated for by subsequent efforts. The fast population recovery of wild boar in resource-rich habitats (Bieber and Ruf 2005; Hone 2012) has been largely attributed to the cessation of hunting-related mortality and disturbance (Tolon et al. 2009; Johann et al. 2020) combined with spring–summer recruitment of pre-reproductive and reproductive individuals and in-migration (Hone 2007). More generally, small variations in juvenile survival disproportionately influenced the population growth rates and sizes of heavily hunted ungulates when their abundance was near equilibrium (Gaillard et al. 2000; Bieber and Ruf 2005; Servanty et al. 2011; Hone 2012). In our study, juveniles were consistently underrepresented among the culled wild boar (Gürtler et al. 2017) and most likely fueled the upsurge at 6 YPI. However, current data cannot assess the relative roles of in-migration and cessation of hunting. The rapid reduction in seedling mortality following 2004–2005 control efforts may in part be attributed to both increasing disturbance and culling effort because wild boar numbers were still high over 2006–2007.

Whether dog-related disturbance displaced wild boar from established home ranges and increased their exposure to shooting or the reverse was a source of conflict between hunters and program managers and remains controversial. Sometimes wild boar responded to hunting disturbance by expanding its home range size (Maillard and Fournier 1995; Saïd et al. 2012) or restricting its short-term mobility, and sometimes boar were apparently unaffected depending on the type and intensity of hunting effort and shelter availability (Massei et al. 2011 and references therein).

Hunting with dogs proved highly effective in the park and elsewhere as a standalone method or as a component of an integrated strategy (e.g. Schuyler et al. 2002; Mayer et al. 2009; Parkes et al. 2010; Massei et al. 2011). In Hawaii Volcanoes National Park, hunting with dogs handled by expert teams was chosen to eradicate wild boar from large fenced areas (Stone and Taylor 1984). In a systematic review, 89% of ground-based shooting operations that also used dogs achieved their objectives whereas 47% of those that did not use dogs were successful (Bengsen et al. 2020). Hunting with dogs can target specific habitats and problem individuals not reached by other methods; its effectiveness largely depends on hunter and dog skills, group size, terrain, and weather conditions (Mayer et al. 2009). However, dogs not well trained and supervised may affect native wildlife (Cruz et al. 2005) and animal welfare issues hinder the use of dogs in some settings; in others, it is a long-standing and socially accepted sport or pest control method. Sticking to a code of good practice is essential. In the park, collateral effects on native wildlife and handlers were rare (Gürtler et al. 2017).

The 10-year follow-up shows the success of *organized* recreational hunting to keep wild boar at bay within the frame of a structured program in a protected area with no shortage of water sources, cover and nutritious food (including yatay fruit: Ballari et al. 2015), and no wild boar predator. Shooting and poisoning were considered the most cost-effective and quickest methods to reduce wild boar population size (Massei et al. 2011). Shooting has been viewed either favorably despite being time-consuming (e.g., Burt et al. 2011; Coblentz and Baber 1987) or as unable to control wild boar in the hands of recreational hunters, especially in food-rich habitats (e.g., Choquenot et al. 1996; Hanson et al. 2009; West et al. 2009; Massei et al. 2011; Ditchkoff and Bodenchuk 2020). "Recreational hunting" (i.e., non-professional, sport, unpaid, amateur, and public hunting) usually means unorganized, casual hunting. However, hunters are a diverse, loosely-defined group whose main motivations often revolve around meat consumption, recreation, trophies, and forest damage control (Andersen et al. 2014). "Opportunistic shooting" and bait stations were considered useful as add-on techniques though economically not feasible (Mayer 2009b, p. 321). Conversely, "amateur hunters" in Australia significantly contributed to wild pig control and produced an economic gain, while their labor applied to conservation goals frequently met obstacles in protected areas (Tisdell 1982, p. 125 and 262). In a systematic review, 60% of ground-based shooting operations that used "volunteer shooters or recreational hunters" reduced herbivore density or damage and half of them achieved their stated objectives; failure to do so was often attributed to insufficient removal rates (Bengsen et al. 2020). But removal rates are also determined by factors decided by resource managers (e.g., length of hunting season and the number of licenses issued).

Organizational capacity, program structure and implementation, and long-term institutional commitment were essential ingredients for meeting conservation objectives, as in other long-term efforts (e.g., Schuyler et al. 2002). The precise nature, intensity and executors of culling operations were also key to program success and sustainability. Park hunters were carefully selected by program managers. Most had long-standing hunting experience and established a long-term relationship with the park in exchange for unpaid access to hunting opportunities. Hunters with dogs and hunters with rifles differed in their views on what hunting meant; affiliation to hunting clubs; allowed prey, and program permanence. Hunters who used dogs spontaneously discontinued their efforts when wild boar hunting success plummeted to move elsewhere, as predicted by harvest and optimal foraging theories (Hone 2007, p. 60), whereas hunters with rifles tended to stick to their blinds as axis deer thrived. Hunter turnover was slow, and as the program matured, prospective hunters spent a training period as assistants to established hunters. With trophy hunting discouraged, the main motivations of park hunters were reportedly recreation and meat consumption rather than financial gain. Travel costs, vehicle maintenance, baiting, shooting gear, and building hunting blinds (all of which were paid by the hunters) implied large, recurrent expenses and sizable contributions to the program, including unpaid labor and a share of the prey to support disadvantaged local groups. This food subsidy program, unique to Argentina, played an essential role in the social sustainability of culling efforts in times of hardship and rising unemployment. As with white-tailed deer in North America, "Hunters have been the engine behind the conservation, management and research…" (Hewitt 2015) of exotic ungulates in the park. Effective shots to wild boar and axis deer in the park over 2019 were reportedly placed at an average distance of 146 m and ranged up to 340 m. Thus, hunter activity qualifies as sharpshooting over bait (DeNicola and Williams 2008), considered the most efficient method to cull white-tailed deer in a protected area (Doerr et al. 2001). Park hunters' activity may be cataloged as recreational or harvest-oriented, while their degree of specialization, experience, dedication, gear and regular practice makes many of them virtually indistinguishable from professional hunters.

Program records provided accurate measurements of hunting effort and catch amenable to standardization and linkage to damage data. Such standardized measures are both rare and valuable for modeling wild boar abundance (Croft et al. 2020). However, hunting effort is multi-faceted and includes other unmeasured components that modify hunter effectiveness, such as prior experience, gear type, and baiting practices (Milner-Gulland and Rowcliffe 2007). Park hunters asserted that wild boar were less attracted to bait when yatay fruit was available during late summer-early fall, matching summer habitat use (Goveto 1999), and diet (Ballari et al. 2015). In the park, shooting effort and occupancy increased over time at a different pace: the former via growing numbers of blinds and sessions whereas occupancy increased by adding shooters to fill in any absence. Occupancy also reflects the degree of the simultaneous spatial coverage of shooting effort and increasing firearm noise potentially disturbing the prey.

Crude shooting effort was boosted over 7–9 YPI by the ever-increasing abundance of axis deer, which kept hunter motivation up and contributed to program sustainability (Gürtler et al. 2018). Every January, program managers decided the annual number of hunting sessions based on a rough assessment of average session and annual catch, tempered by logistic constraints while keeping in line with past practices and anecdotal information. These informal procedures have dominated decision making in conservation management programs (Pullin and Knight 2005). As the program lacked a quantitative target for yatay seedling mortality and failed to monitor it from 5 YPI onwards, the intensity of control efforts at that time was assumed to be sufficient for meeting goals. Although crude shooting efforts at 0 and 9 YPI were roughly similar in hunting party hours, session duration was halved and the frequency of participating parties doubled. Their joint effects, apparently inconsequential for population trend analysis, require further research.

Conclusions

We show that *organized* sport hunting may contribute to the sustainability of long-term control of overabundant and invasive wildlife or pests. It may play a key role in stopping the propagation of emerging wildlife infectious diseases. Carefully structured and managed sport hunting can be an important component of conservation programs (Mysterud et al. 2020) and generate resources to invest in conservation and other societal goals (Festa-Bianchet 2007). How hunting may contribute to sustainable conservation efforts requires more research and evidence (Di Minin et al. 2021).

Our case study provides several lessons for invasive species management programs and highlights crucial needs: to consider well-established principles of applied ecology (Hone et al. 2015) at the planning stage before launching interventions; to preserve the data collected in an accessible format for future use; to invest more in long-term resource monitoring using appropriate designs and sampling efforts, including more current data on palm-tree recruitment and seedling mortality; to estimate ground rooting surface and vegetation recovery rates across main habitats, including patch-level changes in composition, and to implement an adaptive management strategy that links the spatiotemporal distribution of effort to explicit outcomes and target values.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10344-023-01668-0.

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Author contribution REG and JEC originally formulated the idea; AAM and SAB designed and performed the experiments; REG and JEC analyzed the data; REG wrote the manuscript; other authors provided editorial advice.

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Data availability All data generated or analyzed during this study are included in this published article as Online Resource 1.

Declarations

Ethics approval As the culling of exotic ungulates was conducted as part of regular pest control measures in a federally protected area, no approval by an ethics committee was required.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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