



'Reserve effect': An opportunity to mitigate human-wild boar conflicts

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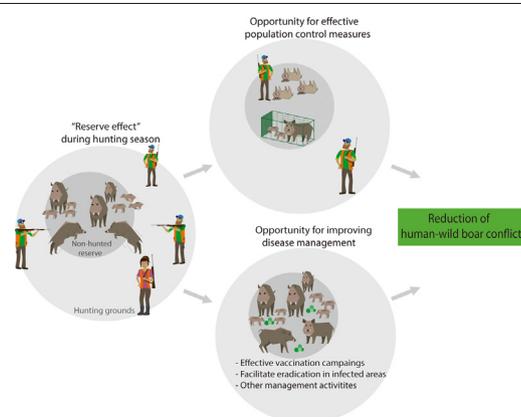
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HIGHLIGHTS

- Wild boar impacts are growing, in parallel with the species' numbers and range.
- Camera traps showed wild boar congregate in reserves where hunting is banned.
- A drastic reduction of wild boar in reserves was observed after a single hunt.
- Population control and disease management can benefit from 'Reserve effect'.
- 'Reserve effect' offers opportunities to mitigate human-wild boar conflicts.

GRAPHICAL ABSTRACT



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ABSTRACT

Wild boar growth in numbers and range is associated with increasing economic and environmental impact. Hunting has been traditionally used to reduce wild boar numbers. Areas where hunting is not allowed may attract wild boar from neighbouring hunting grounds. This phenomenon is called 'reserve effect' and could cause temporarily localised, high densities of wild boar in areas where hunting is banned. To investigate the occurrence of 'reserve effect', this study was conducted in two natural reserves of 400 and 250 ha inside the Montseny Natural Park, Catalonia, Spain where regular hunting of wild boar is not permitted, and only sporadic driven hunts/year are authorised for population control. The aims of the study were to evaluate if wild boar use these reserves as a refuge when hunting is carried out in the surrounding areas and to assess the effects that occasional drive hunts inside these reserves may have on wild boar numbers and social organization. From 2012 to 2015 camera traps were placed in the two reserves without using any bait. Cameras operated for 1.759 days, including hunting and non-hunting seasons, and 37.574 wild boar images were obtained. A 'reserve effect' was detected, as following hunting in the surroundings grounds, the number of wild boar increases inside reserves. Occasional driven hunts conducted in the reserves are effective in reducing the number of individuals and the effects persist for at least 45 days. Hunting disrupts wild boar social organization, as group size was significantly reduced. These results suggested that targeting refuge areas, once hunting in the surroundings causes wild boar to concentrate in these areas, is effective for population control. These findings could also be used to design strategies to optimise population control and offer opportunities for disease management such as vaccination, or to facilitate eradication in areas affected by disease outbreaks. Crown Copyright © 2021 Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

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1. Introduction

Wild boar occur in a wide range of habitats and climates, have few natural predators and are characterised by high reproductive rates. This has led to a fast populations growth that has increased in recent decades across Europe, resulting in high population densities in many countries (Bieber and Ruf, 2005; ENETWILD consortium, 2019a; Massei et al., 2015; Náhlik and Sándor, 2003; Sáenz-Royuela and Tellería, 1986) and causing a wide range of conflicts with conservation and human activities.

This species has significant economic and environmental impacts such as damages to crops, urban areas and infrastructures (Cai et al., 2008; Ficetola et al., 2014; González-Crespo et al., 2018; Ikeda et al., 2019; Schley and Roper, 2003) and reduction of biodiversity richness and species abundance (Bongi et al., 2017; Calevo et al., 2017; Carpio et al., 2016; Genov and Massei, 2004; Herrero et al., 2005). Wild boar also pose threats to public health and livestock, due to traffic accidents and to transmission of diseases, such as African swine fever (ASF), classical swine fever and foot and mouth disease (González-Barrio et al., 2015; Guberti et al., 2019; Rossi et al., 2015; Sáenz-De-Santa-María and Tellería, 2015). All these impacts have important economic implications as the costs derived from traffic accidents, crop and urban areas damages and the consequences of disease outbreaks can amount to billions of euros (Barrios-García and Ballarí, 2012; Forman et al., 2009; Guo et al., 2016; Halasa et al., 2016).

To mitigate these impacts, wild boar population control is required and supported by wildlife managers, landowners, farmers, and public administrations including health services. Population control is carried out mainly by recreational hunting (e.g., driven hunts, solo hunts, etc.) and to a much lesser extent by trapping. Understanding the factors affecting the species' behavioural response to hunting is crucial to apply effective and evidence-based population control.

In most countries, hunting is the main cause of wild boar mortality (Keuling et al., 2013; Massei et al., 1997, 2015; Nores et al., 2008; Toigo et al., 2008; Virgós, 2002). Hunting affects population size but may also influence spatial, social and temporal behaviour, and in particular home ranges size, habitat use, activity patterns and group composition (Baubet et al., 1998; Keuling et al., 2008; Maillard and Fournier, 2014; Scillitani et al., 2010; Thurfjell et al., 2013; Vassant et al., 1988). When driven hunts are carried out, neighbouring areas where hunting is not allowed may be used as a refuge by wild boar. This phenomenon, known as 'reserve effect' has been described in previous studies (Frank et al., 2015; Grignolio et al., 2011; Sodeikat and Pohlmeier, 2003; Tolon and Baubet, 2010). Understanding how wild boar use these reserves is essential to optimise population control and disease management strategies, particularly when the latter are based on a mosaic of areas where culling may or may not be allowed (Keuling et al., 2018; Tolon et al., 2009). Furthermore, no studies have addressed the impact of driven hunts on wild boar behaviour and numbers inside reserves adjacent to areas where hunting occurs. This is particularly relevant for management of diseases such as ASF that rely on core and buffer zones around the outbreak where culling is temporarily banned, and on an intensive hunting area, surrounding the buffer zone, where culling is encouraged (Jori et al., 2020; More et al., 2018).

As wild boar impact is often associated with local population density, the effectiveness of interventions employed to reduce such densities is based on estimating the number of animals before and after population control has been implemented. Of the methods available to estimate wild boar population density (Engeman et al., 2013), several require significant resources, making their implementation unfeasible. One of the most widespread methods is based on hunting statistics, which allows monitoring of large areas with reasonable costs and staff time (ENETWILD consortium, 2019b; Gamelon et al., 2012). Camera traps can also be used to obtain consistent estimates of populations size (Chauvenet et al., 2017; Keuling et al., 2018; Massei et al., 2017; Minuartia, 2020; Rowcliffe et al., 2008). Moreover, camera trap images

allow to collect data on individual behaviour, social interactions, group composition, reproductive output, activity patterns and responses to human presence and hunting (Erdtmann and Keuling, 2020; Lashley et al., 2018; Oliveira-Santos et al., 2013; Palencia et al., 2019; Rowcliffe et al., 2014, 2016). This study used camera traps to monitor changes in wild boar numbers, group size and composition before and after hunting occurred.

The aims of the study were 1. to evaluate if wild boar use reserves as a refuge when hunting is carried out in the surrounding areas; 2. to assess the effects that occasional drive hunts inside these reserve have on wild boar numbers; and 3. to determine the effects of hunting on wild boar group size and composition. The hypotheses were that i) following hunting in the surroundings grounds, the number of wild boar increases inside these reserves; ii) occasional driven hunts conducted in the reserves are effective in reducing the number of individuals and iii) hunting disrupts wild boar social organization.

2. Materials and methods

2.1. Study area

The study was carried out in the Montseny natural park which covers 31.064 ha and is situated in the Catalan pre-littoral mountain range (NE Spain) 17 km from the coastline, with an altitude ranging from 100 to 1.700 m a.s.l. (Fig. 1). The area is located in the Mediterranean region but at the higher altitudes above 1.000 m, the climate is temperate, creating a marked gradient of climate and vegetation. Average annual rainfall is 1.053 mm. Mean annual temperature at the highest altitudes is 7.1 °C with a maximum monthly mean in July of 15.5 °C and a minimum in January of 1.0 °C. At lower altitudes, mean annual temperature is 14.8 °C with a monthly mean maximum in July of 23.6 °C and a minimum on January with 7.2 °C (Servei Meteorològic de Catalunya, 2016).

Inside the natural park, there are eight areas with special protection known as natural reserve areas (here after NRA), with occupying a total of 2606 ha (8.4% of the total surface of the natural park) where regular hunting is not permitted. This study was carried out in the two largest areas: Matagalls-Sant Marçal-Vall de Riudeteix (hereafter referred as Riudeteix) and Vallforners, which together occupy 1515 ha.

Riudeteix is situated between 670 and 1.697 m a.s.l and includes an area of 1.117 ha. The vegetation is composed mainly by dense forests dominated by holm oak (*Quercus ilex*) forest, intermixed with beech (*Fagus sylvatica*) and chestnut (*Castanea sativa*) forests. At higher altitudes, the vegetation is dominated by bushes such as junipers (*Juniperus communis* ssp. *nana*) and broom (*Genista purgans*), mesophilic and xerophilous meadows, wet meadows and reedbeds (OTPAT, 2008).

Vallforners includes an area of 389 ha with a high diversity of habitats situated between 700 and 1.300 m a.s.l. The vegetation is dominated by sclerophyllous species, mainly holm oak, but also conifers and riparian forest, and at the higher altitudes, open habitats dominated by grassland and shrubs as in Riudeteix.

2.2. Hunting data – wild boar monitoring program

In Catalonia a wild boar monitoring program was implemented in 1998, based on data provided by hunting teams at the end of the hunting seasons. Participants deliver a notebook where data from each driven hunt are recorded and include date, number of hunters and dogs, number of wild boar hunted, and number of animals observed but not hunted. These data are used to estimate wild boar density in each of the 22 participant areas in Catalonia. Currently more than 173 hunting groups participate in the program, providing information on about 5.000 hunts each year. The complete database contains data about more than 85.000 driven hunts. These data are analysed to monitor population trends across the whole region, with reports annually published by the Catalan Ministry of Agriculture, Livestock, Fisheries

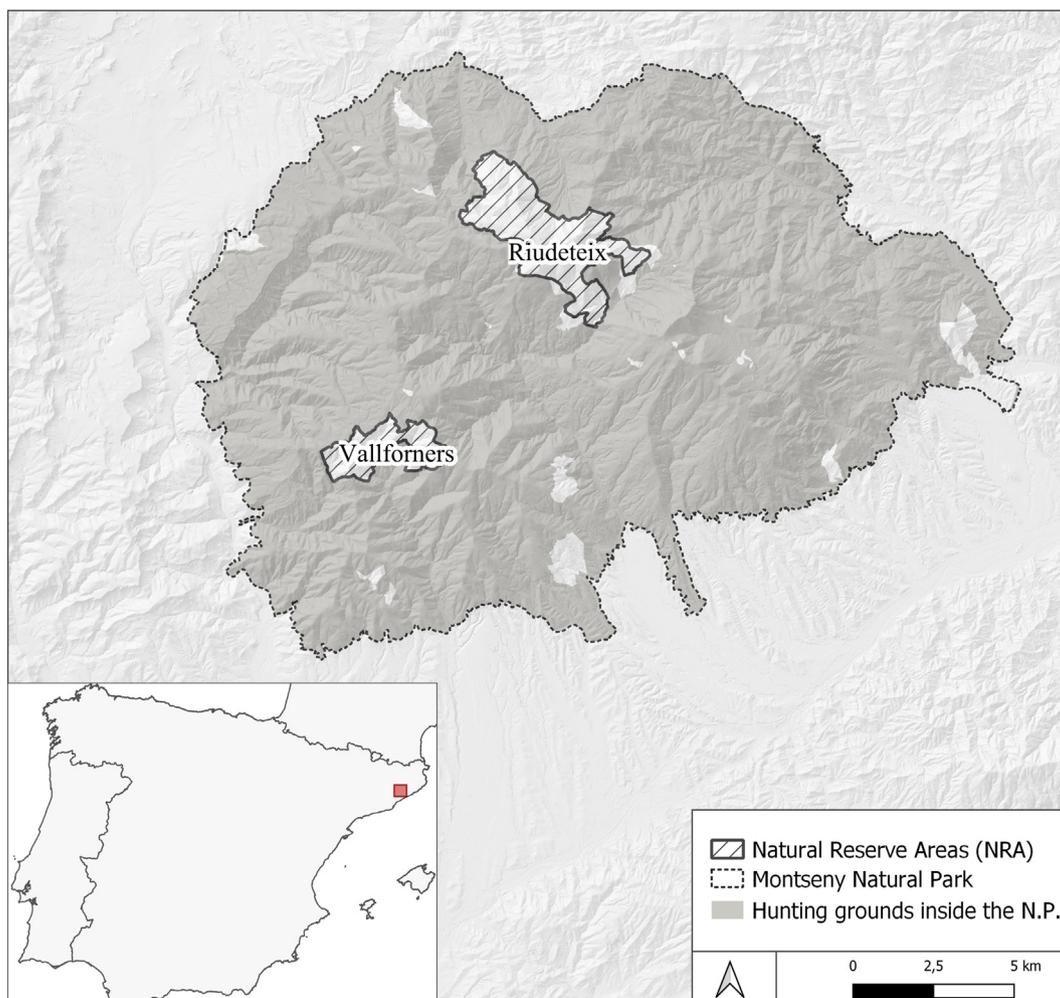


Fig. 1. Location of the two study sites, the Natural Reserve Areas (NRA) of Vallforners and Riudeteix situated within the Montseny natural park, Catalonia, Spain. Hunting areas occupy almost the whole area of the natural park except the NRA and other small sites.

and Food since 1998 (DARP, 2020). Since 1998, Montseny natural park participates to the Catalan Wild boar Monitoring Program.

Two wild boar density indices are calculated each year: 1. a relative density index (Rosell, 1998) which takes into account the total number of wild boar harvested, the hunting effort and the surface of the hunting area and 2. an estimate of the absolute density (Saez-Royuela and Telleria, 1987), considering the ratio of wild boar hunted vs. observed per area (Table 1). These methods are often used for monitoring wild boar trends (Gamelon et al., 2012; Keuling et al., 2018; Massei et al., 2015). Moreover, recent comparison with other density estimation methods based on camera trap, such as the Random Encounter Model (Chauvenet et al., 2017; Rowcliffe et al., 2008) carried out in the Montseny natural park, have provided similar density estimations

(Minuartia, 2020), reinforcing the field operatives' confidence in the method based on hunting data.

During the study period (2012 to 2015) wild boar density estimate by the wild boar monitoring program in Montseny natural park increased from 10 individuals/km² in 2012/2013 to 16 individuals/km² in 2015/2016 (Table 1), the maximum ever registered in the 20 years monitoring period (DARP, 2016).

Throughout the whole natural park, surrounding the two NRA, there was a relatively high hunting pressure during the study periods according to the monitoring program, as on average 110 hunts (SE = 0.95) were carried out each month (from September to February), representing around 1.4 hunts/km². Hunts had a mean participation of 24 (SE = 0.44) hunters and 19 (SE = 0.37) dogs (Table 1).

Table 1
Wild boar density estimates and hunting pressure parameters in the Montseny Natural Park during the study period. Data from the Catalan Wild Boar Monitoring Program (DARP, 2016).

Variable	2012/2013	2013/2014	2014/2015	2015/2016
Wild boar density (individuals/km ²)	10.29	11.59	11.31	16.34
Number of hunts/year/km ²	1.40	1.37	1.33	1.54
Mean number of hunts/month	110.16	107.33	104.00	117.17
±SE	7.10	6.20	5.20	4.12
Mean number of hunters/hunt	23.14	23.61	24.10	24.05
±SE	0.43	0.45	0.45	0.39
Mean number of dogs/hunt	18.79	18.94	18.21	18.02
±SE	0.37	0.40	0.36	0.32

Population control driven hunts were exceptional hunts carried out inside the NRA. These were authorised by the natural park authorities with the objective of culling the maximum number of wild boar inside these areas. These control driven hunts carried out once or twice per year, during the winter months, attracted a higher number of participants, with an average of 31 (SE = 0.58) hunters and 27 dogs (SE = 0.49), compared to regular driven hunts carried out in the surroundings areas.

2.3. Data collection

Camera trapping was conducted to monitor abundance and group composition of wild boar inside the two reserves. No bait was used to attract the animals. Reconyx RC55 and HC500 camera traps were situated in trees next to active wild boar trails.

Five camera trap locations (two in Riudeteix and three in Vallforners respectively) were in operation during the whole period and were considered for the analysis. Camera traps operated for 1759 days (Table 2). Other cameras were placed in the NRA during these years but were not working for the whole period and have not been included in the present study. Nevertheless, the data provided by these extra cameras has been used to check consistency of the results obtained. The same patterns of numbers of individuals inside the reserve are during the hunting and non-hunting season were coincident with the ones observed in the cameras selected for this study. Moreover, the fact that the results obtained in the present paper by the 5 cameras are consistent across the four years of study, together with the high number of day in operation and registers obtained, reinforce the robustness of the dataset and the conclusions that can be drawn.

In Riudeteix two camera traps were placed in an area of 250 ha situated between 875 and 1050 m a.s.l., covered mainly with Mediterranean oak and excluding the higher open areas of the NRA. In Vallforners three camera traps were distributed across the whole area of the NRA, dominated by Mediterranean oak. Cameras were placed in locations without attractive resources for wild boar, in points with conditions and habitats similar to the whole study area. Locations were chosen to assure that camera traps had a good area of vision of wild boar movements, avoiding areas with dense vegetation that interfere in the camera traps range.

2.4. Data analysis

Visual identification was used to define the minimum number of individuals, the age class and group size for each group of wild boar that visited the camera traps. Photographs taken less than 10 min apart were considered the same visit (Massey et al., 2017). Group composition was classified in four categories, matriarchal groups, solitary males, subadults or indeterminate; group size was determined by counting the total number of individuals in each group. Matriarchal groups were described as any group of one or more adult sows with their youngs.

Subadult groups are composed by small number of subadults. Camera traps recorded a sequence of 5 consecutive photos and the minimum time lag between bursts was selected (0.6 s). For each sampling location, the daily mean number of wild boar (minimum count of individuals recorded in the photos taken per day in each camera trap) was calculated. Before any analysis, the autocorrelation between the daily individual counts was tested indicating that each daily observation was independent from the previous and following days.

2.4.1. 'Reserve effect' analysis

To investigate the 'reserve effect', camera traps were used to assess the presence of wild boar inside the reserve areas. The study periods of 2014/2015 and 2015/2016 were selected, since they are the years that present complete camera trap data for the regular hunting and no hunting seasons. The number of wild boar individuals recorded by the camera traps inside the NRA (where hunting is normally forbidden) during regular hunting and non-hunting season in the surroundings areas was analysed. Differences of this variable in each site and season between hunting and non-hunting periods, and before and after the population control hunt, were tested using Mann-Whitney tests. Sequential Bonferroni corrections (Rice 1989), in which alpha was 0.05 (number of years by NRA) were used for the first comparison. Differences in group composition before and after the regular hunting season and before and after the population control driven hunt were tested by chi-square tests. Only the period before the first population control driven hunt inside the NRA was considered, as after the disturbance the NRA could not be considered a hunting reserve anymore.

2.4.2. Population control driven hunt inside the reserves

For testing the effects of the population control driven hunt inside the reserves on wild boar numbers and group composition camera traps were used to assess the number of individuals before and after the hunts. The four study periods in which the camera traps were in operation during the hunting season were considered (2012/2013, 2013/2014, 2014/2015 and 2015/2016). An analysis before / after the hunting control within the reserve was carried out to assess the effect of hunting on numbers and group composition. A period of 45 days after the first population control driven hunt was considered, as previous studies reported that the effects of a driven hunt on wild boar home ranges can be detected during a period of 4 to 6 weeks (Sodeikat and Pohlmeier, 2003). In addition, the present study also tested whether the effects of the population control driven hunt on wild boar numbers and group composition persisted for longer periods, specifically for 60 days, in the instances where data were available.

To evaluate the effectiveness of the population control hunt in decreasing the number of wild boar inside the NRAs, an Interrupted time series analysis (ITS) was carried out. The ITS examined changes in the slope of the trend of daily mean number of wild boar detected/camera

Table 2

Duration of the camera trap monitoring in each NRA during both open hunting season (September to February) and closed hunting season (February to September) in the surrounding areas of the Montseny Natural Park. Two and three camera traps were used in Riudeteix and Vallforners respectively.

Natural Reserve Area	Hunting season	Installation	Removal	Proportion of days in operation
Riudeteix	Hunting 2012/2013	30/10/2012	12/03/2013	82%
	Hunting 2013/2014	06/11/2013	23/02/2014	100%
	Non-hunting 2014	24/02/2014	06/09/2014	100%
	Hunting 2014/2015	07/09/2014	22/02/2015	100%
	Non-hunting 2015	23/02/2015	06/09/2015	99%
	Hunting 2015/2016	06/09/2015	18/02/2016	100%
	Total			97%
Vallforners	Hunting 2012/2013	-	-	
	Hunting 2013/2014	03/10/2013	23/02/2014	81%
	Non-hunting 2014	24/02/2014	31/08/2014	100%
	Hunting 2014/2015	01/09/2014	22/02/2015	76%
	Non-hunting 2015	23/02/2015	05/09/2015	100%
	Hunting 2015/2016	06/09/2015	18/02/2016	100%
	Total			92%

trap/day in each study site during the hunting season in Montseny natural park before and after the population control hunts were carried out inside the reserves (Bernal et al., 2017).

Before the ITS analysis was carried out, data autocorrelation (tendency of observations closer in time to be more similar between each other) and overdispersion (variability greater than the expected by the model) were tested. As the data did not show autocorrelation but tested positive for overdispersion, a Quasi-poisson distribution was used, which allows the variance to be proportional rather than equal to the mean. The ITS analyses were carried out using the script available on Bernal et al. (2017). All data analyses were carried out in R (R Core Team, 2020).

3. Results

3.1. 'Reserve effect'

During 2014/2015 and 2015/2016 seasons, camera traps were in operation for 723 and 724 days respectively (Table 2) and recorded 7800 and 12,908 wild boar images in Riudeteix and Vallforners respectively. Wild boar were detected in all operational camera traps, with an average daily number across sites and seasons of 2.45 (SE = 0.11, range = 0–41) wild boar /day.

Comparison of the number of individuals between regular hunting and non-hunting season, showed that wild boar concentrate in the NRA when hunting occurs in the surroundings areas. The average number of individuals was significantly higher inside the NRA during the hunting season, than the non-hunting season for both years in the Vallforners site (2014/2015: Mann-Whitney U test $W = 4785.5$, $n_1 = 195$, $n_2 = 85$, $P < 0.001$; 2015/2016: $W = 7732$, $n_1 = 193$, $n_2 = 91$, $P < 0.001$) and for the 2015/2016 period in the Riudeteix site (U test $W = 6815$, $n_1 = 194$, $n_2 = 82$, $P < 0.001$), but not for Riudeteix during 2014/2015 ($W = 12,962$, $n_1 = 195$, $n_2 = 131$, $P = 0.811$) (Fig. 2).

For both study sites, the mean group size detected inside the NRA was higher during the regular hunting season than the non-hunting

season for both years in the Vallforners site (2014/2015: Mann-Whitney U test, $W = 3712$, $n_1 = 287$, $n_2 = 151$, $P < 0.001$; 2015/2016: U test, $W = 31,775$, $n_1 = 171$, $n_2 = 185$, $P < 0.001$) and for 2015/2016 in the Riudeteix site (U test, $W = 5715.5$, $n_1 = 163$, $n_2 = 162$, $P < 0.001$) but not for Riudeteix during 2014/2015 ($W = 21,168$, $n_1 = 207$, $n_2 = 151$, p -value = 0.576). Mean group size for each period are reported in supplementary materials (Table S1).

Group composition differed between the non-hunting and the regular hunting season for both sites and study periods after Bonferroni correction (Vallforners: 2014/2015: $X^2_3 = 42.90$, $P < 0.001$; 2015/2016: $X^2_3 = 55.71$, $P < 0.001$. Riudeteix: 2014/2015: $X^2_3 = 32.04$, $P < 0.001$; 2015/2016: $X^2_3 = 23.09$, $P < 0.001$). The proportion of matriarchal groups was higher inside the NRAs during the hunting season than during the non-hunting season in all cases. No consistent patterns were observed on proportions of solitary males and subadults across years and sites (Fig. 3).

3.2. Effects of population control driven hunt inside the reserves

During the hunting seasons from 2012/2013 to 2015/2016, two and three camera traps were in operation for 1102 days (Table 2) and recorded 17,532 and 20,042 wild boar images in Riudeteix and Vallforners respectively. Wild boar was detected in all operational camera traps, with an average daily number of individuals across sites and seasons of 2.75 (SE = 0.10, range = 0–41).

The population control driven hunts inside the reserve were carried out once per season except for Vallforners in 2014/2015 and 2015/2016, when two population control hunts were carried out but only the period after the first hunt has been considered for the analysis.

The mean number of wild boar detected/camera trap for a period of 45 days after the population control hunt was lower than that before the hunt for all years in Vallforners (2013/2014: Mann-Whitney U test, $W = 278$, $n_1 = 105$, $n_2 = 45$, $P = 0.001$; 2014/2015: $W = 501.1$, $n_1 = 30$, $n_2 = 45$, $P < 0.001$, 2015/2016: $W = 427.5$, $n_1 = 91$, $n_2 =$

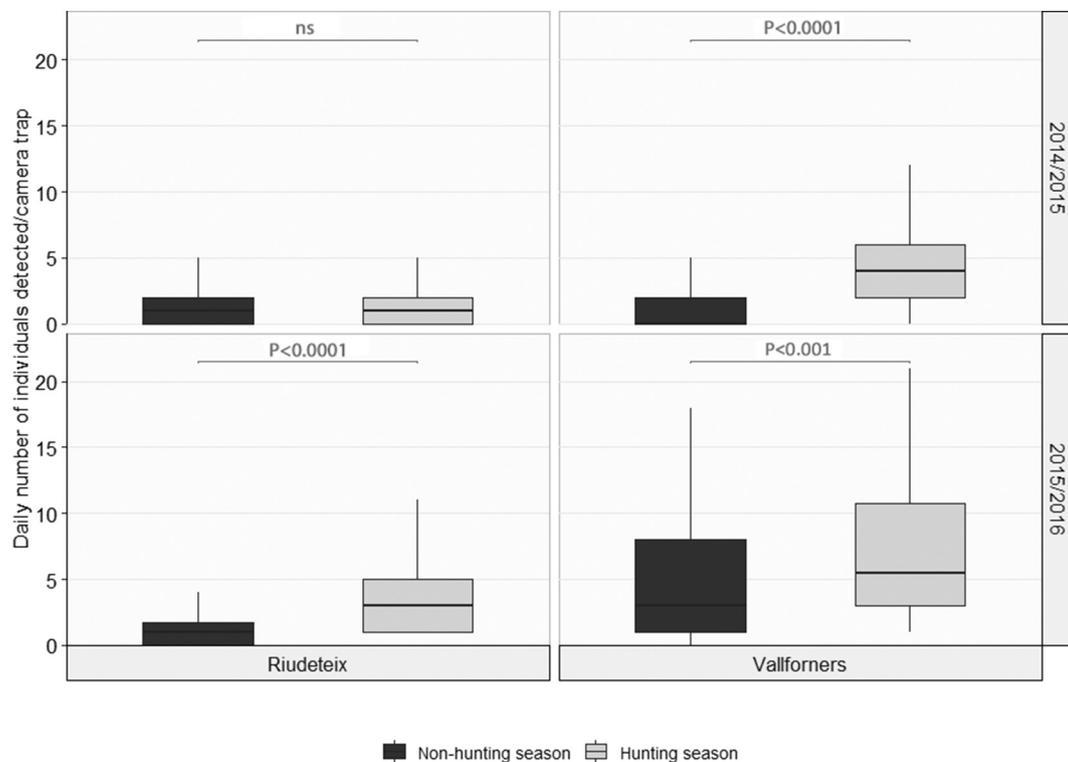


Fig. 2. Daily number of wild boar individuals detected/camera trap inside the NRAs during non-hunting season (spring and summer) and hunting season (autumn and winter) in the Montseny natural park before any population control hunt was carried out inside the NRAs. The line inside the box represents the median, lower and upper box boundaries represent 25th and 75th percentiles respectively and lower and upper error lines; 10th and 90th percentiles respectively. ns: $p > 0.05$.

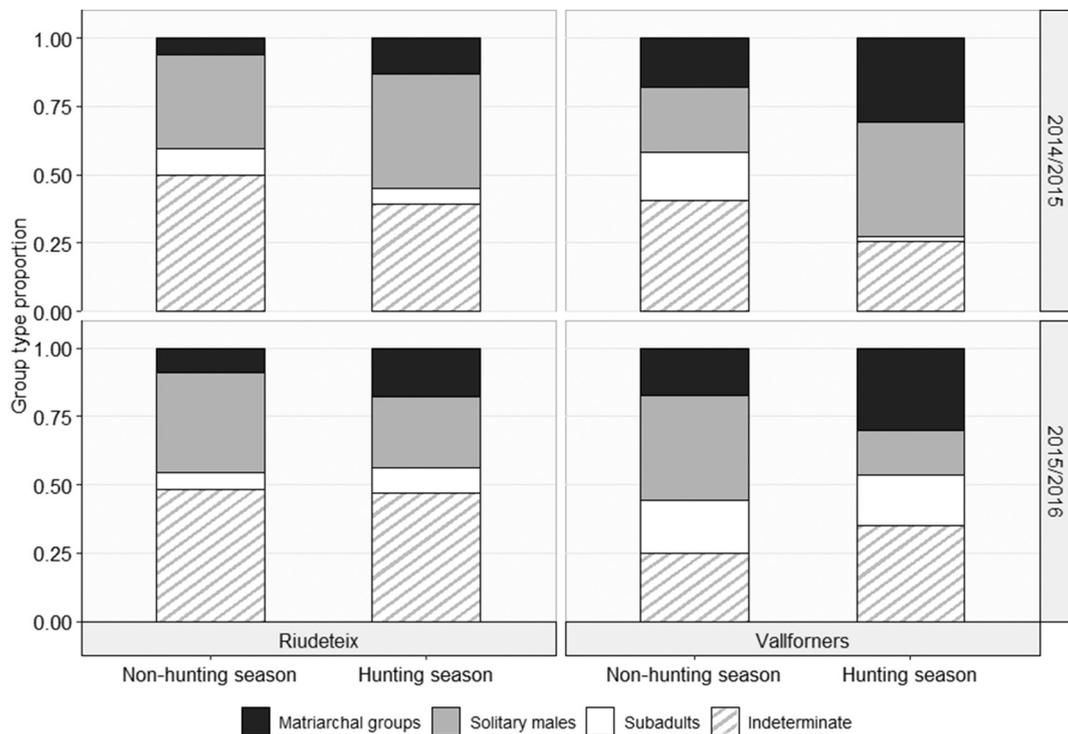


Fig. 3. group composition proportions observed in the two non-hunted study sites during non-hunting and hunting season in the other hunted parts of the Montseny natural park.

45, $P = 0.019$) and for the first three years in Riudeteix (2012/2013: $W = 532.5$, $n_1 = 53$, $n_2 = 45$, $P < 0.001$; 2013/2014: $W = 488$, $n_1 = 152$, $n_2 = 34$, $P < 0.001$; 2014/2015: $W = 1501$, $n_1 = 131$, $n_2 = 42$, $P < 0.001$). Only the 2015/2016 season in Riudeteix the decrease was not significant ($W = 287.5.5$, $n_1 = 67$, $n_2 = 45$, $P = 0.079$) (Fig. 4). Data of 60 days after the hunt were only available in four cases (Riudeteix 2012/2013 and 2015/2016 and Vallformers 2014/2015 and 2015/2016). In these cases, differences in wild boar numbers before and after the population control driven hunt were significant only in Riudeteix for the season 2012/2013 (Mann-Whitney U test, $W = 651$, $n_1 = 53$, $n_2 = 60$, $P < 0.001$), in all other cases (Riudeteix 2014/2015, and Vallformers 2014/2015 and 2015/2016) differences were not significant (Mann-Whitney U test, $W < 800$, $P > 0.049$).

The interrupted time series analysis showed that the population control driven hunts inside the reserves reduced wild boar numbers and that the effects were still lasting after 45 days (Fig. 5). In all study periods for both sites, the observed trend based on the regression model of individual numbers detected per day was lower than the predicted trend if the intervention had not been carried out.

The effect of single population control driven hunts inside the reserves on group size was not consistent across areas and years (Table S2). At Vallformers, there was a significant decrease in mean group size for all the three seasons (2013/2014: Mann-Whitney U test: $W = 35,355$, $n_1 = 285$, $n_2 = 181$, $P < 0.001$; 2014/2015: $W = 54,655$, $n_1 = 162$, $n_2 = 208$, $P < 0.001$, 2015/2016: $W = 42,640$, $n_1 = 153$, $n_2 = 214$, $P < 0.001$). At Riudeteix, mean group size differed for the 2015/2016 season ($W = 6694$, $n_1 = 109$, $n_2 = 85$, $P < 0.001$) but not for the first three seasons ($W < 22,066$, $P > 0.164$), although the same trend in decreased group size was observed.

Where individual and groups could be identified, consistent but only borderline significant differences in group composition frequencies emerged when comparing the period before the population control driven hunt and the 45 days after the hunt (Fig. 6). No differences were observed in Vallformers (after Bonferroni correction) for all three study periods (2013/2014: $X^2_3 = 9.11$, $P = 0.028$; 2014/2015: $X^2_3 = 10.56$, $P = 0.032$; 2015/2016: $X^2_3 = 6.52$, $P = 0.030$) and in Riudeteix only 2015/2016 ($X^2_3 = 17.98$, $P < 0.001$) was significant after Bonferroni

correction ($X^2_3 < 7.82$, $P > 0.049$). Bonferroni correction is a very conservative test and in all cases the p values were very close to significance.

4. Discussion

This study substantiated the hypotheses that i) following hunting in the surroundings grounds, the number of wild boar increases inside reserves; ii) occasional driven hunts conducted in the reserves are effective in reducing the number of individuals; and iii) hunting disrupts wild boar social organization.

In particular, the study confirmed that when driven hunts, that involve tens of hunters and dogs, are carried out, wild boar seek refuge in reserve areas where hunting is banned. The results also indicated that this behaviour seems particularly apparent in matriarchal groups and that hunting affects group size and composition. This was also the first study that investigated the effects that control driven hunts inside refuge areas have on wild boar numbers and on group composition. Although few camera traps were employed during the study, albeit for consecutive years, the results were reasonably consistent across the two reserves and the years.

The 'reserve effect' for wild boar was detected in this study, similarly to what described in previous studies (Amici et al., 2012; Rosell et al., 2004; Tolon et al., 2009; Tolon and Baubet, 2010). Amici et al. (2012) found that the presence of non-hunted areas close to cultivated areas was a significant factor affecting crop damage by wild boar, supporting the hypothesis of a 'reserve effect'. Tolon et al. (2009) showed that wild boar moved to the reserve during the open hunting season but also that there was a threshold distance (2.1 km) beyond which animals did not respond to hunting disturbance as they might have not perceived the safety in the reserve. As the two reserves in the present study are more than 5 km apart, it is likely that the wild boar attracted to one of the reserves were not affected by the other one. Rosell et al. (2004) found the maximum number of wild boar in the non-hunted reserves in a wetland area during the autumn months, which coincided with the start of the hunting season in the surroundings. This also coincided with the lack of food resources in the neighbouring areas, which were

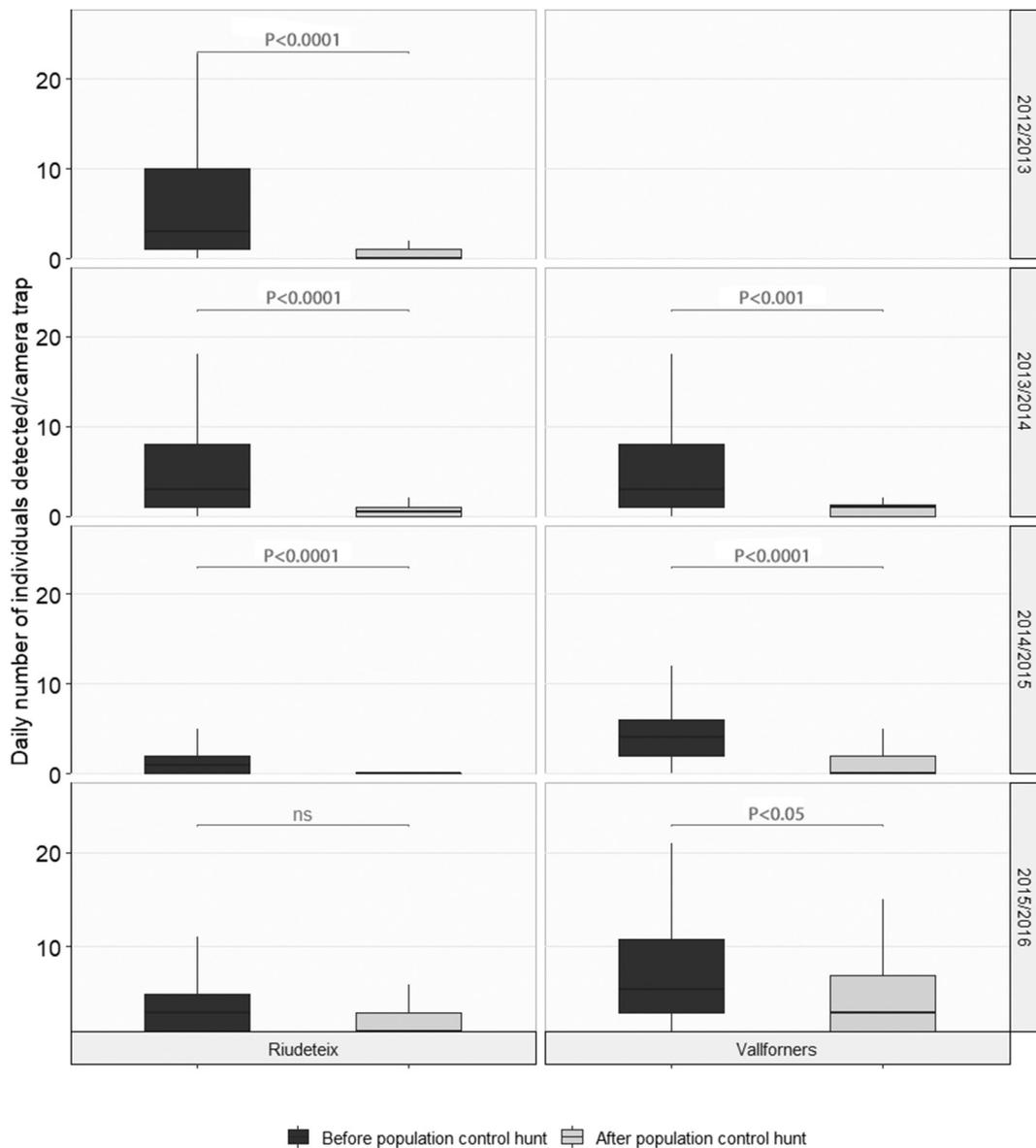


Fig. 4. Daily number of wild boar detected/camera trap during the hunting season in Montseny natural park before and 45 days after the population control hunts in each site and study period. The line inside box represents the median, lower and upper box boundaries represent 25th and 75th percentiles respectively and lower and upper error lines; 10th and 90th percentiles respectively. ns: $p > 0.05$.

occupied mainly by cereal crops harvested at the end of summer and might have encouraged wild boar towards the reserves where food resources are available during autumn and winter. The same study also observed larger group size during the mating season which coincided with the hunting season. The present study showed that group size and proportion of matriarchal groups increased significantly inside the reserves during the hunting season (autumn and winter). These variations could be due to both the hunting pressure but also to seasonal variations in social organization at the beginning of the mating season as in Rosell et al. (2004).

A 'reserve effect' has also been described for other ungulate species, for instance roe deer (*Capreolus capreolus*) sought refuge in protected areas when hunting with dogs was conducted in the surroundings, even though this species was not targeted by these hunts (Grignolio et al., 2011). Similarly, farmland (Casas et al., 2009) and wetland birds species (Bregnballe and Madsen, 2004; Madsen, 1998) during the hunting season switch their resting areas to sites where hunting is banned.

Conversely, Brogi et al. (2020) did not find any evidence of 'reserve effect' in wild boar and attributed the increased number of animals in

a non-hunted areas during autumn to the presence of food resources inside these areas. In the present study, food resources appeared equally distributed as there is the same type of habitat, dominated by holm oak, intermixed with beech and chestnut forests inside and outside the reserves. The increase of wild boar numbers was very likely due to the safety that non-hunted areas offered during the hunting season, as partly indicated by the sudden shift in numbers once the hunting season had started.

Where the 'reserve effect' occurs, adaptive management is required to achieve population reduction objectives across a whole area. For this reason, one or two control driven hunts per year were authorised inside the NRAs in Montseny natural park where hunting is normally banned. This study confirmed the hypothesis that these occasional hunts are effective in decreasing number of wild boar in the reserves. The effect of these hunts persisted for at least 45 days, in agreement with previous studies that showed that after a single hunt wild boar returned to their original home ranges within four to six weeks (Sodeikat and Pohlmeier, 2002). The reduced numbers of wild boar inside the reserves post-occasional driven hunts could be due to a combination of

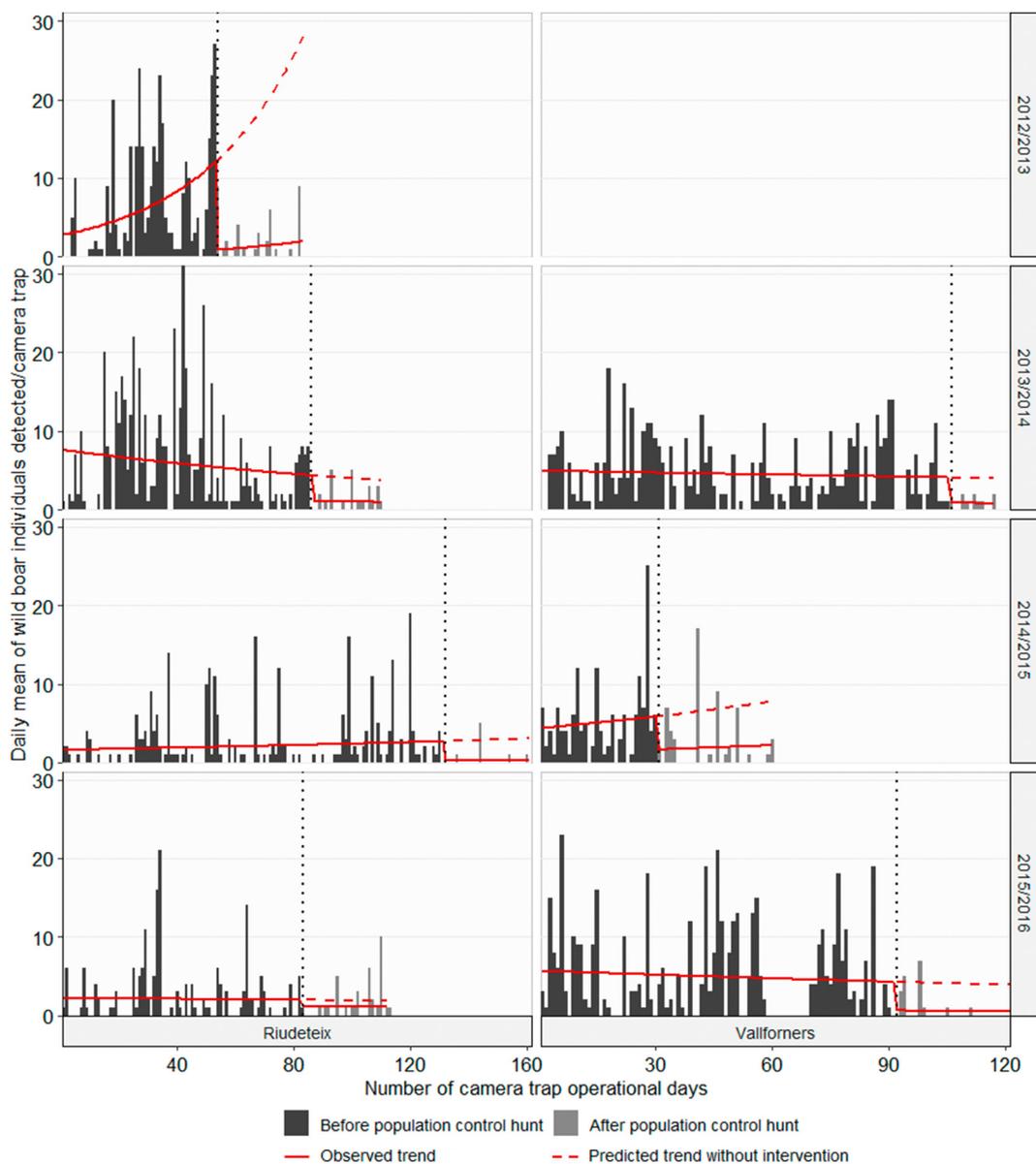


Fig. 5. Daily mean number of wild boar detected/camera traps in each site and study period during the hunting season in Montseny natural park before and after the population control hunts (represented by vertical black dotted lines) were carried out inside the reserves. Solid lines show the actual trend before and after the driven hunt. Dashed lines show the predicted trend based on regression model if the population control hunt had not been carried out. The ‘after’ period includes 45 days after the population control hunt.

individuals that have been culled and animals that emigrated outside the reserves. Spatio-temporal variations of risk perception are major drivers of animal distribution especially for intensely preyed upon or harvested species responding to the so called “landscape of fear” (Brown et al., 1999; Thurfjell et al., 2013; Tolon et al., 2009). Future studies using camera traps inside and outside the reserves to estimate wild boar numbers throughout the year should establish whether the persistent decreased number of wild boar inside the reserves, following a single hunting event, is due to numbers removed by hunters, to emigration or to both.

The results show that single driven hunts carried out inside the reserves resulted in a decrease of group size. This may be caused by loss of individuals that have been culled but also from group disruption or individuals leaving the original groups. Previous studies found that hunting, even a single driven hunt affects social behaviour, activity patterns and spatial use (Keuling et al., 2008; Maillard and Fournier, 2014; Miguel et al., 2020). Nevertheless, the effects caused by hunting on wild boar social organization are uneven across sites and different studies do

not agree on how wild boar respond to hunting (Massei et al., 2011; Podgórski and Śmietanka, 2018).

Group composition was only affected by population control driven hunts inside the reserves in one case, for Riudeteix in 2014/2015, when the proportion of matriarchal groups decreased while that of solitary males and subadults increased. This tendency was observed in all the other study cases, although the difference was not significant. These variations could be partly explained by regular season variations in group compositions. However, previous studies showed that the proportion of matriarchal groups during autumn and winter remain stable (Rosell et al., 2004), while the results of the present study show that there was a significant decrease during these periods in both study sites, supporting the idea that the hunting intervention was the cause of the severe reduction of the number of matriarchal groups observed. The fact that matriarchal groups decrease after disturbance can be attributed to these groups being more easily hunted as they are more detectable by hunting dogs, but also to the leading sows being more cautious and having a lower threshold of risk perception than subadults

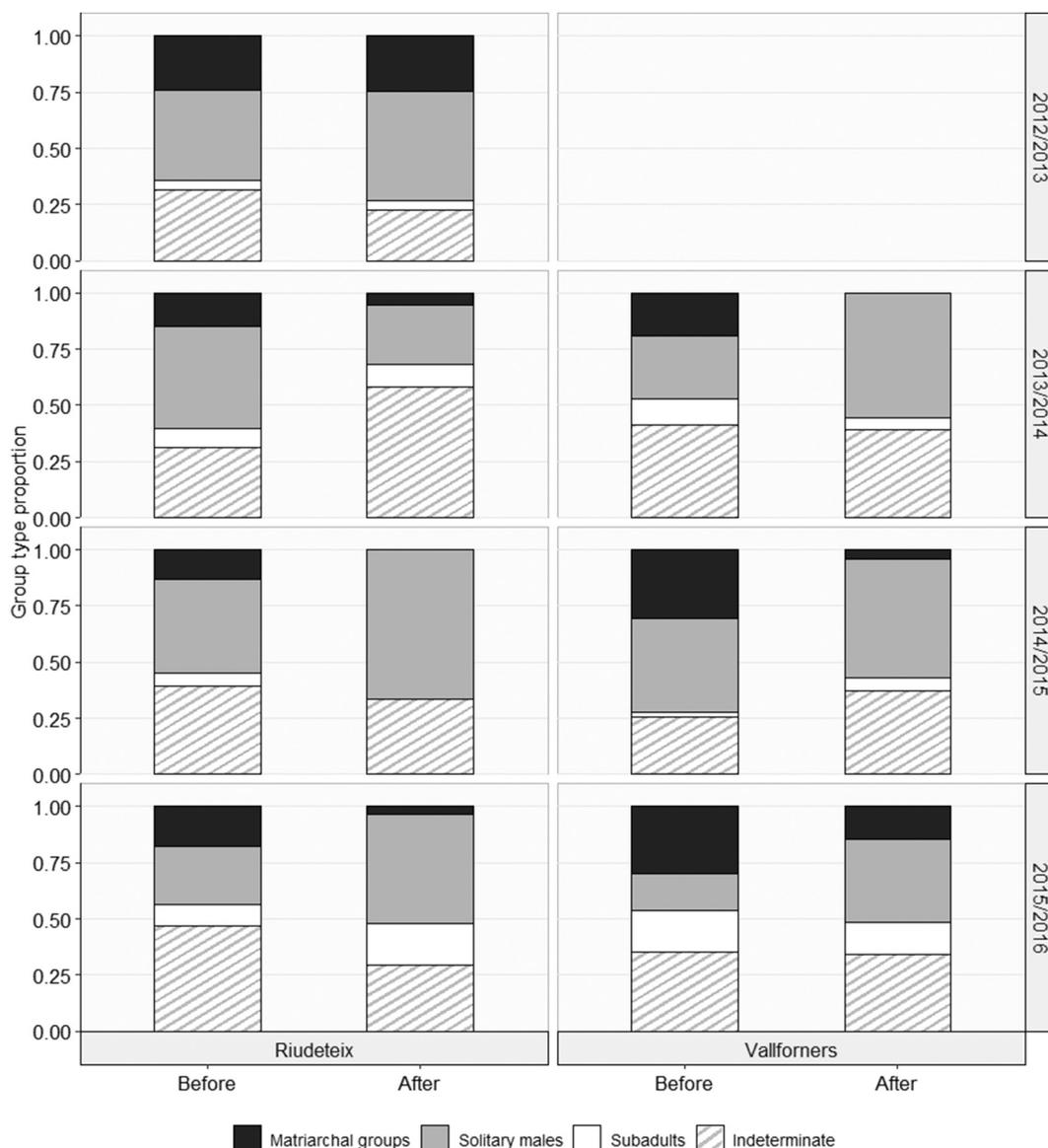


Fig. 6. Group composition proportions observed in the two study sites before and after the population control hunts inside the reserves.

and solitary males, as suggested by Saïd et al. (2012). Iacolina et al. (2009) reported that high hunting pressure may lead to an increase of aggregations of unrelated adult females suggesting that hunting may increase contact rates between otherwise different matriarchal groups. Wild boar group disruption, especially if the leading sow and other adult females are culled can also cause an increase of the juvenile dispersion (Moennig et al., 1999), once again leading to a potential increase in contact rate, which represents a major risk of disease transmission (Podgórski et al., 2018).

Little attention has been paid so far to the effect of hunting on wild boar social disruption, although the latter could have significant effects on disease control, particularly for those diseases that are contact-rate or density dependent. For instance, culling-induced social perturbation, reported in European badgers (*Meles meles*), led to increased contacts between neighbouring social groups and was in turn associated to a rise of bovine tuberculosis prevalence (Riordan et al., 2011). Similar results were reported for alpine ibex (*Capra ibex*) as home range perturbations due to culling led to a brucellosis re-emergence (ANSES, 2015).

These findings have major implications for mitigating human-wild boar conflicts. In contexts where wild boar high densities are associated with negative impacts, such as crop damage, reduction of biodiversity,

and vehicle collisions, reserves may act as sinks when hunting occurs in the surrounding grounds but also as sources of wild boar once the hunting season is over. This study suggests that single population control driven hunts carried out in non-hunted areas may achieve a significant reduction of individual numbers. Thus, banning hunting in some areas during a part of the hunting season will concentrate wild boar which will later allow to increase the effectiveness of methods such as culling or trapping.

These results are also relevant to manage disease outbreaks. For instance, current recommendations to control ASF include establishing a core area around the outbreak, surrounded by a buffer zone, which is in turn surrounded by an outer zone. Soon after the outbreak declaration, hunting is banned in the core and buffer zones and allowed only in the outer zone. After a certain time, the core and buffer areas are to be depopulated through intensive culling (Jori et al., 2020). Recent studies based on modelling of wild boar contact rates in North America, suggest that a 2 km culling radius around the disease detection might be sufficient to stop the spread, nevertheless, it would vary depending on the density and home range of the infected populations (Yang et al., 2021). The method used for culling should be chosen as the most efficient, causing the least possible disturbance and taking into account the local habitat and hunting traditions (Jori et al., 2020). In the study area driven hunt is

by far the most used hunting method while other methods such as lying-in wait or stalking are barely practiced. The findings of this study confirm that regular driven hunts are an effective method of concentrating wild boar in relatively small areas where animals can then be removed by culling. Nevertheless, as highlighted by a recent study in South Korea, the human intervention in ASF infected areas represents an important risk of disease spread, particularly if biosecurity measures are not properly adopted, and trapping methods can be the most effective intervention in some situations (Jo and Gortázar, 2021).

The results of several studies suggest that driven hunts can increase the wild boar movements over wider areas (Maillard et al., 1996; Sodeikat and Pohlmeyer, 2003) and cause group disruptions, as we found in the present study, potentially leading to an intensification of contacts with other wild boar groups and to an increased risk of disease transmission. Yang et al. (2021) did not detect any effect of culling on contact rates in low removal situations but suggest that higher culling pressure could lead to an increase of contact rate and disease spread.

The 'reserve effect' and the fact that wild boar densities temporary increase in non-hunted areas could also be exploited to maximise the impact of vaccination campaigns based on baits containing drugs such as classical swine Fever vaccines. Future studies should explore this idea and assess whether a temporary, hunting-induced increase in concentration of wild boar can be used to increase bait uptake.

4.1. Conclusions

This study corroborated the 'reserve effect' as wild boar use non-hunted areas as a refuge when hunting occurs in the surroundings. The results also demonstrate that exceptional population control driven hunts undertaken inside these areas, are an effective method in reducing number of individuals, but may also cause a disruption of wild boar social groups, potentially increasing contact rates between groups. These findings indicate that detecting or creating these refuge areas could be used to improve the efficiency of population control and to mitigate the conflicts caused by this species. The results also support the creation of different types of areas around outbreaks of diseases such as ASF, where culling is either banned or encouraged according to the need to reduce disease transmission and minimise wild boar movements between areas.

CRediT authorship contribution statement

Joana Colomer: Data curation, Formal analysis, Writing – original draft. **Carne Rosell:** Conceptualization, Methodology, Resources, Writing – review & editing. **José Domingo Rodríguez-Teijeiro:** Supervision, Methodology, Writing – review & editing. **Giovanna Massei:** Supervision, Conceptualization, Writing – review & editing.

Declaration of competing interest

No conflict of interest exists.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.148721>.

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