

# How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.?

Oliver Keuling · Norman Stier · Mechthild Roth

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**Abstract** Increasing wild boar (*Sus scrofa* L.) population densities all over Europe cause severe economic problems. In popular belief, the wild boar is a more or less diurnal species, causing only minor problems when undisturbed, but is assumed to become nocturnal and wide-ranging when opposed to hunting pressure. In our study, we investigated the impact of hunting and several environmental factors on movements, spatial utilisation and activity patterns by radiotelemetry. Activity pattern revealed a mean proportion of diurnal activity of 12% of all localisations with a monthly change. The wild boar showed increased diurnal activity on undisturbed feeding habitats, especially in early summer. Different hunting methods did influence activity and spatial utilisation in terms of activity and smaller home ranges in areas with only single hunt, although this might be biased by seasonal effects. Flight distances increased significantly after single hunt and capture incidents, but still ranged inside the annual home ranges. Battues did not influence the spatial utilisation before and after hunt significantly. In only 14% of the observed cases did wild boar show small scaled escape movements after battues. The overlaps of home ranges did not change after battues.

**Keywords** Hunting impact · Influencing factors · Battue · Activity pattern · Hunting management

## Introduction

Rapidly increasing wild boar *Sus scrofa* L. densities are regarded to be responsible for severe economical problems in many parts of Europe, as they can cause enormous damages notably in crop fields and forest ecosystems (Bratton 1975; Singer et al. 1984; Labudzki and Wlazelko 1991; Groot Bruinderink and Hazebroek 1996; Killian et al. 2006) and are suspected of transmitting disease to domestic livestock (Killian et al. 2006; Gortázar et al. 2007). Consequently, farmers and animal health authorities claim for a stringent reduction of wild boar populations (Bieber and Ruf 2005; Killian et al. 2006; Sodeikat and Pohlmeier 2007). To develop an effective and biologically based wild boar management, detailed information about population structure, reproduction and spatial usage is required. This need for knowledge is in particular true for family groups dominated by females who are the main subject of regulatory management measures.

Activity patterns of wild boar were described by many authors (e.g. Briedermann 1971; Gerard and Campan 1988; Cousse et al. 1995; Russo et al. 1997). The activity rhythm is biphasic or polyphasic with a high intraspecific variability; the main part of activity is used for foraging (Briedermann 1990; Cuartas and Braza 1990; Cousse et al. 1995; Cahill et al. 2003); the start of activity is closely correlated to sunset (Gerard and Campan 1988; Cousse et al. 1995; Lemel et al. 2003). Although some authors observed higher nocturnal than diurnal activities in wild boar (Briedermann 1971; McLroy 1989; Boitani et al. 1992, 1994; Lemel et al. 2003), in popular belief, wild boar are more or less diurnal with small scaled movements when undisturbed (Meynhardt 1989, 1990; Hennig 1998), as this is assumed to be the natural behaviour (Briedermann 1971, 1990). On the other hand, they are supposed to become nocturnal and wide-

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O. Keuling (✉) · N. Stier · M. Roth  
Institute of Forest Botany and Forest Zoology,  
Chair of Forest Zoology, Dresden University of Technology,  
Pienner Str. 7,  
01737 Tharandt, Germany  
e-mail: oliver.keuling@googlegmail.com

ranging under hunting pressure (Briedermann 1971; Beuerle 1975; Hennig 1998).

As wild boar should behave more natural when less disturbed, diurnal activity should increase when wild boar are exposed only to minor, short-term hunting pressure (e.g. only few battues per year, no single hunt). Permanent hunting pressure (single hunt, repeated battues) was assumed as the main factor for larger home ranges in winter/hunting season (Maillard and Fournier 1995; Baubet et al. 1998; Calenge et al. 2002). Contrariwise, in some cases, wild boar reacted on hunting with smaller (and sometimes after battues shifted) home ranges in secure places (Baubet et al. 1998; Calenge et al. 2002; Sodeikat and Pohlmeier 2002). Battues seem to be less and only short time disturbing than single hunt, but they may cause escape movements or higher overlap of home ranges (Maillard and Fournier 1995; Sodeikat and Pohlmeier 2007). Higher dispersal may enhance crop damages and provide contact for spreading disease, however, it is still unknown which hunting method has least influence on wild boar movements.

In this study, we investigated the impact of different hunting methods on activity and spatial patterns as well as the influence of seasonal activity cycles and environmental factors on diurnal activity of wild boar. As solitary male wild boar cause less damage in agriculture and are not the reproducing animals of interest for population management, our study focused on female groups as basics for further investigations.

## Study area

The study area was located 60 km east of Hamburg in the federal state of Mecklenburg-Western Pomerania (north-eastern Germany, 53.28° N, 10.55° E). The landscape was formed by the Vistula glaciation and rises from 20 up to 100 m above sea level. The study area of 20,000 ha was divided into a relatively flat outwash plain (one third), which enables an easy and precise work on radiotelemetry, and surrounding moraines. Agriculture and forestry combined with low human settlement (20 inhabitants/km<sup>2</sup>) were the main features of the area: the study area consisted of 40% agricultural land, 34% forest stand, 23% meadows and pastures with 3% housing estates. The agricultural land was characterised by large fields of a mean size of 20 ha (up to 150 ha maximum). The core area, surrounded by a mosaic of fields, grassland and small forests, comprised 2,400 ha unfragmented forest, which consisted of 71% coniferous tree species, important for shelter (57% pine *Pinus sylvestris*, 7% spruce *Picea* spec. and 7% other). The most important deciduous trees were oak (*Quercus robur*, *Q. petraea*, *Q. rubra*, 6%), beech (*Fagus sylvatica*, 6%), alder

(*Alnus glutinosa*, *A. viridis*, 7%) and birch (*Betula pendula*, 7%). During the observation period, there was abundant mast of acorns (2002, 2003 and 2005) and beechnuts (2004). Based on the Atlantic climate, the average annual rainfall amounted to 680 mm and the mean annual temperature was 8.2°C. The density of the wild boar population is unknown. However, the mean annual harvest of wild boar in the whole study area increased continuously from 2.83 individuals per 100 ha in 1999/2000 to 5.13 individuals per 100 ha in 2005/2006. Thus, we assume even higher densities within the forested core area.

As the intensity of hunting (e.g. hunters per 100 ha, attempts per shot wild boar) is rarely stated in other studies, it is difficult to assess the level of hunting pressure. Some authors describe about ten hunters, five beaters and one to five dogs per 100 ha as optimal for conducting drive hunts on ungulate species (Eisenbarth and Ophoven 2002; Happ 2002; Wölfel 2003), which is similar to our study area where battues were conducted with 8.3 hunters, 5.3 beaters and 2.7 dogs per 100 ha driven forest area. Battues were normally conducted once a year on the same area. Where population densities were assumed to be still high, another small battue was arranged. Within battues, 68 man-hours were operated per 100 ha, five wild boar were shot per 100 ha. Thus, 14 man-hours were needed to shoot one wild boar (for comparison, see Elliger et al. 2001, 41 h per wild boar). On these battues also other ungulates, mainly fallow deer *Dama dama* (in higher amounts at the same hunt), were shot. To shoot one sow on single hunt, about six attempts were needed (for comparison, see Liebl et al. 2005, ten attempts for one shot wild boar). Thus, about 24 single hunt attempts on wild boar were conducted per 100 ha and year. These were 72 man-hours per 100 ha (plus another 50 h per 100 ha for shooting other ungulates), which were about 18 man-hours per shot animal (for comparison, see Elliger et al. 2001, 36 h per wild boar). Areas where only single hunt was conducted took 74.5% (66% fields, 8.5% forest) of the analysed areas. On 17% of the study area single hunt and battues were both conducted in forest, on 8.5% of area wild boar were hunted only at battues. Sixty percent of the animals were shot on single hunt from hides at baiting stations, 28% were shot at the edge of fields (hides, stalking) or during harvest (hunters surrounding harvested field), 7% were shot at battues, and in 5%, the hunting method was unknown to us.

## Materials and methods

### Radiotelemetry

The data presented in this paper were recorded from 18th Nov. 2002 to 25th Nov. 2006. We captured wild boar in big cage

traps of 5×2×2 m and fitted them with ear tag transmitters (Andreas Wagener Telemetricanlagen, Cologne, Germany) with a weight of about 50 g. The transmitters had a beep ratio of 20 beeps per minute with a maximum lifespan of 3 years (mean lifespan 363 days), reaching up to 3 km. From 152 captured wild boar 68 females of 29 different groups were fitted with ear tag radiotransmitters. Eleven of these groups appeared as yearling groups, 12 as family groups. Another six groups survived from the age of yearling up to family group and thus appear within the data as both. The mean weight of captured piglets during capturing period (September to February) was 32 kg alive ( $N=143$ , sex ratio 1:0.88), that of adult females (November to May) was 75 kg ( $N=8$ ). The age structure of shot animals was 45% piglets (younger 12 months,  $N=47$ , sex ratio 1:0.91), 41% yearlings (13–24 months,  $N=43$ , sex ratio 1:0.65) and 14% adults (older 24 months,  $N=14$ , sex ratio 1:2.75). The group structure of the observed population is described in Table 1. The peak of parturition was in early April. All observed animals presented in this paper were of good health and body condition at capture, sightings and when shot.

We localised the wild boar once at daytime about four times a week and one to five times at night at least twice a week. Thus, we achieved a mean of 381 localisations per year and animal. To avoid disturbances, we performed the localisations with car-mounted four-element YAGI antennas (self-made) using TRX-1000S receivers (Wildlife Materials Inc., USA). As recommended by Garrott et al. (1986), we used multiple triangulations with at least three bearings per localisation to eliminate reflected signal errors. Moreover, only acceptable bearings, producing error polygons less than 4 ha, were used to minimise the telemetry error (Zimmerman and Powell 1995), and the centre of the polygon was taken as positioning of a particular wild boar. We mapped all localisations and recorded additional information, e.g. activity, date and time as well as bonus notes, like sightings, group size and structure, disturbances, shooting of a marked group member and the presence of other groups nearby. The telemetry error was at median 60 m between assumed and real transmitter location (Keuling et al. 2008).

We transcribed the wild boar positionings with a Calcomp® SummaSketchIII digitising tableau to Esri® ArcView 3.2 using the Movement 2.0 extension (Hooge and Eichenlaub 2001). Telemetry data were analysed with Ranges 6 v1.2 (Kenward et al. 2003). Home ranges were calculated for every season (see Keuling et al. 2008) to test the impact of different hunting methods on seasonal home range sizes as kernel home ranges 95% core weighted default settings (KHR95), describing the home range (Burt 1943). We assumed an absolute minimum time interval of 2 h between localisations as sufficiently independent to calculate kernel home ranges (see de Solla et al. 1999;

Keuling et al. 2008). To investigate the direct impact of battues on periodical home ranges 2 weeks before and after battues, respectively, these were estimated as (a) kernel home ranges (KHR95) and as (b) minimum convex polygons (MCP), which describes the maximum used space (100% of localisations). We calculated the spatial shift of home ranges by the distance between centres of temporary kernel home ranges 2 weeks before and 2 weeks after the battues. Diurnal activity was defined as activity (alternating strength of signals) during daytime, i.e. between sunrise and sunset.

## Statistics

As wild boar behaved similarly in space utilisation within groups and in different age classes (Keuling et al. 2008), we used the data of only one animal per group as representative for its group and pooled the data of different groups and age classes for the analyses.

We used a binary logistic regression to test the impact of six main categories of factors potentially influencing diurnal activity. For every factor every localisation has been assigned to an area of specified characteristics of each factor. These factors were: (1) month: 1–12 (Jan–Dec); (2) forest–open land; (3) habitat category: dense coniferous forest, open coniferous forest, dense deciduous forest, open deciduous forest, grassland, bearded cereals (barley, rye, triticale), beardless cereals (wheat, oat), reed, rapeseed, maize; (4) structure: open (mown grassland and fields), dense low (rapeseed, maize, reed), dense high (forest with dense understorey, thickets), open low (high grassland, cereals), open high (older forest without understorey); (5) human disturbance (distance to human structures: roads and settlement): (a) <50 m against >50 m, (b) <150 m against larger distances; (6) hunting method: (a) only one to two battues per year, (b) single hunt plus battues, (c) only single hunt all over the year in forest, (d) only single hunt in agricultural fields.

With Kruskal–Wallis  $H$  test, we tested the influence of different hunting methods (defined as under regressions,

**Table 1** Observed group structure

| Type  | Percentage | $N$ |
|---|------------|-----|
| Single sow  | 7.7        | 3   |
| Yearling groups                                       | 30.8       | 12  |
| One sow with piglets (some temporary with yearlings)  | 17.9       | 7   |
| Two sows with piglets (some temporary with yearlings) | 25.6       | 10  |
| Three or more sows with piglets and yearlings         | 12.8       | 5   |
| Piglets without sow                                   | 5.1        | 2   |

factor 6) on seasonal home range size, as post hoc test, we used Nemenyi test. The respective hunting method was assigned to every home range depending on the situation of the home range centre (KHR).

To detect the dimension of “flight distances” of family groups after disturbance (hunting/capture), the difference in distances between daytime resting on the day before and after hunting incident (distance of surviving group members when one marked member of the group was shot during the night by single hunt) and hunting site as well as captures were tested with the Wilcoxon rank-sum test. We compared these groups with the Mann–Whitney  $U$  test.

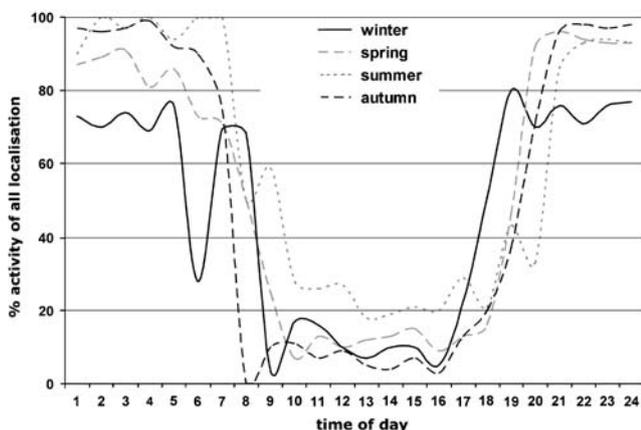
Differences in home range estimates 2 weeks before and after battues were compared with the Wilcoxon rank-sum test. For differences in home range measurements between hunted (battues) wild boar groups and unhunted control groups, we used the Mann–Whitney  $U$  test. We examined the differences in overlapping home ranges of neighbouring groups before and after battue (and control) with the Wilcoxon rank-sum test as well as the differences between hunted and control sample with the Mann–Whitney  $U$  test, and when not any, one or both groups, respectively, have been hunted with the Kruskal–Wallis  $H$  test.

We accomplished the Nemenyi test with Excel and further analyses in SPSS 12.0. Unless otherwise noted, all values are presented as mean $\pm$ SE. All tests were two-tailed with level of significance of  $p\leq 0.05$ .

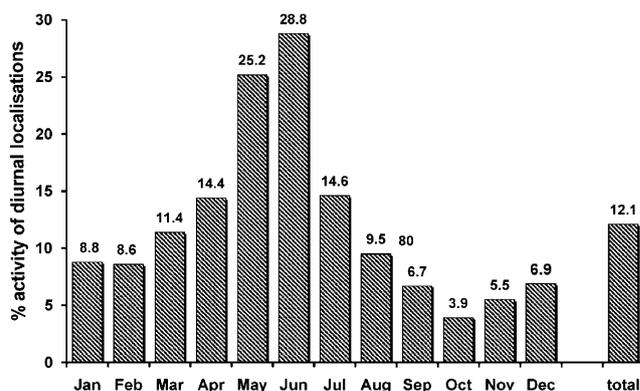
## Results

### Diurnal and nocturnal activity patterns

In winter, female wild boar (Fig. 1) showed relatively low nocturnal activity (70% of all nocturnal localisations). Corresponding to the short daytime, the resting period



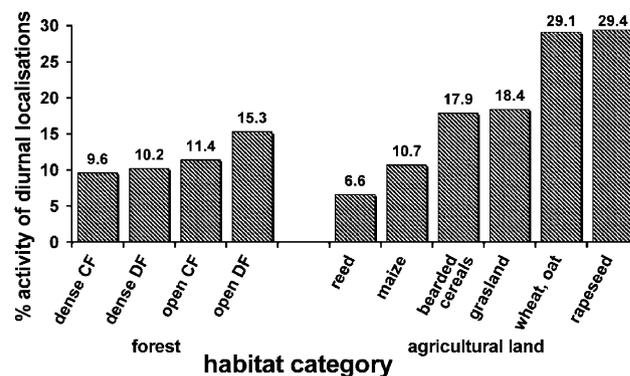
**Fig. 1** Seasonal activity patterns of female wild boar expressed as percentage of telemetry locations (100%=all localisations during hourly time of day, total localisations  $N=10,388$ )



**Fig. 2** Seasonal change of diurnal activity throughout the year based on radiotelemetry locations [bar shows percentage of locations with activity of all diurnal (sunrise to sunset) locations]

was also short with a low rate of diurnal activity (about 10% of all diurnal localisations). In spring, the nocturnal activity rose and the resting period increased in length as well depending on longer daytime periods, maintaining the same proportion of diurnal activity. In summer, the nighttime activity achieved nearly 100%, but during the long daytime, the activity was also relatively high (about 25%, Fig. 1). The activity pattern of autumn was similar to that of spring.

The regression analyses showed a seasonal impact on diurnal activity of wild boar groups (diurnal localisations  $N=5,138$ ; Table 2, Fig. 2). In May and June, diurnal activity was significantly higher, in October lower than in the other months, with an annual mean diurnal activity of 12.1%. Habitat type also influenced diurnal activity: Higher activity during daytime was recorded in fields of unbarbed cereals (wheat and oat) as well as in rapeseed compared to other agricultural habitats and forests (Table 2, Fig. 3). The structure of vegetation did not influence diurnal activity (Table 2), but the distance to human structures did (Table 2).



**Fig. 3** Diurnal activity of wild boar in different habitat categories based on radiotelemetry locations [bar shows percentage of locations with activity of all diurnal (sunrise to sunset) locations]. CF coniferous forest, DF deciduous forest

**Table 2** Binary logistic regression of seven factors potentially affecting diurnal activity of wild boar

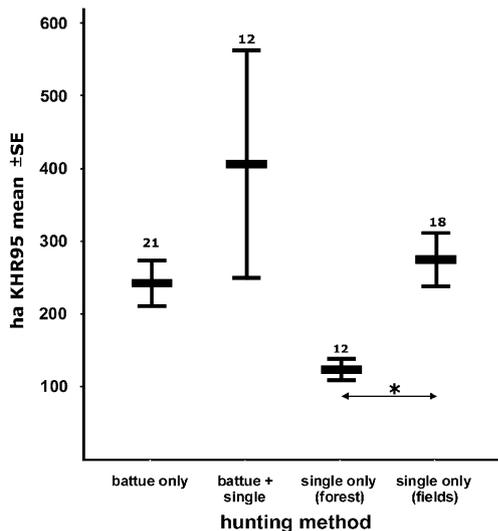
| Factor           | $r_B$  | $\pm SE$ | Wald    | $df$ | $p$          |
|------------------|--------|----------|---------|------|--------------|
| Month            |        |          | 173.305 | 11   | $\leq 0.001$ |
| Hunting method   |        |          | 41.938  | 3    | $\leq 0.001$ |
| Distance, 150    | 0.302  | 0.096    | 9.858   | 1    | 0.002        |
| Habitat category |        |          | 47.100  | 9    | $\leq 0.001$ |
| Constant         | -1.723 | 0.084    | 424.460 | 1    | $\leq 0.001$ |
| Distance, 50     |        |          | 2.168   | 1    | 0.141        |
| Structure        |        |          | 1.851   | 4    | 0.763        |
| Forest/open      |        |          | 0.002   | 1    | 0.964        |

For the model:  $\chi^2=359.761$ ,  $df$  16,  $p\leq 0.001$ ,  $2LL=3,447.954$ , Nagelkerkes  $R^2=0.129$ . For description of factors, see text.

Thus, wild boar showed higher diurnal activity at locations farther than 150 m from roads, tracks and buildings. The hunting method also seemed to affect diurnal activity (Table 2): In areas with only one to two battues per year, wild boar were active in 10.6% of all diurnal localizations. In areas with battues and single hunt, they were active in 8.0%. In forest areas with only single hunt, 18.1% of localisations showed activity, and within fields, where also only single hunt was undertaken, wild boar were active in 17.7% of the cases.

Impact of hunting methods on seasonal home ranges

The hunting method modified the size of seasonal home ranges of wild boar groups (KHR95) (Kruskal–Wallis  $H$  test:  $\chi^2=11.654$ ,  $df=3$ ,  $N=63$ ,  $p=0.009$ ; Fig. 4). On



**Fig. 4** Home range sizes (mean ha $\pm$ SE) of wild boar groups located (kernel home range center) on areas managed with different hunting methods;  $N$  shown above error bars, asterisk: Nemenyi:  $p\leq 0.05$

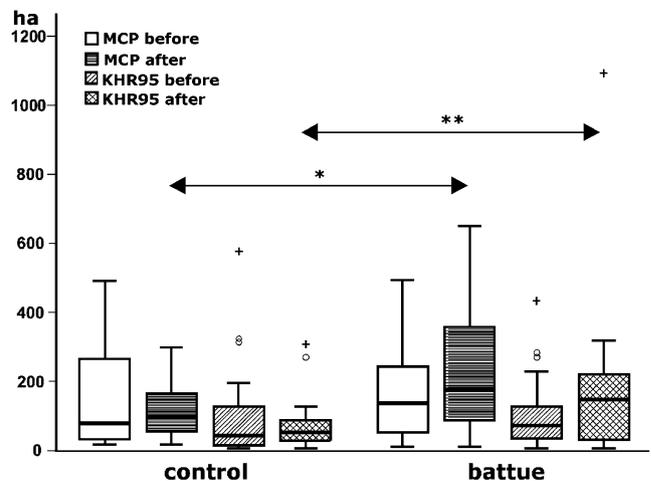
forested areas with only single hunt, mean home range size was significantly smaller than on fields with single hunt (Nemenyi test:  $\chi^2=7.81$ ,  $df=3$ ,  $N=63$ ,  $p\leq 0.05$ ; no significant difference between the other hunting methods).

Impact of single hunt and capture on location of daytime resting sites

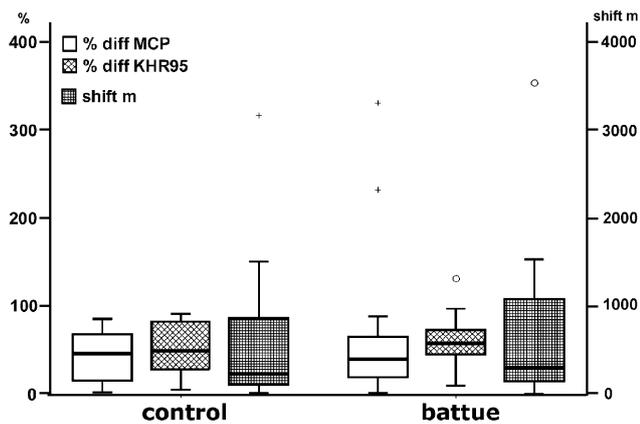
The distance between daytime resting and hunting site (single hunt) of family groups was significantly larger after the hunting incident ( $1,317.6\pm 178.3$  m) than before ( $747.1\pm 153.7$  m; Wilcoxon:  $Z=-2.807$ ,  $N=17$ ,  $p=0.005$ ), similar to distances between daytime resting and catching site before and after recapture (before recapture,  $351.1\pm 61.7$  m; after recapture,  $800.0\pm 124.2$  m; Wilcoxon:  $Z=-2.371$ ,  $N=9$ ,  $p=0.018$ ). For those wild boar which had been captured for the first time, the flight distances were slightly but not significantly larger ( $1,190.3\pm 146.7$  m,  $N=31$ ; Mann–Whitney  $U$  test:  $Z=-1.006$ ,  $N=40$ ,  $p=0.314$ ) than those of recaptured ones. Consequently, there was no significant difference in flight distances between hunted and captured wild boar (Mann–Whitney  $U$  test:  $Z=-1.223$ ,  $N=57$ ,  $p=0.221$ ).

Impact of battues on wild boar spatial usage

We found no difference in home range size 2 weeks before and after battue in wild boar groups, which had been involved in battues (Fig. 5; Wilcoxon,  $N=22$ , MCP:  $Z=-1.282$ ,  $p=0.200$ ; KHR95:  $Z=-1.640$ ,  $p=0.101$ ) or in the unhunted control groups in the same time periods (Fig. 5;



**Fig. 5** Home range sizes (MCP and KHR95) of wild boar groups involved in battues ( $N=22$ ) 2 weeks before and after the battue as well as unhunted control groups ( $N=20$ ) during the same time periods. Box and whisker plots show median (horizontal line within box), 25% and 75% percentiles (box) and range (whiskers); circles indicate statistical outliers (observations between 1.5 and 3 interquartile ranges); plus sign indicates extreme values.  $U$  test:  $*p=0.044$ ,  $**p=0.047$



**Fig. 6** Changes of home range sizes and locations of wild boar groups located 2 weeks before and after battues ( $N=22$ ) as well as unhunted control groups ( $N=20$ ) during the same time periods. Box and whisker plots show median (horizontal line within box), 25% and 75% percentiles (box) and range (whiskers); circles indicate statistical outliers (observations between 1.5 and 3 interquartile ranges); plus sign indicate extreme values. % diff MCP: percentage of mcp home range changes, % diff KHR95: percentage of kernel home range (95%) changes, shift m: shifting of khr centres

Wilcoxon,  $N=20$ , MCP:  $Z=-0.149$ ,  $p=0.881$ ; KHR95:  $Z=-0.485$ ,  $p=0.627$ ). Before battues, home ranges of hunted and unhunted groups were similar in size (Fig. 5; Mann-Whitney  $U$  test,  $N=42$ , MCP:  $Z=-1.259$ ,  $p=0.208$ , KHR95:  $Z=-0.579$ ,  $p=0.562$ ). After hunts, the MCP and KHR95 were different between hunted and unhunted groups (Fig. 5; Mann-Whitney  $U$  test,  $N=42$ , MCP:  $Z=-2.015$ ,  $p=0.044$ , KHR95:  $Z=-1.990$ ,  $p=0.047$ ). However, the relative changes of MCP and KHR95 home ranges (percental difference in home range sizes before and after battues) and the shift of home range centres did not differ between wild boar involved in battues and the unhunted control group (Fig. 6; Mann-Whitney  $U$  test,  $N=42$ , MCP-diff:  $Z=-0.101$ ,  $p=0.920$ , KHR95-diff:  $Z=-0.730$ ,  $p=0.465$ , shift:  $Z=-1.007$ ,  $p=0.314$ ). All these measures did not differ between yearling and family groups (Mann-Whitney  $U$  test,  $N=42$ , MCP difference:  $Z=-0.267$ ,  $p=0.790$ , KHR difference:  $Z=-0.160$ ,  $p=0.873$ , shift:  $Z=-1.574$ ,  $p=0.115$ ). Only in three cases (13.6%) did slight escape movements (max. 2.1 km beyond annual home range) for less than 7 days follow a battue. In one of these cases, the group has been observed in the same area in September of the following year without any previous disturbance.

The overlap of kernel home ranges of neighbouring wild boar groups did not change after battues in which at least one of both groups had been involved (Wilcoxon:  $Z=-0.604$ ,  $N=21$ ,  $p=0.546$ ). The same applied to the control groups (not involved in battue) in the corresponding periods of time (Wilcoxon:  $Z=-0.357$ ,  $N=10$ ,  $p=0.721$ ). Thus, the overlap of KHR95 did not differ between control and hunted pairs (Mann-Whitney  $U$  test,  $N=31$ : before:  $Z=-0.170$ ,  $p=0.865$ ;

after:  $Z=-0.642$ ,  $p=0.521$ ). There were also no differences between pairs of wild boar groups (a) that had not been hunted, (b) when one or (c) when both groups had been involved in a battue (overlap before,  $11.37\pm 3.04\%$ ; after,  $7.01\pm 1.58\%$ ; Kruskal-Wallis  $H$  test:  $N=31$ ,  $df=2$ ; before:  $\chi^2=3.254$ ,  $p=0.196$ ; after:  $\chi^2=0.550$ ,  $p=0.760$ ).

## Discussion

The various hunting methods seem to influence wild boar behaviour in similar and only moderate intensities. This is particularly true for activity and movement patterns. However, we found some significant effects to be discussed in the following.

### Activity

The activity patterns reflected seasonal daytime length and weather conditions as well as energetic requirements of female wild boar. During winter, wild boar do not need to be active persistently in long nights. Especially when frozen soil prevents rooting, it is more efficient to stay at the resting site and use fat deposits than wander around. Reduced activity during cold winter months, also described by Briedermann (1971), saves energy (Gundlach 1968; Massei et al. 1997). Nights are long enough without the need for diurnal activity in winter, spring and autumn. During summer, when piglets are still small, adult females have enhanced energy requirements due to nursing. Thus, they have to forage during the entire short summer nights and also show a higher proportion of diurnal activity. In Italy, females showed polyphasic instead of biphasic activity pattern during farrowing season, with a tendency to increasing diurnal activity in June and July (Russo et al. 1997). Thus, wild boar seem to be most active during periods of short nighttimes (see also Briedermann 1971) with a relatively high proportion of diurnal activity. The large rapeseed and wheat fields, which many wild boar used during summer (Keuling et al. 2008), offered the possibility for undisturbed diurnal activity providing shelter and food (see also Meriggi and Sacchi 1992a, b). Juveniles from 3 to 8 months were mainly diurnal, while adults were nocturnal (Cousse et al. 1995). This might be another reason for higher diurnal activity of female wild boar with piglets during summer. Thus, the results reflect an interaction between habitat types and season, as availability of food, shelter and other resources change seasonally within different habitats.

The higher diurnal activity in fields and forest with only single hunt may be either a reaction on the hunting method or on seasonal influences, which must not be mutually exclusive. Although a tendency towards higher daytime

activity might be caused by nocturnal hunting, we assume other effects like seasonal influences to be more likely. The influence of the hunting method on activity pattern is hardly to assess compared to all other impacts and influencing biases. However, a perturbation by man does exist, as wild boar are more active when farther from human structures and as they prefer cereal fields far from human structures (Meriggi and Sacchi 1992b). This conclusion does not allow any reverse, less permanent hunting pressure which does not cause inevitably higher proportions of diurnal activity, and hence, other factors may be mainly decisive.

Meynhardt (1989) observed a certain diurnal activity in undisturbed areas. In our study area, some diurnal activity was always obvious, although to a lower degree than in other studies (see McIlroy 1989; Boitani et al. 1992, 1994). Other authors observed mainly nocturnal activity and less diurnal activity in areas with low or without hunting pressure (Caley 1997; Russo et al. 1997). Activity cycles seem to depend mainly on age and sex (McIlroy 1989; Cuartas and Braza 1990; Cousse et al. 1994, 1995; Janeau et al. 1995), weather conditions (Caley 1997; Lemel et al. 2003) or food and water resources (Caley 1997; Massei et al. 1997). Cousse et al. (1994) described slightly different spatial patterns of post-weaning piglets and their mothers. Piglets are closely associated with their mother and siblings, their initial movements being very small scaled and bound to the site of birth. The increasing degree of independence of post-weaning piglets leads to temporary separation from their mother while exploring the expanded home range (Cousse et al. 1994; Janeau et al. 1995). Those solo attempts occur mainly during diurnal resting phases, as we could record by video observation (Saebel et al., unpublished data). In the study of McIlroy (1989) in New Zealand, immature feral pigs were more active than adults, and males were more active than females. Feral pigs showed more nocturnal (49%) than diurnal (33%) activity (McIlroy 1989). In addition, Boitani et al. (1992) observed in captivity reared wild boar a significantly higher nocturnal (70%) than diurnal (40%) activity. These proportions of daily activity did not change within 8 weeks after release and were similar to those of free ranging wild boar (Boitani et al. 1994). Briedermann (1971) described diurnal activity for wild boar in captivity and assumed hunting pressure to increase nocturnal activity in free ranging wild boar.

#### Impact of hunting and other disturbances on wild boar movements

Hunting is often proposed as a main cause for size changes and shifting of home ranges in winter, e.g. the hunting season (Boitani et al. 1994; Maillard and Fournier 1995; Baubet et al. 1998; Calenge et al. 2002; Sodeikat and

Pohlmeyer 2002, 2007), although size of core areas remained stable. Maillard and Fournier (1995) estimated seasonal home ranges varying stronger under hunting pressure, but their sample size was small. However, all these authors do not presume any impact of hunting pressure on dispersion of wild boar. Wild boar enlarging their home range during hunting season are more likely to get shot (Baubet et al. 1998). Although hunting seems to have an influence on home range size, there might be other internal and extrinsic factors triggering the seasonality of spatial utilisation patterns such as weather, availability of food and water resources, vegetation cover, sibling of piglets, population density (Boitani et al. 1994; Massei et al. 1997) and intraspecific variability (Lott 1989). Especially when resources are sparse, activity is higher and home ranges are larger (Massei et al. 1997). Therefore, it would be very difficult to prove hunting as the only factor of changing seasonal home range sizes.

In areas with combined hunting methods, home ranges tended to be slightly larger and showed more variation than in other areas, whereas in forested areas with only single hunt, home ranges were significantly smaller. As home range size did not differ significantly between seasons in our study area (Keuling et al. 2008), varying home range sizes may be influenced by different hunting methods (besides many other factors) as assumed in other studies (Boitani et al. 1994; Maillard and Fournier 1995; Dexter 1996; Baubet et al. 1998; Calenge et al. 2002; Sodeikat and Pohlmeyer 2002). Some authors assumed hunting as the main factor for larger home ranges in winter/hunting season, with animals trying to avoid hunters and searching for secure areas (Maillard and Fournier 1995; Baubet et al. 1998; Calenge et al. 2002), despite observing many animals not changing their home ranges or including dispersing subadults to analyses (e.g. Calenge et al. 2002). To the contrary, in some cases, wild boar reacted on hunting with smaller (sometimes shifted) home ranges in secure places (Baubet et al. 1998; Calenge et al. 2002; Sodeikat and Pohlmeyer 2002). There seem to be two main anti-predator strategies: (a) mainly staying in well-known home range, perhaps reducing space into more secure places and (b) enlarging or shifting home range to avoid predators or hunters respectively (see also Baubet et al. 1998; Sodeikat and Pohlmeyer 2007). We assume other influences like seasonal resources, habitat availability within individual home ranges and intraspecific variability as more important than the hunting method.

Although distances increased after disturbance (single hunt, capture) between disturbed and resting site, all movements remained within the seasonal home range measurements (Keuling et al. 2008). Singer et al. (1981) observed even smaller daily movements after human disturbance. Thus, single hunt and capture for scientific

purposes (see also Sodeikat and Pohlmeier 2004) apparently do not increase wild boar movements.

According to literature data, battues with high beating pressure and many dogs partly caused temporary shift or increase of home ranges (Maillard and Fournier 1995; Sodeikat and Pohlmeier 2002, 2003, 2007). However, in France, home range shifts occurred only after repeated disturbances (Maillard and Fournier 1995). In Germany, wild boar returned after 4 to 6 weeks to their previous area; in some cases, home range size even decreased (Sodeikat and Pohlmeier 2002). Shooting feral pigs from helicopters in Australia as a pest control induced non-significant smaller home ranges after hunting (Dexter 1996). Dexter (1996) assumed that direct contact to humans and dogs by ground battues may displace wild boar, but not shooting from helicopters.

In our study, we could not document a significant impact of hunting on wild boar home range size or location. Being well adapted to human disturbances and hunting (see also Meynhardt 1990), only minor reactions to single hunt and battues could be observed under good nutritional conditions. Most variation in activity or spatial usage patterns seemed to be rather induced by seasonal changes (Boitani et al. 1994; Maillard and Fournier 1995; Massei et al. 1997; Keuling et al. 2008). Therefore, we assume the influence of hunting on increasing animal movements as negligible if hunting pressure is moderate (e.g. only few effective battues per year instead of repeated “monterias”). Hence, hunting may be conducted as management tool for regulating or even reducing population densities and thus may reduce the risk of spreading epidemics.

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All experiments comply with the current laws of Mecklenburg-Western Pomerania.

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# Wild boar (*Sus scrofa*) harvesting using the *espera* hunting method: side effects and management implications

Carlos Braga · Nuno Alexandre ·  
Pedro Fernández-Llario · Pedro Santos

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**Abstract** Harvesting of wildlife by man has been linked to demographic and evolutionary impacts in many populations. We investigated the sex ratio and age class structure in hunting bags of wild boar harvested by *espera*—nocturnal single hunt at bait—during four hunting seasons in Alentejo (Portugal). In addition, we assessed whether the hunting method is a significant predictor of the probability

of harvesting an animal of a particular gender, of particular age class or of a particular combination of these two attributes. We found that the *espera* hunting method allows very selective harvesting regimes, and thus, it seems a highly effective population management tool. Removing a large proportion of adult males, however, may bias the population sex ratio towards females, reduce male life expectancy and raise the degree of polygyny. Our results suggest that recruitment rates are resilient to this skewed sex ratio, and possibly the higher proportion of females in the adult population may even increase productivity.

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C. Braga  
Comissão de Coordenação e Desenvolvimento Regional do Alentejo,  
Av. Engenheiro Arantes e Oliveira, 193,  
7004-514 Évora, Portugal  
e-mail: ca.braga@netcabo.pt

N. Alexandre  
Departamento de Paisagem, Ambiente e Ordenamento,  
Colégio Luís António Verney,  
R. Romão Ramalho 59, Universidade de Évora,  
7000-671 Évora, Portugal  
e-mail: nbalexandre@gmail.com

P. Fernández-Llario  
Departamento de Biología y Geología,  
Instituto de Enseñanza Secundaria “Santa Lucía del Trampal”,  
10160 Alcuéscar, Cáceres, Spain  
e-mail: pfernandezllario@gmail.com

P. Santos  
Departamento de Paisagem, Ambiente e Ordenamento,  
Colégio Luís António Verney,  
R. Romão Ramalho 59, Universidade de Évora,  
7000-671 Évora, Portugal

P. Santos (✉)  
ICAAM—Instituto de Ciências Agrárias e Ambientais  
Mediterrânicas, Universidade de Évora—Núcleo da Mitra,  
Apartado 94,  
7002-554 Évora, Portugal  
e-mail: aps@uevora.pt

**Keywords** Selective harvesting · Population structure · Conservation · Alentejo (Portugal)

## Introduction

Modern sport hunting is often selective of sex or age, or of morphological characteristics, either for hunting regulation purposes or because of a hunter's preferences (Festa-Bianchet 2007). The common preference of hunters to shoot males with large horns, antlers or teeth ('trophy' males) is likely to lead to artificial selection in natural populations, also producing a bias in the sex ratio in favour of females and reducing the survival of elderly animals (Milner-Gulland et al. 2003; Torres-Porras et al. 2009).

In the Iberian Peninsula, population sex ratio and age composition were determined mainly through *montaria* game bag analysis. *Montaria* is a hunting method in which dog teams chase wild boar towards hunters waiting at fixed points; there is no limit to the number each hunter may shoot and they are allowed to shoot piglets, yearlings and adults of both sexes (Fernández-Llario et al. 2003), as in similar drive hunts conducted elsewhere in Europe

(Maillard and Fournier 1995; Monaco et al. 2003; Keuling et al. 2008a; Scillitani et al. 2009). *Montaria* hunting bag analysis has been considered a correct method to estimate sex ratio and age class distribution in wild boar populations (Fernández-Llario and Mateus-Quesada 1998; Massolo and Mazzoni della Stella 2006). In Alentejo County (Portugal), *montaria* hunting bag analysis showed that the majority of the harvested animals were aged <1 year and sex ratio favourable towards females (Santos 2002).

*Espera* hunting method involves the use of bait to attract wild boar to the shooting range of elevated hunting stands, and it is supposed to promote the selective targeting of specific animals according to a given management criterion. However, there is a need for studies in order to assess if targeting criteria have been taken into consideration or if, on the contrary, the hunting bag departs from selective criteria.

In this study, we analyse sex ratio and age class structure in wild boar *espera* hunting bags during four hunting seasons. Furthermore, we assess whether the hunting method (*montaria* versus *espera*) is a significant predictor of the probability of harvesting an animal of specific gender and age.

## Materials and methods

### Data collection

Data were collected in Alentejo (38°22'–38°35' N, 7°35'–7°43' W), a Portuguese county belonging to the Mediterranean Ibero-Atlantic Province which comprises an area of 26,766 km<sup>2</sup> (see Fernández-Llario et al. 2003).

We gathered data all year round during four hunting seasons—2005/2006, 2006/2007, 2007/2008 and 2008/2009—on a 920-ha private hunting estate (not fenced) where *montaria* is only occasionally practised and *espera* is the main hunting method, representing more than 80% of the total hunting bag. Wild boar is the only big game species present in the area. The harvested wild boars were aged in the field according to coat colour patterns and to chronology of teeth eruption (Fonseca et al. 2004; Santos et al. 2006); three age classes were considered: piglets—under 12 months old; yearlings—between 12 and 24 months old; adults—older than 24 months.

Hunting by *espera* took place mainly from February to October, avoiding the hunting season of small game species, and promoted the targeting of trophy animals. In each hunting season, about 20 tonnes of wheat grain and 3 tonnes of almond nuts were used to attract wild boar to the shooting range of 15 elevated hunting stands, approximately two times more than the amount of bait provided in central Europe (Keuling et al. 2008b). Besides baiting, no

supplementary food was supplied in order to improve carrying capacity. Baiting was done every day from the first quarter moon until full moon and on alternate days during the rest of the lunar cycle. Every month, about six of the stands were used by hunters over three nights, from sunset until approximately 4 h later. The hunting nights were distributed over a period of 10 days, starting on the eighth day before full moon and ending on the first day after the full moon. For each hunting night, the total number of wild boar observed by the hunters was recorded.

### Data analysis

Data were analysed using the SPSS software (SPSS software version 16, SPSS, Chicago, IL, USA). We performed one-way between-groups ANOVAs, with post hoc tests, to find out whether the mean number of harvested wild boar per hunting night and the mean number of wild boar observed per hunting night differed among the four studied hunting seasons. To analyse the sex ratio in *espera* hunting bags, we made a binomial test determining whether the proportion of males was different from 0.5. Finally, to see if the sex ratio and age class proportion were related to the hunting season, we used the chi-square test and the Fisher's exact test (for independence of two categorical variables).

To assess whether the hunting method (*montaria* versus *espera*) is a significant predictor of the probability of harvesting a male, of harvesting an animal older than 1 year, of harvesting a male older than 1 year and of harvesting a male older than 2 years, we also used *montaria* unpublished data presented elsewhere (Santos 2002). These data concern 248 wild boars harvested during two hunting seasons in 20 different private estates ecologically similar to our study area. We used the SPSS software procedure called binary logistic to perform logistic regressions by the forward:LR method with the aforementioned dependent variables, separately. To evaluate the relative amount by which the odds of the outcome increase or decrease when the value of the predictor variable increases by 1 unit, i.e. the hunting method changes from *montaria* to *espera*, we used the odds ratio (exponential of the logistic coefficient *B*).

## Results

During the four hunting seasons, 192 wild boars were harvested on 127 hunting nights (Table 1). Since about six stands were used on each hunting night, a total of approximately 762 *esperas* took place and near 0.25 wild boars were shoot per *espera*. The mean number of harvested wild boar per hunting night, as well as the mean number of observed wild boar per hunting night, varied

**Table 1** Wild boar *espera* game bags during four hunting seasons in Alentejo (Portugal)

|   | Hunting seasons |              |                |                | Total          |
|---|-----------------|--------------|----------------|----------------|----------------|
|   | 2005/2006       | 2006/2007    | 2007/2008      | 2008/2009      |                |
| Number of hunting nights  | 35              | 31           | 24             | 37             | 127            |
| Mean number of harvested wild boar per hunting night (standard variation) | 2.00 (1.372)    | 0.81 (0.946) | 1.46 (1.103)   | 1.73 (1.170)   | 1.53 (1.240)   |
| Mean number of observed wild boar per hunting night (standard variation)  | 14.63 (11.847)  | 6.90 (7.884) | 17.67 (14.547) | 17.24 (13.162) | 14.08 (12.607) |
| Number of wild boar harvested per 100 ha                                  | 7.60            | 2.83         | 3.70           | 6.74           | 20.87          |
| Gender of harvested wild boar   |                 |              |                |                |                |
| Male  | 40              | 19           | 19             | 34             | 112            |
| Female  | 30              | 7            | 15             | 28             | 80             |
| Total   | 70              | 26           | 34             | 62             | 192            |
| Age of harvested wild boar  |                 |              |                |                |                |
| Piglets   |                 | 4            |                | 0              | 4              |
| Yearlings   |                 | 5            |                | 14             | 19             |
| Adults  |                 | 13           |                | 46             | 59             |
| Total   |                 | 22           |                | 60             | 82             |

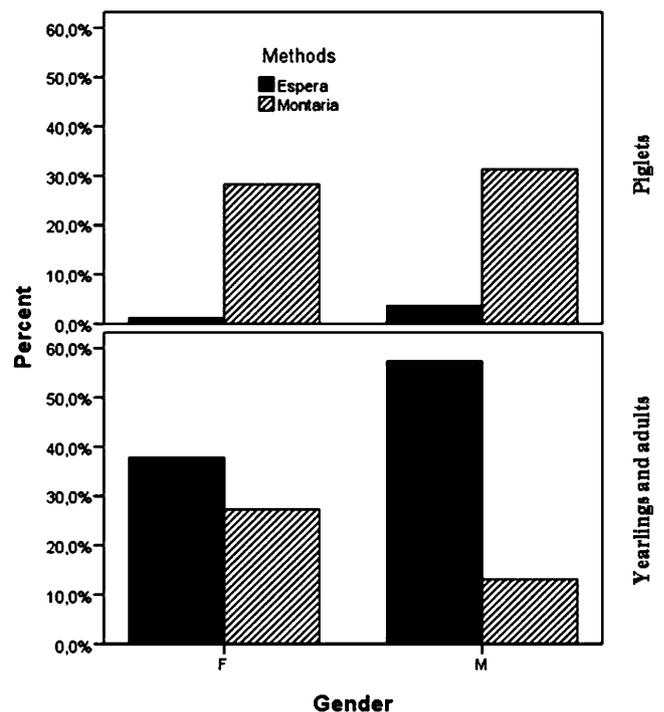
significantly among the hunting seasons (ANOVA:  $F=6.234$ ,  $p=0.001$ ; ANOVA:  $F=5.283$ ,  $p=0.002$ ), reflecting hunting quota adaptation to population fluctuations.

In the hunting seasons of 2005/2006 and 2007/2008, lack of logistical support did not allow to correctly identify the age class of a significant number of harvested wild boar; thus, for age structure analysis, only the hunting seasons of 2006/2007 and 2008/2009 were taken into consideration. The harvested population is male-biased (binomial test,  $p<0.001$ ) and largely composed of yearlings and adults (Table 1). The mean number of harvested and observed wild boar per night, as well as the proportion of animals older than 1 year (Fisher's exact test,  $p=0.004$ ), increased from 2006/2007 to 2008/2009, without significant differences in sex ratio between these two hunting seasons (Pearson  $\chi^2=2.762$ ,  $p=0.430$ ).

There were highly significant differences between *espera* (data from this study) and *montaria* (unpublished data collected by Santos 2002 in the same region) concerning sex ratio (Pearson  $\chi^2=7.596$ ,  $p=0.006$ ) and age class distribution (Pearson  $\chi^2=82.386$ ,  $p<0.001$ ). Furthermore, the graphical comparison of sex ratio and age structure between *espera* and *montaria* shows opposed harvesting selectivity (Fig. 1). In fact, contrary to what happens in *espera* hunting bags, in *montaria* hunting bags, the sex ratio is female-biased and the majority of the harvested animals are <1 year old.

The logistic regressions showed that the hunting method (*montaria* versus *espera*) significantly affects the probability of harvesting a male ( $\chi^2_{\text{Wald}}(1) = 7.427$ ,  $p=0.006$ ), of harvesting an animal older than 1 year ( $\chi^2_{\text{Wald}}(1) = 41.387$ ,  $p<0.001$ ), of harvesting a male older

than 1 year ( $\chi^2_{\text{Wald}}(1) = 68.030$ ,  $p<0.001$ ) and of harvesting a male older than 2 years ( $\chi^2_{\text{Wald}}(1) = 72.413$ ,  $p<0.001$ ). When *espera* instead of *montaria* is the hunting method used, the odds of harvesting a male are 1.957 times higher, the odds of harvesting an animal older than 1 year are 28.743 times higher, the odds of harvesting a male older than 1 year



**Fig. 1** Gender distribution (F female, M male) by age classes in *espera* ( $n=82$ ) and in *montaria* ( $n=428$ ) wild boar hunting bags in Alentejo (Portugal)

are 8.920 times higher, and the odds of harvesting a male older than 2 years are 8.336 times higher.

## Discussion

Our results show that *espera* hunting bags, conversely to *montaria* hunting bags (Fernández-Llario and Mateus-Quesada 1998; Santos 2002), are male-biased and adult-biased and that the odds of harvesting an adult male are much higher. Our *espera* hunting bags also diverge from those obtained outside the Iberian Peninsula using hunting methods similar to *montaria* (Dzieciolowski and Clarke 1989; Ahmad et al. 1995; Boitani et al. 1995; Durio et al. 1995; Moretti 1995; Berger et al. 1998; Massolo and Mazzoni della Stella 2006).

*Espera* selectivity is clearly pointed out by the sharp difference between the mean number of wild boar observed per hunting night and the mean number of wild boar actually harvested per hunting night (Table 1). In addition, yearling and adult males represent almost 60% of the *espera* hunting bag (Fig. 1), a proportion that clearly departs from those observed in both natural and hunted wild boar populations in the Iberian Peninsula (Fernández-Llario 1996; Fernández-Llario and Mateus-Quesada 1998) and elsewhere in Europe (Moretti 1995; Berger et al. 1998; Massolo and Mazzoni della Stella 2006).

The studied hunting estates are not fenced, and thus, a comparison between *espera* and *montaria* harvesting per hectare may be misleading. However, *espera* seems to be a rather effective hunting method considering that only about four attempts were needed to shot a wild boar, considerably less than that in central Europe (Liebl et al. 2005; Keuling et al. 2008a). Despite this high efficacy, *espera* yields conservative results that allow wild boar renewal and its sustained use.

*Espera* hunting bags reveal that harvest criteria are usually observed, presumably because the hunters are able to carefully watch the target and have plenty of time to make the right decision before shooting. Conversely, in *montaria*, the harvest criteria may be difficult to observe, particularly when the targets are running through thick vegetation in hilly ground (Martínez et al. 2005). Allowing higher selectivity than *montaria*, *espera* seems to be more effective in terms of the population structure management, regardless of management goals.

The *espera* hunting method does not mimic the patterns of wild boar natural mortality since the large majority of animals (75–95%) eaten by wolves (*Canis lupus*) are non-adults (Jędrzejewski et al. 1992; Mattioli et al. 1995; Nores et al. 2008). Thus, according to Bischof et al. (2008), if the management goal is to minimise the demographic disturbance induced by artificial harvest, a neutral hunting

method, such as *montaria*, should be recommended. On the other hand, if assuring prey availability to large carnivores, like wolf or Iberian lynx (*Lynx pardinus*), is a management goal, then *espera* seems a rather suitable hunting method.

In light of this study, *espera* is a hunting method that allows highly selective harvesting regimes, and thus, it seems a very effective tool for population structure regulation whatever the management goals may be. *Espera* may be suitable for both cropping large trophy males and removing numerous piglets and yearlings, as well as the best reproductive females, if the goal is agricultural damage prevention as it happens in many parts of Europe (see Schley et al. 2008).

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# Mortality rates of wild boar *Sus scrofa* L. in central Europe

Oliver Keuling · Eric Baubet · Andreas Duscher · Cornelia Ebert ·  
Claude Fischer · Andrea Monaco · Tomasz Podgórski · Céline Prevot ·  
Katrin Ronnenberg · Gunter Sodeikat · Norman Stier · Henrik Thurfjell

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**Abstract** In many parts of Europe, wild boar *Sus scrofa* population increase, and thus, high densities and dispersal into new areas are accompanied by economic problems. Due to many factors like insufficient hunting strategies as well as underestimation of population densities and reproduction rates, harvest rates seem to be insufficient. Thus, we calculated mortality rates of several wild boar populations from 1998 to 2009, to show the efficiency of hunting within several studies distributed over eight European states. For calculating mortality rates, the daily probability of survival of radio

telemetrically observed wild boar was analysed according to Mayfield (Wilson Bull 73:255-261, 1961) and with survival analysis in R for three age classes (0, 1,  $\geq 2$  years) and both sexes. The mortality rates of wild boar per annum, especially piglets, were comparably low (about 0.5 for piglets and similar for total population). About three third of all observed animals survived at least until the next period of reproduction. Mortality rates differed between some study areas, the sexes and age classes. The sex ratio of the shot piglets equals the sex ratio of captured piglets; there seems to be no sex-biased

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O. Keuling (✉) · K. Ronnenberg · G. Sodeikat  
Institute for Terrestrial and Aquatic Wildlife Research,  
University of Veterinary Medicine Hannover,  
Bischofsholer Damm 15,  
30173 Hannover, Germany  
e-mail: oliver.keuling@tiho-hannover.de

E. Baubet  
CNERA Cervidés-Sangliers, Office National de la Chasse  
et de la Faune Sauvage, Avenue de Wagram 85 bis,  
75017 Paris, France

A. Duscher  
Research Institute of Wildlife Ecology,  
University of Veterinary Medicine Vienna, Savoyenstraße 1,  
1160 Vienna, Austria

C. Ebert  
Research Institute for Forest Ecology and Forestry,  
Hauptstraße 16,  
67705 Trippstadt, Germany

C. Fischer  
hepia, Filière Gestion de la Nature, 150 route de Presinge,  
1254 Jussy, Switzerland

A. Monaco  
National Wildlife Institute, Via Cà Formacetta,  
9-40064 Ozzano dell'Emilia, Bologna, Italy

T. Podgórski  
Mammal Research Institute, Polish Academy of Sciences,  
Waszkiewicza 1c,  
17-230 Białowieża, Poland

C. Prevot  
Laboratoire Faune sauvage et Cynégétique,  
Département de l'étude du milieu naturel  
et agricole, Service Public de Wallonie,  
avenue Maréchal Juin 23,  
5030 Gembloux, Belgium

N. Stier  
Institute of Forest Botany and Forest Zoology,  
Dresden University of Technology, Piennner Str. 7,  
01737 Tharandt, Germany

H. Thurfjell  
Department of Wildlife, Fish, and Environmental Studies,  
Swedish University of Agricultural Sciences,  
901 83 Umeå, Sweden

hunting in this age class, but in an older age. Shooting was the main cause of death; only very few animals died by natural causes, e.g. diseases. The comparative analysis of all studies reflects a low mortality of wild boar in highly productive populations. Our results certified the findings of several studies that predation, natural mortality, and road mortality have only small impact on wild boar populations, whereas especially, nutrition or hunting are mainly decisive. Assuming net reproduction rates of more than 200 % according to literature data, our results indicate that harvest rates are not sufficient at our study sites. In all our studies, mortality rates and, thus, harvest rates are less than the assumed total net reproduction. Especially, the harvest rate of piglets seems to be insufficient. Thus, the population will increase further. High reproduction has to be counteracted by regulating mainly the reproductive animals. For regulating a population, combined and effective hunting methods have to be conducted to harvest at least the net reproduction. Thus, we recommend higher hunting rates of piglets (80 % of the offspring should be harvested) and of adult females. Intensified hunting of piglets by drive hunts and at an early age as well as intensified single hunt on adult females might help regulating wild boar populations.

**Keywords** *Sus scrofa* · Mortality rates · Hunting efficiency · Sex ratio · Wildlife management · Human dimension

## Introduction

In many parts of Europe, wild boar *Sus scrofa* L. population increase and dispersal into new areas is accompanied by economic problems, like high risk of epidemics and increasing agricultural damages, especially in agricultural regions (e.g. Labudzki and Wlazelko 1991; Groot Bruinderink and Hazebroek 1996; Gortázar et al. 2007; Schley et al. 2008). Briedermann et al. (1986) already recommended higher hunting pressure by changed hunting methods and efficiencies as well as by convincing hunters of the necessity of reduction. These authors (Briedermann et al. 1986) also suggested increasing harvest rates for regulating populations by shooting higher proportions of female wild boar. However, it seems that nothing happened until today. This might be due to underestimation of reproduction rates (Genov et al. 1994; Gethöffer et al. 2007; Cellina 2008) and thus insufficient harvest rates, as already delineated by Keuling et al. (2010).

For regulating a population, effective hunting methods, combining single hunt and different types of driven hunts within one area, have to be conducted to harvest at least the net reproduction (Briedermann 1990; Happ 2002; Keuling et al. 2008b, 2010). Some authors describe different models to accomplish regulation of wild boar populations by hunting different proportions of age classes (Bieber and Ruf 2005;

Servanty et al. 2005; Sodeikat et al. 2005; Servanty 2008; Keuling et al. 2010). In common opinion, biased sex and age ratios as well as high hunting pressure (Servanty et al. 2009, 2011) cause higher reproduction, although food conditions have been demonstrated as the main cause for higher reproduction (Gethöffer et al. 2007; Cellina 2008).

Radio telemetry allows for calculation of survival or mortality rates (Kenward 2001), without a bias of animals with unknown fate. Thus, we calculated mortality rates of several wild boar populations, to indicate the efficiency of hunting, as hunting may only be efficient, when mortality rates equal reproductive rates.

Are there any differences in mortality rates of wild boar between

- Nations (combined study areas)?
- Age classes?
- Sexes?

If there is a sex bias, is there a sex bias due to hunting within different age classes?

## Methods

The data were collected within 12 years (1998–2009) from studies conducted in 15 different study areas distributed over eight states all over central Europe (Table 1, see also Online Resource 1). For animals which died during observation period, the causes of death were notified.

For calculating mortality rates, the daily probability of survival  $p$  of radio telemetrically observed wild boar was analysed according to Mayfield (1961; Kenward 2001):

$$p = \frac{\text{observed days with active transmitter}}{(\text{observed days with active transmitter} + N \text{ dead individuals})}$$

The survival rate ( $P$ ) per year or any defined period ( $x$ ) is calculated  $P=p^x$ , where  $x$  is the number of days within the defined period. Thus, the mortality rate ( $M$ ) per defined period is  $1-P$ . For each country, mortality rates were calculated separately males and females within the age classes piglets (<12 months), yearlings ( $\geq 12$ –23 months) and adults ( $\geq 24$  months). As the exact date of birth was not known, April 1 was taken as reference date for reaching the next age class. Piglets were normally tagged at an age of more than 5 months; thus, the calculation was done for September 1 to February 28 (=181 days), which is also the period where hunting is allowed in most countries. Thus, the reference period was 365 days for yearlings and adults and 181 days for piglets. However, as natural mortality is quite low in piglets older than 3 months (Martys 1982; Keuling et al. 2010), we assume this mortality rate as relevant for hunted populations and regard this mortality rates as annual mortality rates of piglets.

**Table 1** Study areas: location, size, period, number of observed animals and used telemetry technique

| Name of study area/region                   | Name of author/partner       | Country                | °N      | °E      | Size [ha]                 | Duration                                 | N radio observed animals | VHF  | GPS                         | Citation of previous study/report   |
|---|------------------------------|------------------------|---------|---------|---------------------------|--|--------------------------|--|-----------------------------|---|
| 1 Bogesund                                  | Henrik Thurffell             | Sweden                 | 59°24'N | 18°12'E | 10,000                    | Aug 2005–Jan 2007                        | 1                        |  | 1 Vectronics                |   |
| 2 Östermalma                                | Henrik Thurffell             | Sweden                 | 58°57'N | 17°09'E | 10,000                    | April 2006–Dec 2006                      | 1                        |  | 1 Vectronics                |   |
| 3 Österlen                                  | Henrik Thurffell             | Sweden                 | 55°32'N | 14°03'E | 16,000                    | April 2004–May 2007                      | 20                       |  | 20 Vectronics               | Thurffell et al. (2009)   |
| 4 Białowieża Primeval Forest                | Tomasz Podgórski             | Poland                 | 52°47'N | 23°48'E | 4,000 within total forest | March 2007–Oct 2009                      | 57                       | 15 ATS<br>42 Wagener                                 |                             | Podgórski et al. (2013)   |
| 5 Schildfeld, Mecklenburg-Western Pomerania | Oliver Keuling, Norman Stier | Germany                | 53°28'N | 10°55'E | 20,000                    | Nov 2002–June 2007                       | 79                       | 85 Wagener   |                             | Keuling (2009), Keuling et al. (2008a, b, 2009); Keuling et al. (2010)      |
| 6 Behren, Lüneburger Heide                  | Gunter Sodeikat              | Germany                | 52°48'N | 10°28'E | 10,000                    | Jan 2004–Jan 2006                        | 54                       | 55 Biotrack  |                             |   |
| 7 Betzhorn Leu, Lüneburger Heide            | Gunter Sodeikat              | Germany                | 52°39'N | 10°37'E | 15,000                    | Jan 1998–Dec 2003                        | 74                       | 80 Biotrack  |                             | Sodeikat and Pohlmeier (2007)   |
| 8 Wildforschungsgebiet Pfälzerwald          | Ulf Hohmann                  | Germany                | 49°12'N | 7°45'E  | 10,000                    | March 2006–Jan 2009                      | 19                       | 19 Wagener   | 6 Vectronics (additional)   | Ebert et al. (2009, 2010)   |
| 9 St Hubert, Ardenne centrale               | Céline Prévot                | Belgium                | 50°08'N | 5°27'E  | 11,000                    | March 2006–Aug 2010                      | 56                       | 11 ATS<br>28 Televilt                                | 4 Televilt<br>5 Vectronics  |   |
| 10 Hertogenwald, Hautes Fagnes              | Céline Prévot                | Belgium                | 50°39'N | 6°10'E  | 8,000                     | Nov 2003–Aug 2010                        | 15                       | 3 Televilt   | 8 Televilt<br>10 Vectronics |   |
| 11 Donation Royale, Famenne                 | Céline Prévot                | Belgium                | 50°12'N | 5°11'E  | 8,000                     | June 2005–Aug 2010                       | 16                       |  | 6 Televilt<br>10 Vectronics |   |
| 12 Châteauvillain-Arc-en-Barrois            | Eric Baubet                  | France                 | 48°02'N | 4°55'E  | 11,000                    | March 2003–March 2008                    | 59                       | 59 Televilt  |                             | Baubet et al. (2009)  |
| 13 Basin of Geneva                          | Claude Fischer               | Switzerland and France | 46°13'N | 6°00'E  | 40,000                    | May 2002–May 2007                        | 158                      | Biotrack<br>ATS                                      | Lotek                       | Hebeisen et al. (2008); Tolon et al. (2009)                                 |
| 14 NP Neusiedler See                        | Andreas Duscher              | Austria                | 47°46'N | 16°48'E | 500 within 9,700 NP       | Feb 2006–March 2007                      | 11                       | 3 Biotrack<br>3 Televilt                             | 2 Vectronics                | Reimoser et al. (2009)  |
| 15 Emilia Romagna - Northern Appennines     | Andrea Monaco                | Italy                  | 44°19'N | 11°28'E | 20,000                    | Aug 1998–Nov 2000/<br>June 2003–May 2009 | 41                       | 3 Wagener<br>9 Televilt<br>23 Biotrack<br>2 Sirtrack |                             | Monaco and Carnevali (2004); Fenati et al. (2008); Scillitani et al. (2010) |

We calculated the sex ratios (SR) of captured piglets, and additionally we calculated the proportions of sex and age classes (age determination by dentition) of marked individuals that have been shot to estimate a potential sex bias within hunting bags. This was done only for those study areas where the number of captured animals was high enough (at least five animals per sex and age class) to calculate reasonable ratios for both captured and shot wild boar (Table 3).

According to the aims of the studies and due to better probabilities of capturing females than males, more females were marked. Thus, in some studies, the mortality rates of some age classes and sex are not reliable and might only be considered within the total pooled data. In total, 661 wild boar have been observed by VHF or GPS-telemetry (Table 1). Several animals have been observed longer than 1 year; thus, the total number of observed animals/years was 810.

The differences in mortality rates (according to Mayfield) between countries (data of different study areas of one nation combined), age classes and sexes were tested in a linear regression (lm R 2.15.2, R Core Team 2012). For comparison, we additionally conducted a non-parametric survival analysis with censoring (survivors with unknown fate get less weighting) with the package “survival” (Therneau 2012) in R 2.15.0. The main effects country (data of different study areas of one nation combined), age class and sex were tested; interactions between factors had to be neglected because some levels of factors were missing in several studies.

## Results

Out of 661 studied animals, 233 died during the total observation of 127,030 days (Table 2). The mortality rates of wild boar, especially piglets, were low (Table 2). In the Białowieża Primeval Forest, Poland, a non-hunted area with large predators such as wolves, the mortality rates were lowest of all study areas (Table 2, Figs. 1 and 2); thus, they were not used for calculating total mortality rates. All in all, 67 % of all animals survived the observed period, 73 % survived at least until the next breeding season (Figs. 1 and 2).

With the linear regression (Call: glm(formula =  $M \sim \text{sex} + \text{age} + \text{study area}$ ), intercept  $\Pr(>|Z|) = 0.004$ , deviance residuals: min -0.5431, 1Q -0.111, median 0.010, 3Q 0.082, max 0.703; for further details, see Online Resource 2) of the Mayfield (1961) calculations, we proved a tendency for male-biased sex ratio mortality ( $p = 0.053$ ) and a difference between mortality rates in Białowieża Primeval Forest, Poland, and the study area in Sweden ( $p = 0.011$ ). By survival analysis (non-parametric survival analysis with censoring: coxph(formula =  $\text{Surv}(\text{days\_observed}, \text{dead}) \sim \text{study area} + \text{sex} + \text{age}$ ),  $n = 883$ , number of events = 218 (ten observations deleted due to

missingness); for further details, see Online Resource 3), some more differences between countries were observed, with Belgium ( $p = 0.012$ ), Switzerland ( $p = 0.023$ ), France ( $p = 0.013$ ) and Poland ( $p < 0.001$ ) showing significantly lower mortality rates than Sweden (Figs. 1 and 2). Yearlings ( $p = 0.044$ ) differed and juveniles tended to differ ( $p = 0.079$ ) from adults (Fig. 1) as well as a sex bias towards males was confirmed ( $p = 0.019$ , Fig. 2).

Detailed causes of death were not reported in France and Switzerland. In Białowieża Primeval Forest, Poland, only four animals were shot by hunters when these left the protected area, only one was killed by wolves and one starved. However, reliable datasets are only available for yearlings and adults, piglets are non-representative. Within the other 14 studies, 85 % of dead animals were shot, 3 % died by diseases or starvation, 3 % died by traffic accidents and another 9 % death causes could not be proven, but many of them were shot and found later by radio telemetry after unsuccessful trail.

Sex ratios of wild boar are varying from region to region and year to year. The literature search also did not reveal a general trend in Table 3. SR of shot piglets equals this of captured piglets. Although in total the SR of shot wild boar seems to be balanced as shown by own and published data (Table 3), in our present study, we find mortality rates higher for males ( $p = 0.019$ ) and especially male yearlings (Table 2 and Fig. 2, see also Online Resource 3).

## Discussion

This is the first comprehensive study on mortality rates in eight European countries and gives valuable insights in population dynamics. Overall, we found a bias between reproductive and harvest rates which leads to growing wild boar populations. Thus, a need for a change in management and population regulation is apparent to counteract economic problems. A reduction of high populations seems to be inevitable, especially to stop infection chains and to reduce crop damages (Keuling et al. 2008a). To control the reproduction, a regulation of the reproductive animals is necessary. Nowadays, all age classes of females are highly reproductive; thus, mainly piglets and females of all ages have to be shot (Bieber and Ruf 2005; Sodeikat et al. 2005; Gethöffer et al. 2007; Cellina 2008; Servanty 2008).

Samples of less than ten observed animals deliver unreliable results and have to be considered carefully. However, analyses of the overall mortalities give consistent and reliable results. The total analysis of all studies reflects a comparably low mortality of wild boar in highly productive populations (Gethöffer et al. 2007; Cellina 2008; Servanty et al. 2009). In all our study areas (with exception of Italy), mortality rates and, thus, harvest rates are less than the total

**Table 2** Mortality rates of wild boar observed by radio telemetry in central Europe

| Study area                           | Age + sex | <i>N</i> animals | <i>N</i> dead | <i>N</i> days observed | Daily probability of survival | Mortality rate (reference period) |
|--------------------------------------|-----------|------------------|---------------|------------------------|-------------------------------|-----------------------------------|
| 1–3 S                                | AF        | 20               | 7             | 3,715                  | 0.9981                        | 0.498                             |
|                                      | AM        | 2                | 2             | 369                    | 0.9946                        | 0.862                             |
| 4 PL no hunting                      | PF        | 6                | 0             | 523                    | 1                             | 0                                 |
|                                      | PM        | 5                | 1             | 412                    | 0.9976                        | 0.356                             |
|                                      | YF        | 15               | 1             | 3,084                  | 0.9997                        | 0.112                             |
|                                      | YM        | 12               | 1             | 2,785                  | 0.9996                        | 0.123                             |
|                                      | AF        | 30               | 0             | 6,971                  | 1                             | 0                                 |
|                                      | AM        | 16               | 0             | 3,253                  | 1                             | 0                                 |
| 5 D                                  | PF        | 57               | 16            | 3,784                  | 0.9958                        | 0.536                             |
|                                      | PM        | 9                | 4             | 251                    | 0.9841                        | 0.945                             |
|                                      | YF        | 41               | 14            | 7,112                  | 0.9980                        | 0.513                             |
|                                      | YM        | 7                | 4             | 1,010                  | 0.9960                        | 0.765                             |
|                                      | AF        | 16               | 4             | 4,998                  | 0.9992                        | 0.253                             |
| 6+7 D                                | PF        | 54               | 17            | 3,500                  | 0.9951                        | 0.586                             |
|                                      | PM        | 45               | 15            | 2,868                  | 0.9948                        | 0.613                             |
|                                      | YF        | 15               | 7             | 1,415                  | 0.9951                        | 0.836                             |
|                                      | YM        | 12               | 4             | 673                    | 0.9941                        | 0.886                             |
|                                      | AF        | 2                | 0             | 223                    | 1                             | 0                                 |
|                                      | PM        | 4                | 0             | 255                    | 1                             | 0                                 |
| 8 D                                  | YF        | 3                | 1             | 1,041                  | 0.9990                        | 0.296                             |
|                                      | YM        | 9                | 2             | 802                    | 0.9975                        | 0.598                             |
|                                      | AF        | 3                | 2             | 440                    | 0.9955                        | 0.810                             |
|                                      | AM        | 4                | 2             | 413                    | 0.9952                        | 0.830                             |
| 9–11 B                               | AF        | 70               | 17            | 14,631                 | 0.9988                        | 0.346                             |
|                                      | AM        | 50               | 10            | 8846                   | 0.9989                        | 0.338                             |
| 12 F                                 | YF        | 33               | 12            | 6,290                  | 0.9981                        | 0.502                             |
|                                      | YM        | 5                | 1             | 440                    | 0.9977                        | 0.564                             |
|                                      | AF        | 37               | 9             | 8,584                  | 0.9990                        | 0.318                             |
|                                      | AM        | 1                | 1             | 106                    | 0.9906                        | 0.969                             |
| 13 CH                                | PF        | 24               | 9             | 3,042                  | 0.9970                        | 0.415                             |
|                                      | PM        | 22               | 5             | 2,499                  | 0.9980                        | 0.304                             |
|                                      | YF        | 46               | 14            | 8,565                  | 0.9984                        | 0.450                             |
|                                      | YM        | 19               | 7             | 3,118                  | 0.9978                        | 0.560                             |
|                                      | AF        | 44               | 9             | 9,965                  | 0.9991                        | 0.281                             |
|                                      | AM        | 19               | 5             | 4,125                  | 0.9988                        | 0.358                             |
| 14 A                                 | PF        | 1                | 0             | 123                    | 1                             | 0                                 |
|                                      | PM        | 2                | 1             | 91                     | 0.9890                        | 0.982                             |
|                                      | YM        | 2                | 0             | 226                    | 1                             | 0                                 |
|                                      | AF        | 1                | 0             | 71                     | 1                             | 0                                 |
| 15 I                                 | PF        | 5                | 3             | 468                    | 0.9936                        | 0.688                             |
|                                      | PM        | 7                | 5             | 691                    | 0.9928                        | 0.731                             |
|                                      | YF        | 14               | 9             | 2,507                  | 0.9964                        | 0.731                             |
|                                      | YM        | 16               | 10            | 1,922                  | 0.9948                        | 0.851                             |
|                                      | AF        | 4                | 2             | 823                    | 0.9976                        | 0.589                             |
| Total hunted populations (without 4) | PF        | 141              | 45            | 10,917                 | 0.9959                        | 0.527                             |
|                                      | PM        | 89               | 30            | 6,655                  | 0.9955                        | 0.559                             |
|                                      | P         | 230              | 75            | 17,572                 | 0.9957                        | 0.539                             |
|                                      | YF        | 152              | 57            | 26,930                 | 0.9979                        | 0.539                             |

**Table 2** (continued)

| Study area | Age + sex | <i>N</i> animals | <i>N</i> dead | <i>N</i> days observed | Daily probability of survival | Mortality rate (reference period) |
|------------|-----------|------------------|---------------|------------------------|-------------------------------|-----------------------------------|
|            | YM        | 70               | 28            | 8,191                  | 0.9966                        | 0.713                             |
|            | Y         | 222              | 85            | 35,121                 | 0.9976                        | 0.587                             |
|            | AF        | 197              | 50            | 43,450                 | 0.9988                        | 0.343                             |
|            | AM        | 76               | 20            | 13,859                 | 0.9986                        | 0.410                             |
|            | A         | 273              | 70            | 57,309                 | 0.9988                        | 0.360                             |
| Σ hunted   |           | 725              | 230           | 110,002                | 0.9979                        | 0.534                             |
| Σ          |           | 809              | 233           | 127,030                |                               |                                   |

Numbers in italics show results of small sample sizes, reference period in piglets=181 days, in yearlings and adults=1 year  
*P* piglets <12 months, *Y* yearlings, *A* adults >24 months, *F* female, *M* male

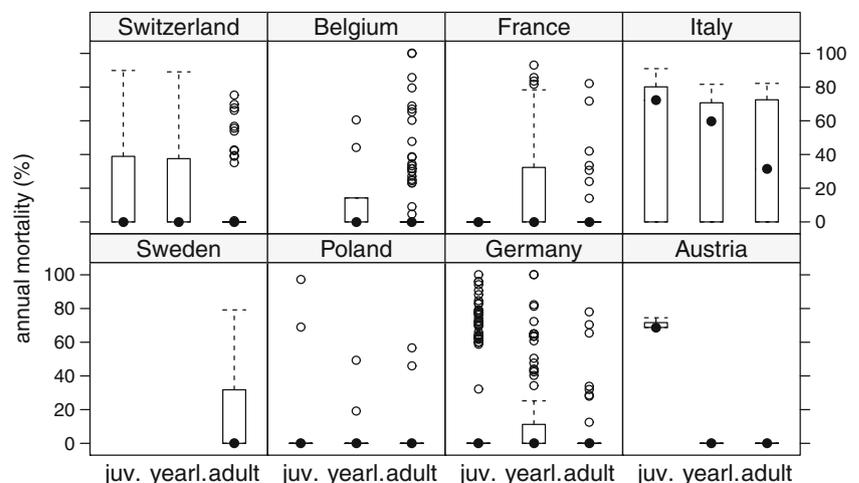
net reproduction. Our results reflect the permanently increasing annual hunting bags as shown in Online Resource 4. The population will increase further; a fact that Genov et al. (1994) already reported for most European countries. This bias between reproductive rate and harvest is based on an underestimation of population densities and reproduction rates (Genov et al. 1994). The reproduction amounts up to 300 % increase of basic population (Gethöffer et al. 2007; Cellina 2008); in the Federal State of Lower Saxony, Germany, the mean reproductive rate from 2002 to 2011 was 260 % (Gethöffer et al., unpublished data). Assuming a peri- and postnatal mortality of 20 % (Martys 1982), the mean annual increase is about 210 %. Thus, about 65 % of the summer population has to be harvested. This would come up to a mortality rate of 0.65. Especially, the harvest rate of piglets seems to be insufficient. Only in the Italian study area that the mortality rates achieve the requested values, which might be due to a high hunting pressure and, of course, to the low number of observed animals. Out of the piglets, 80 % should be harvested (Happ 2002) besides yearlings and adults. It is of big importance to shoot more piglets at an early age (Genov et al. 1994; Bieber and Ruf 2005) to prevent them from becoming pubescent to

reduce population increase. In summer, many wild boar groups live predominantly within fields, causing high damages (Gerard et al. 1991; Cahill et al. 2003; Keuling et al. 2008b, 2009). Also, a higher number of yearlings might increase the risk of infections and damages, as they behave more spacious than family groups (Keuling et al. 2008a, b, 2009). The reduction of wild boar populations in woodland during winter as well as hunting small piglets early and intense inside agricultural fields in summer is a precondition for regulation and prevention of damages in agricultural fields (Briedermann 1977; Mazzoni della Stella et al. 1995; Liebl et al. 2005; Keuling et al. 2008a, b, 2009).

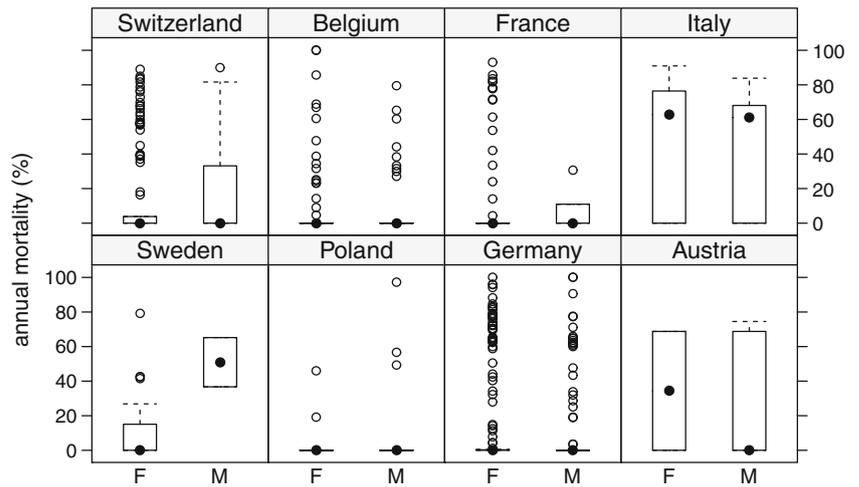
However, like Genov et al. (1994), we recommend a higher hunting rate of older females, especially on single hunt (“espera” sensu, Braga et al. 2010). Reduction or regulation of a population is achieved easier by increased shooting of female yearlings and adults (Bieber and Ruf 2005; Servanty 2008). How to transport this point to private hunters is another problem. Wildlife managers will also have to incorporate hunters willingness into management concepts (Keuling 2009).

Our results certified the findings of several studies that predation, natural mortality and road mortality have only

**Fig. 1** Annual mortalities (censored, i.e. for the animals with confirmed deaths) for different age classes (data of different study areas of one nation combined). A median of 0 means that more than 50 % of the observed animals survived the observation period. Significant differences between countries and age classes, see Online Resource 2. *juv.* = piglets (<12 months), *yearl.* = yearlings (>12–24 months), *adults* (>24 months)



**Fig. 2** Annual mortalities (censored, i.e. for the animals with confirmed deaths) for different sexes (data of different study areas of one nation combined). A median of 0 means that more than 50 % of the observed animals survived the observation period. Significant differences between countries and sexes, see Online Resource 2. *juv.* = piglets ( $\leq 12$  months), *yearl.* = yearlings ( $>12$ –24 months) *adults* ( $>24$  months)



**Table 3** Overview on literature data and own analyses of sex ratios of different wild boar age classes; c captured, all other hunted

| Foeti  | Piglets            | Yearlings          | Adults               | Total    | Region            | Author  |
|--------|--------------------|--------------------|----------------------|----------|-------------------|---|
|        | 1.14:1<br>1.13:1 c | 1.53:1             | 0.57:1               | 1.20:1   | 5, MV, D          | Keuling et al. (2010), this study   |
|        | 1.04:1             | 1.27:1             | 1.41:1               | 1.15:1   | NI, D             | Sodeikat, official hunting bags of Lower Saxony 2003–2008                     |
|        | 0.91:1 c           |                    |                      |          | c: 6+7, NI, D     | c: this study   |
|        | 0.55:1<br>0.65:1 c | 0.50:1<br>0.65:1 c | 0.55:1<br>0.41:1c    | 0.53:1   | 13, Geneve, CH    | This study  |
|        |                    |                    | 0.71:1               |          | 9-11, Wallonie, B | This study  |
|        | 1.14:1<br>1.13:1 c | 0.97:1             | 1.05:1               | 1.06:1   | 15, Appennines, I | This study  |
|        | 0.83:1 c           | 0.71:1 c           |                      |          | 4, Bialowieza, PL | This study  |
| 1.12:1 | 1.2:1              | 1.19:1             |                      |          | n-DDR (D)         | Briedermann (1971)  |
| 0.85:1 |                    |                    |                      | 1.11:1   | DDR (D)           | Stubbe and Stubbe (1977)  |
| 0.8:1  | 1.25:1<br>1.14:1 c | 1.26:1             | 0.76:1<2<br>0.42:1>2 |          | w-PL              | Fruzinski and Labudzki (2002)   |
|        |                    |                    |                      | 1.01:1   | LUX               | Cellina (2008)  |
| 1.08:1 |                    |                    |                      | 0.98:1   | e-F               | Servanty (2008)   |
|        |                    |                    |                      | 1.24:1 c | s-CH              | Moretti (1995)  |
|        | 1.14:1             | 0.88:1             | 0.65:1               | 0.92:1   | Bologna, I        | Fenati et al. (2008)  |
| 0.83:1 | 0.92:1             | 1.75:1             | 0.99:1               | 1.17:1   | Piedmont, I       | Durio et al. (1995)   |
|        |                    |                    |                      | 1.19:1   | Tuscany, I        | Boitani et al. (1995)   |
| 0.83:1 |                    |                    |                      |          | Tuscany, I        | Massolo and Mazzoni della Stella (2006)                                       |
|        | 1.75:1             | 1.12:1             | 0.42:1               | 1:1      | H                 | Náhlík and Sándor (2003)  |
|        | 0.72:1             | 0.71:1             |                      |          | Pyrenees, E       | Herrero et al. (1995)   |
| 0.88:1 | 0.74:1             | 0.44:1             | 0.39:1               | 0.8:1    | Barcelona, E      | Cahill and Llimona (2004)   |
| 1.1:1  |                    |                    |                      | 0.81:1   | w-E               | Garzon-Heydt (1992)   |
|        |                    |                    |                      |          | Cáceres, w-E      | Fernández-Llario et al. (1999),<br>Fernández-Llario and Mateos-Quesada (2003) |
|        |                    |                    |                      | 1.6:1    | N.T., AUS         | Caley and Ottley (1995)   |
|        |                    |                    |                      | 1:1 c    | N.S.W, AUS        | Saunders (1993)   |

small impact on wild boar populations, whereas the environment, especially nutrition or hunting is mainly decisive (Okarma et al. 1995; Kanzaki and Perzanowski 1997; Peris et al. 2005; Nores et al. 2008; Toïgo et al. 2008). Mammal populations without or with low predation are strongly dependent on environment and food (Saether 1997). Although predation seems to be a low impact factor on yearlings and adults in Białowieża Primeval Forest, Poland, higher mortality rates by large predators like wolf may be assumed for piglets (Jędrzejewski et al. 2000), especially at an earlier age (before radio observation, less than about 5 months of age). Optimal nutritional conditions within agricultural-formed environments, supported by supplemental feeding, increase reproduction and population of wild boar (Boutin 1990; Saether 1997; Geisser and Reyer 2005; Gethöffer et al. 2007).

As the sex ratio of the shot piglets equals the SR of captured piglets, there seems to be no sex-biased hunting (as main mortality factor) in this age class. This is due to the missing ability of hunters to distinguish the sex in this age class within the sounders. Notably, mortality of male yearlings is higher than that of females. This might be due to intensified movements depending on migration, especially during summer within fields. Additionally, hunters try to avoid hunting females with piglets. Mortality of adult males is quite high, when trophy hunt is one of the aims, like it is in most of European countries. In such case, males should be shot at an older age. Especially, male yearlings and perhaps young adult males should be preserved (Braga et al. 2010). Sexual and age class population data have to be reliable, not to destabilise social structures and the dominance hierarchy by biased shooting of age and sex (e.g. by trophy hunt: Milner-Gulland et al. 2004; Milner et al. 2007).

The high reproductive success has to be counteracted by high harvest rates to regulate populations and thus to regulate damages. All in all, mortality rates seem not to be sufficient all over Europe. Thus, hunting efforts have to be intensified. "... wildlife managers should consider hunter willingness to harvest piglets and females..." (Toïgo et al. 2008); therefore, hunters have to be stimulated (hunting as leisure activity, Ueda and Kanzaki 2005). Intensifying comprehensive drive hunts and small battues especially for wild boar may increase the proportion of this method at annual hunting bags and, also, a comprehensive combination of hunting methods might be an effective management tool (Briedermann 1977; Calenge et al. 2002; Sodeikat and Pohlmeier 2007; Keuling 2009). Only a cooperation of hunters can raise hunting efficiency and, thus, prevent officially ordered culling.

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RESEARCH ARTICLE

# Stochastic assessment of management strategies for a Mediterranean peri-urban wild boar population

Carlos González-Crespo<sup>1</sup>, Emmanuel Serrano<sup>1,2</sup>, Seán Cahill<sup>3</sup>, Raquel Castillo-Contreras<sup>1</sup>, Lluís Cabañeros<sup>3</sup>, José María López-Martín<sup>4</sup>, Joan Roldán<sup>5</sup>, Santiago Lavín<sup>1</sup>, Jorge Ramón López-Olvera<sup>1\*</sup>

**1** Wildlife Ecology & Health Group and Servei d' Ecopatologia de Fauna Salvatge (SEFaS), Departament de Medicina i Cirurgia Animals, Facultat de Veterinària, Universitat Autònoma de Barcelona (UAB), Bellaterra, Barcelona, Spain, **2** Departamento de Biología & Cesam, Universidad de Aveiro (UA), Aveiro, Portugal, **3** Consorci del Parc Natural de la Serra de Collserola, Barcelona, Spain, **4** Departament d'Agricultura, Ramaderia, Pesca i Alimentació, Serveis Territorials de Barcelona, Generalitat de Catalunya, Barcelona, Spain, **5** Forestal Catalana SA, Generalitat de Catalunya, Barcelona, Spain

\* [Jordi.Lopez.Olvera@uab.cat](mailto:Jordi.Lopez.Olvera@uab.cat)



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## Abstract

Wild boar (*Sus scrofa*) population spread into urban and periurban areas has exacerbated conflicts with humans. There is a need for planned wild boar management strategies, and Population viability analysis (PVA) combined with perturbation analyses allow the assessment of the management effort of control methods. Our study aims to develop stochastic predictive models of the increasing wild boar population of the 80 km<sup>2</sup> peri-urban Mediterranean area of Collserola Natural Park (CNP), located near Barcelona, Spain, as well as assessing specific management measures (including reduced food availability, selective harvest, and reduction in fertility). Population parameters were estimated from previously published census and hunting data provided by the CNP and the local hunting administration. The results revealed that under the current conditions the CNP wild boar population will continue to increase. The most efficient strategy to reduce wild boar abundance was a combination of reducing supplementary anthropogenic food resources and selective removal of juvenile (<1 year) and yearling (1–2 years) wild boar. These strategies will probably be also the most efficient ones in other oversupplemented increasing wild boar populations in similar situations, although specific studies will be needed to fine-tune the best management option for each context. PVA allows the prediction of future population trends and the assessment of the efficacy and efficiency of potential management strategies before implementing management measures.

## Introduction

Wild boar (*Sus scrofa*) population numbers have increased and their distribution area has spread worldwide in the last decades, mainly due to artificial feeding, a reduction in predators

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and translocations [1], changes in land use and decrease of human population in rural areas [2–4]. At least in Europe, climate change is also favoring wild boar populations through milder winters and increased mast productivity [5]. As a generalist species, the wild boar is capable of successfully colonizing and exploiting a wide range of habitats [6], including the interface between urban areas, agricultural landscapes and even highly artificial urban green areas [7,8].

Increasing wild boar population in rural areas and in proximity to urban areas has exacerbated conflicts with humans. Wild boar cause damage to crop fields in cultivated areas, to plant diversity, vegetation composition and regeneration patterns [9,10], they prey on a number of animal species like ground-nesting birds, such as red-legged partridge (*Alectoris rufa*), pheasants (*Phasianus colchicus*), mammals as the red-backed vole (*Clethrionomys gapperi*) and short-tailed shrew (*Blarina brevicauda*) and even domestic livestock [11]. Wild boar are increasingly involved in vehicle collisions [7,8,12,13]. The colonization of urban areas and habituation to humans has also increase damage in parks, green areas, attacks on people and pets, and pose human-health risks [7,8,14].

Regulated wild boar hunting has been the primary method of population control. However, wild boar hunting is declining in some European countries and is currently insufficient to halt wild boar population growth [4]. Suggested methods to control the growth of wild boar populations include the use of toxicants, not approved in Europe but common in other parts of the world such as Australia [15] and fertility control [10,16]. Other methods are aimed to decrease damage and conflicts like the use of repellents, translocation and fencing [10,17]. However, none of these methods provides a definitive solution to control population growth because the high reproductive rate of wild boar compensates for the potential mitigation effects of these measures [17,18].

There is a general need for carefully planned wild boar management strategies [9]. Identifying the vulnerable life stages of pest species and their relative responses to perturbations [19,20] allows the establishment of control methods within the proper focus for management effort [21]. Population viability analysis (PVA) combined with perturbation analyses (i.e. sensitivity and elasticity) are currently the most commonly used methods for this objective [20].

Population Viability Analysis (PVA) is a model-based quantitative risk assessment that, relying on ecological models, identifies the viability requirements and threats to a species population, also evaluating the likelihood of persistence, either for a given time under current conditions or expected from proposed management. Although PVAs were originally developed for threatened species to evaluate the risk of extinction allowing to minimize the risks [22,23], they have also been used to evaluate the impact of disease outbreaks [24] and to assess the effects of management measures aimed at reducing population size for invasive and pest species [20,23].

Both PVA and sensitivity analyses can also be used as a decision-support tool to identify key life cycle stages and/or demographic processes as targets for management interventions for established invasive species [20,23]. This allows the determination of the most cost-efficient management strategies [25] and the effect of different management strategies prior to undertaking them.

The purpose of our study was to develop stochastic predictive models of the wild boar population of the peri-urban Mediterranean area located near Barcelona, Spain. We specifically wanted to use sensitivity analyses [23] to identify the life stages (sex and age) to be targeted with specific management measures (including reduced food availability, selective harvest, and reduction in fertility), in order to achieve the maximum effect for population reduction [26]; and, secondly, to evaluate the effectiveness of the aforementioned management strategies on affecting the most vulnerable life stages and thereby controlling population growth. The results

will provide managers with measures that can be applied to reduce wild boar populations and the attractiveness of urban areas for this species in Mediterranean ecosystems.

## Methods

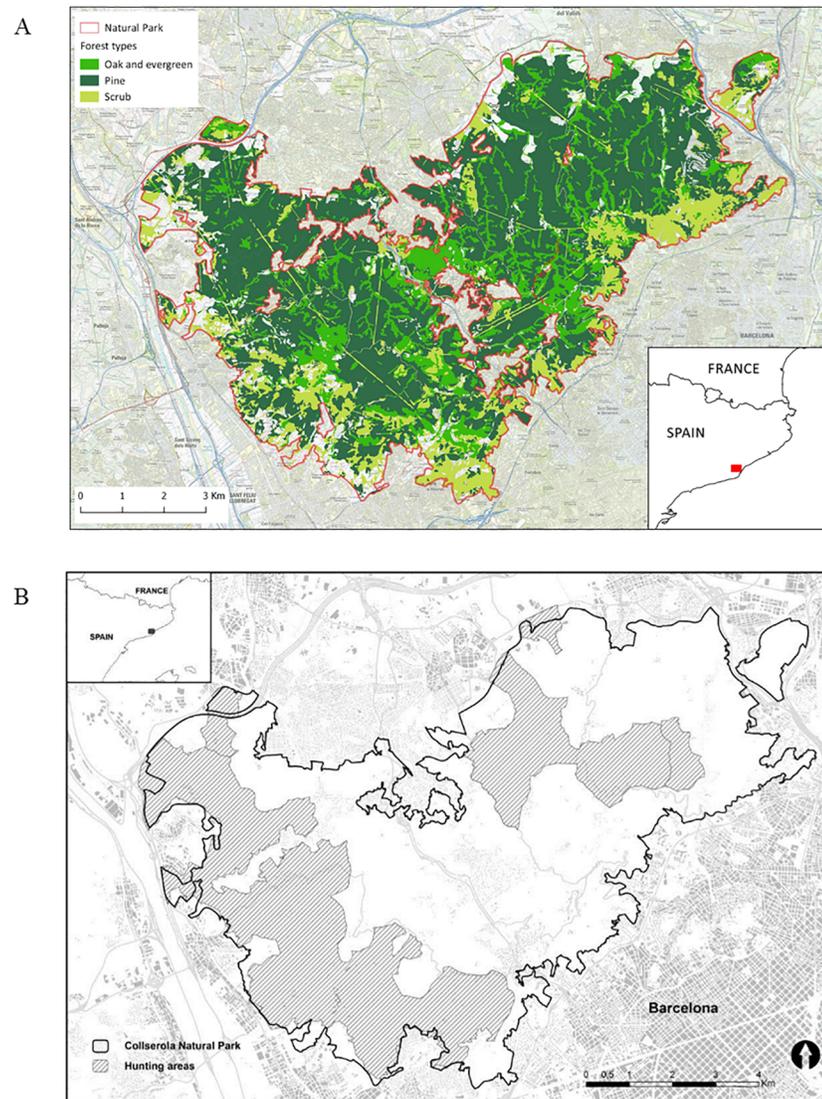
Our study area consisted of the 80 km<sup>2</sup> Natura 2000 Collserola Natural Park (CNP) (41°25'52"N, 2°4'45"E), located in Barcelona, in north-eastern Spain, Wild boar are considered abundant in the province of Barcelona [14,27]. The CNP (Fig 1) is surrounded by urban areas within the Barcelona metropolitan area (AMB, by its acronym in Spanish). The AMB is one of the largest European metropolitan areas, with 36 municipalities occupying more than 636 km<sup>2</sup> and populated by 3.2 million people (population density of 5,000 people per km<sup>2</sup>) (AMB 2015).

The CNP is virtually isolated from the nearby natural and agricultural areas by urban development and road and train networks (Fig 1A) [14], although some corridors and ecological connectors, such as riparian areas and dry riverbeds, are used by wild boar, hence allowing some movements out of this area [28]. The CNP is a Mediterranean hilly area, with an altitude ranging from 60 to 512 meters at the Tibidabo summit. The climate is typically Mediterranean, with warm dry summers and mild wet winters. Annual rainfall is 672 mm and average annual temperatures range from -4°C (minimum) to 35°C (maximum). The vegetation of CNP is mainly composed of Mediterranean scrub (24%) and mixed woodland of Aleppo pine (*Pinus halepensis*) (40%) combined with evergreen oak (*Quercus ilex*) (15%) and deciduous oak (*Q. cerrioides*) (0.7%) [7,29]. The remaining surface is composed by abandoned fields, wastelands and ruderal areas (3.9%), urban areas (3.5%), herbaceous (2.1%) and woody (1.8%) croplands and others (i.e. grasslands, ports, rafts, artificial canals, etc.) (9.0%). Oak acorn production in Mediterranean areas is highly variable, both intra- and inter-annually, mainly due to spring weather conditions during flowering and acorn growth [30,31]. Inter-annual evergreen oak production variation in Catalonia ranges from 58 to 82% [32], and a full mast year takes place every four years on average [32,33]. The wild boar is the only wild ungulate and the largest animal in size inhabiting the CNP. Although some minor piglet predation by medium-sized carnivores such as foxes may happen within the park, no natural predators for adult wild boar thrive inside the park. Therefore, natural predation is likely negligible and has no impact on the wild boar population dynamics.

The wild boar population in the CNP has increased and become habituated to human presence, due to anthropogenic resources, including street bins, waste containers, stray cat colonies, urban green areas and direct feeding by people (Figures A and B in S1 File) [28]. Anthropogenic feeding is facilitated by the proximity of densely vegetated areas close to the city limits [7,34,35].

In CNP, hunting is allowed from October through February as a traditional activity with a management plan in the Controlled Game Area of Collserola, which comprises 38% of the CNP surface and the same proportion of habitats described for the CNP (Fig 1b). Hunting is carried out via drive hunts with hunters at fix positions and hound packs flushing the boars, in about 17.2% of the park. In an attempt to reduce wild boar abundance and damage, hunting pressure has progressively increased since 2004 through night waits (single hunter from a fix position, using bait and spotlights but not hide), granted almost year-round even in non-hunting areas after damage claims[7].

In spite of such hunting pressure, the estimated CNP wild boar population has experienced a 10-fold increase from 2000 to 2015, reaching an estimated relative abundance of around 1,500 wild boar (Table 1). The estimated percentage of harvested wild boar with respect to the estimated wild boar population increased throughout the study period from 10.0% (2000–



**Fig 1. Study area.** Maps of Collserola Natural Park, Barcelona, NE Spain, showing a) the different habitats and b) Controlled Game Area, currently the only hunting areas in the whole massif.

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2003) to 46.5% (2012–2015) (Table 1). However, adults were overrepresented (65.6%) in the battue hunting bag as compared to their proportion in Mediterranean populations (25%) [1,18,36,37], whereas yearlings and juveniles accounted only for 34.4% of the total harvest, far less than their proportion (75%) [1]. Although the scarce detected poaching have been included in the mortality rate, both the amount of wild boar poached and the effect of poaching on the CNP wild boar population are negligible.

Fertility control of the wild boar population of the CNP has not been attempted, and repellents are unlikely to be effective in reducing the impact of wild boar [10]. Finally, fencing of CNP is incompatible with the human uses of this natural area surrounded by a 3.2 million human population.

All the data have been gathered from hunting records and wild boar management projects but no wild boar has been hunted, captured, handled or euthanized for this study.

**Table 1. Wild boar harvested and abundances in Collserola Natural Park from 2000 to 2014.**

| Year | Hunting season | Estimated wild boar population in CNP (CI 95%) | Wild boars hunted in drive hunts | Wild boars hunted in night waits | Registered mortality (% of the estimated population) <sup>+</sup> |
|------|----------------|--|----------------------------------|----------------------------------|---|
| 2000 | 2000/2001      | 165 (0.0–371.4)                                | 19                               | 0                                | 19 (11.5)   |
| 2001 | 2001/2002      | 357 (167.8–546.2)                              | 35                               | 0                                | 35 (9.8)  |
| 2002 | 2002/2003      | 191 (15.4–366.6)                               | 18                               | 0                                | 18 (9.4)  |
| 2003 | 2003/2004      | 280 (98.0–462.0)                               | 27                               | 0                                | 27 (9.6)  |
| 2004 | 2004/2005      | 579 (400.2–757.8)                              | 61                               | 19                               | 128 (22.1)  |
| 2005 | 2005/2006      | -  | 26                               | 35                               | 129   |
| 2006 | 2006/2007      | 558 (295.7–820.3)                              | 26                               | 43                               | 136 (24.4)  |
| 2007 | 2007/2008      | 689 (485.5–892.5)                              | 77                               | 37                               | 173 (25.1)  |
| 2008 | 2008/2009      | -  | 29                               | 44                               | 171   |
| 2009 | 2009/2010      | 809 (580.1–1,037.9)                            | 50                               | 53                               | 168 (20.8)  |
| 2010 | 2010/2011      | 821 (608.0–1,034.0)                            | 72                               | 77                               | 222 (27.0)  |
| 2011 | 2011/2012      | 773 (458.5–1,087.5)                            | 84                               | 108                              | 269 (34.8)  |
| 2012 | 2012/2013      | 1,050 (786.1–1,313.9)                          | 109                              | 171                              | 462 (44.0)  |
| 2013 | 2013/2014      | 759 (596.1–921.9)                              | 114                              | 261                              | 486 (64.0)  |
| 2014 | 2014/2015      | 831 (662.6–999.4)                              | 75                               | 206                              | 326 (39.2)  |
| 2015 | 2015/2016      | 1,500 (1,296.5–1,703.5)                        | 123                              | 432                              | 650 (43.3)  |

<sup>+</sup> Including all the wild boar hunted, killed in car accidents, poached and captured and euthanized.

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### Data collection

Sex, age and abundance data for the local wild boar population (Tables 1 and 2) were collected by the authors from wild boar captured, hunted or found dead from 2000 to 2015. According to age-specific variation in demographic parameters we defined three age classes for each sex [36,38,39]: juveniles (0–1 years), yearlings (1–2 years) and adults (> 2 years). Specific age class abundances were calculated from the aforementioned data collected by the authors and were used to calculate the specific age class mortality rates (Table 2).

Population trend was estimated from hunting bags only from the drive hunt data (S2 Table), a reliable index of wild boar relative abundance [37]. Briefly, the number of wild boar hunted in every hunting event is divided by the hunted surface. This value is corrected by the mean efficiency of the hunting season (total wild boar hunted divided by the total wild boar seen in all the drive hunts of the year) and the result is again divided by the ratio between the number of hunting events in a season and the mean annual number of hunting events. This method was used consistently during the whole study period with minor variations among years (except for 2005 and 2008) in the independent variables: number of drive hunts (18.4 SD 0.97), number of hunting days (9.2 SD 0.48), hunters in each drive hunt (44.1 SD 3.43) and dogs in each drive hunt (46.5 SD 2.96).

We obtained reproductive data (Table 2) from literature review on wild boar biological parameters in neighboring populations in Mediterranean environments [1,18,27,46].

To provide a carrying capacity (K value) allowing to perform our PVA with VORTEX [48], we defined a hypothetical population threshold (HPT) fixed to a number of 3,000 individuals. This value falls just between the 1,000 wild boar value corresponding to a density of 12.5 wild boar/km<sup>2</sup> in the 80 km<sup>2</sup> CNP [12,49], and the 6,400 wild boar corresponding to the maximum wild boar population density value recorded in fenced, food, water and shelter-supplemented Mediterranean environments (80 wild boar/km<sup>2</sup>, Gonçalves-Blanco, Ingulados Co., personal communication).

**Table 2. Input data used in the model scenarios of the Collserola Natural Park wild boar population.** Life history and population attributes: A) Reproduction values; B) Mortality and environment values. EV: Environmental variation.

| A   |                           |            |  |               |
|---|---------------------------|------------|--|---------------|
| Parameters  |                           | Base value | Source   |               |
| <b>Breeding system</b>  |                           | Polygynous | [12]   |               |
| <b>Age of first offspring (year)</b>                              | Females                   | 1          | [12,27]  |               |
|   | Males                     | 2          |  |               |
| <b>Maximum age of reproduction (year)</b>                         | Female                    | 11         | [12]   |               |
|   | Male                      | 11         |  |               |
| <b>Maximum lifespan (years)</b>                                   |                           | 11         | [12]   |               |
| <b>Maximum of broods per year</b>                                 |                           | 2          | [39,40]  |               |
| <b>Maximum of progeny per brood</b>                               |                           | 6          | [12]   |               |
| <b>Sex-ratio at birth</b>   |                           | 1:1        | [27]   |               |
| <b>% females breeding (SD due to EV)</b>                          | 0–1 years                 | 15 (10)    | [12,27]  |               |
|   | 1–2 years                 | 60 (10)    |  |               |
|   | > 2 years                 | 70 (10)    |  |               |
| <b>Distribution of broods per year</b>                            | 0 broods                  | 10         | [39,40]  |               |
|   | 1 brood                   | 85         |  |               |
|   | 2 broods                  | 5          |  |               |
| <b>Number of offsprings</b>                                       | Mean (SD)                 | 3.5 (2)    | [27]   |               |
| <b>% males in the breeding pool</b>                               |                           | 25         | [27]   |               |
| B   |                           |            |  |               |
| Parameters  |                           | Base value | Source   |               |
| <b>Mortality rates<sup>†</sup></b><br>Mean as %<br>(SD due to EV) | Females                   | 0–1 years  | 29 (10)  | Present study |
|   |                           | 1–2 years  | 35 (10)  |               |
|   |                           | > 2 years  | 39 (10)  |               |
|   | Males                     | 0–1 years  | 30 (10)  |               |
|   |                           | 1–2 years  | 43 (10)  |               |
|   |                           | > 2 years  | 35 (10)  |               |
| <b>Catastrophes</b>   |                           |            |  |               |
| <b>1) Severe drought</b>  |                           |            |  |               |
| Frequency   |                           | 15%        | Servei Meteorologic de Catalunya, unpublished data |               |
| Severity  | Reproduction <sup>a</sup> | 0.5        | [27,41,42]   |               |
|   | Survival <sup>b</sup>     | 0.5        | [9,36,43]  |               |
| <b>2) Full mast</b>   |                           |            |  |               |
| Frequency   |                           | 22%        | [32,33]  |               |
| Severity  | Reproduction <sup>a</sup> | 1.5        | [27]   |               |
|   | Survival <sup>b</sup>     | 1.5        | [9]  |               |
| <b>Carrying capacity (K)</b>                                      |                           |            |  |               |
| K value (SD due to EV)  |                           | 3000 (150) | Present study                                      |               |

<sup>†</sup>We estimated the age-class survival rates (*Sac*) from hunting data using the formula [44,45]:  $Sac = \frac{\sum N_{ac+1}(t_{x+1})}{\sum N_{ac}(t_x)}$ , where *Nac* and *Nac* + 1 are the abundances of the ageclasses, and *tx* the census years. *Nac* were calculated from data collected by the authors.

<sup>a</sup> Proportion of wild boar reproducing.

<sup>b</sup> Proportion of wild boar surviving.

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To include environmental stochasticity in the model, we considered the plasticity of Mediterranean wild boar populations, modeling a population characterized by high reproductive rates and high mortality in the first year of life [1], intense responses to food availability and weather conditions, with the proportion of reproducing females varying from 20–30% to

90% depending on food resource availability [39,46,49]. Altogether allows the population to increase even under yearly hunting pressures over 50% [38].

## Modeling

The trend of the CNP wild boar population was modeled from the published and estimated data (Table 2) over a time frame of 36 years (2000–2035) through two scenarios: past and future. We carried out simulation models using VORTEX Version 10.0.8 [47], a free software developed by the Chicago Zoological Society. The software is an individual-based simulation model for PVA that modeled the effect of deterministic and stochastic processes on the dynamics of wildlife populations [45].

We ran 500 iterations for each scenario to allow standard error calculations and we delayed the first year mortality until all annual mortality was done [45], in order to allow the harvest of juveniles. We included the vortex option of “environmental variation concordance of reproduction and survival” as the environmental variation affect reproduction and survival simultaneously [39,43] but not inbreeding effects, nor genetic management or density dependence effects on reproduction in the model.

*Past scenario*—We ran a 16-year (2000 to 2015) simulation with an initial population size of 165 wild boar (the estimated population size in 2000, CNP) to validate the model. We used the HPT value (3,000 individuals) and the parameter values introduced in VORTEX (Table 1). The number of wild boar of each age class harvested each year was modeled through a function (S1 Table).

*Future scenario*—A 20-year projection was run to study the future evolution of the population and to test both the impact of the variation in demographic rates and management strategies on the CNP wild boar population trend. The values for the parameters were taken from the past scenario, initiating the model with a wild boar population size of 1,500 individuals in 2015 (as estimated by the hunting bag analyses and confirmed by the past scenario model). Harvest was calculated to remain at 30% of the population, maintaining the same harvest proportion of each age-class as in the past scenario, and it was modeled by a function (S1 Table). We evaluated three HPT values (3,000, 4,200 and 6,400), corresponding to three different situations depending on the availability of anthropogenic resources under the same management.

## Sensitivity and elasticity analyses

Sensitivity and elasticity analyses estimate respectively the impact of absolute and proportional changes in biological parameters on population growth rate [21]. We tested the sensitivity and elasticity of the CNP wild boar population parameters on wild boar population trend in the CNP for 25 years in the future scenario, using the Sensitivity test (ST) implemented in VORTEX 10. We measured the sensitivity or impact as the total variation in the projected population sizes between the minimum and maximum value of the variable, and the elasticity or effect as the average population variation corresponding to each 10% parameter variation. The demographic variables were modified as follows to estimate the effect of three main different management strategies: 1) decreasing CNP HPT for wild boar (minimum value 500, maximum value 6,500, increment by 500) corresponding to different levels of anthropogenic food availability [9,10,17,50]; 2) reducing the percentage of breeding males and females (minimum value 0, maximum value 100, increment by 10) in each age-class through fertility control corresponding to variable fertility control effort [10,39]; and 3) increasing mortality (minimum value 0, maximum value 100, increment by 10) in sex and age-classes and a combination of them corresponding to variable and selective harvest pressure [1,17,18,38,50]. We also ran a factorial sensitivity analysis on the harvest values to estimate the best combination.

## Evaluation of management strategies

Once the ST determined the sensitivity and elasticity of the demographic parameters of the CNP wild boar population, we tested the effectiveness of reducing supplementary food availability and increasing selective harvest on modifying the variables selected by the sensitivity analyses in the future scenario. We did not evaluate the effectiveness of fertility control because the ST results of this strategy revealed a low effect on the variation in the projected population size. The output of each strategy was measured as the probability (PVA parameter “extinction probability”) of reaching the target population value and as the resulting wild boar population, both at the end of the future scenario period (25 years). The target population size (“extinction”) was set at 500 wild boar, half the theoretical natural carrying capacity of CNP (1,000 wild boar [12]), since this 50% value maximizes recruitment [51]. Wild boar is a native species in the CNP and the aim is not eradicating this species from the CNP but maintaining the population below ‘threshold’ levels not causing negative impacts in the ecosystem [11].

We modeled the decrease of CNP HPT for wild boar through supplementary feeding reduction [9,10,17,50] from the current estimated HPT value of 3,000 to the target value of 1,500, assuming a minimum supplementary food availability for 500 wild boar over the environmental carrying capacity (1,000 wild boar, [12]). We modeled such a decrease at two different rates: an idealistic option, with a 15% annual decrease for 5 years, and a conservative option, with a 5% annual decrease for 15 years. Secondly, we modeled the effectiveness of selective harvest [1,17,18,38,50], focused on increasing harvest in the best combination of values for juveniles and yearlings of both sexes provided by the sensitivity test results. Finally, we also modeled the effectiveness of an integrated management plan including the combination of supplementary feeding reduction and selective harvest.

## Results

### The past scenario

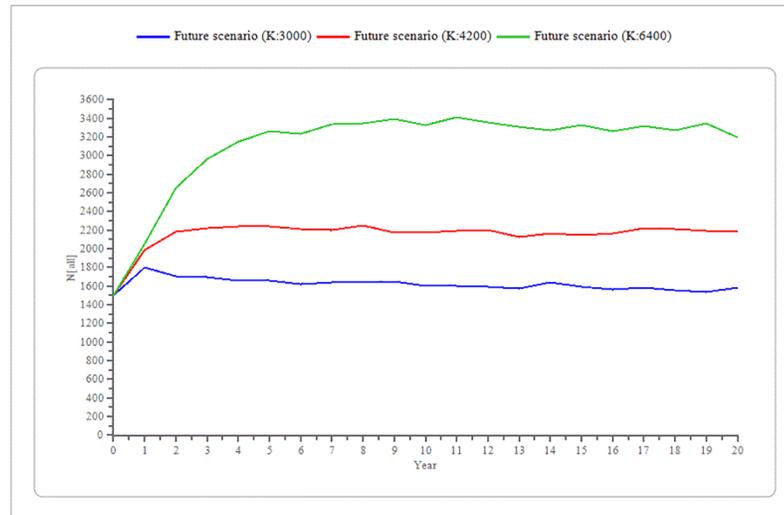
The population model calculated a population of 1,560 (34.42 SE) wild boar in 2015, agreeing with the evolution of the CNP wild boar population estimated from hunting bags, from 165 wild boar in 2000 to 1,500 in 2015. The deterministic annual increase ( $r$ ) in wild boar abundance calculated by VORTEX was 0.3723.

### The future scenario

The VORTEX simulations predicted that under the current conditions the CNP wild boar population will increase an 11.5% (until 1,673 individuals, 26.81 SE), with an 8% probability of decreasing below the target size (500 individuals). Increasing HPT ( $K$  value) to 6,400 produced a consequent progressive increase in the final population size up to a 120.3% (until 3,304 wild boar, 61.56 SE) while the probability of achieving the target population size decreased to 4% (Fig 2).

### Sensitivity analyses

The sensitivity analyses evidenced (Table 3, Figs 3 and 4) food availability as represented by HPT as the most influential parameter in population size (S2 Fig), followed by the mortality rate of juvenile males and females, and the mortality rate of yearling males and females. The impact of adult male and female mortality on the variation in the CNP wild boar population size was not significant (S3 Fig). Overall, the variations in female mortality rate had a stronger effect on population size than male mortality rate for all age-classes (Fig 4).



**Fig 2. Predicted wild boar population trends.** Future scenario results showed a progressive increase in the Collserola Natural Park final population size of: 1,673 wild boar for a K value (Hypothetical population threshold: Anthropogenic food resources availability) of 3,000, 2,281 wild boar for a K value of 4,200 and up to 3,304 wild boar for a K value of 6,400. Lines indicate SE.

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Regarding reproduction, the variation in the percentage of reproductive females had a stronger impact on population size than for males (Table 3). Among females, the impact on wild boar population of the percentage of reproducing females increased with age. However, even though the variation in the predicted CNP wild boar population size due to the variation in the percentage of breeding females was high, only percentages of adult breeding females below 30% had an effect in achieving a significant reduction in CNP wild boar population size (Fig 4, S4 Fig).

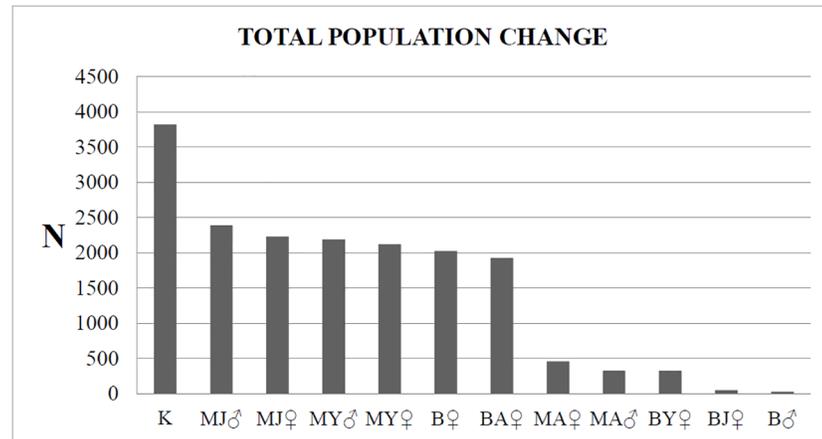
The sensitivity analyses showed that a mortality rate between 40–60% for both juvenile and yearling wild boar, combined with a reduction of CNP HPT to a value of 1,500 wild boar, were

**Table 3. Sensitivity test results for the different parameters tested.**

| Parameter tested in the sensitivity test (minimum-maximum value) |          |                 | Relative population variation <sup>a</sup> |                  | Variation between values (number of individuals) |
|--|----------|-----------------|--|------------------|--|
|  |          |                 | At minimum value                           | At maximum value |  |
| Hypothetical Population Threshold (500–6500)                     |          |                 | -79.6%                                     | +175.0%          | 3,820  |
| Mortality (0–100%)   | Juvenile | Male            | -100.0%                                    | +59.1%           | 2,387  |
|  |          | Female          | -99.4%                                     | +49.0%           | 2,226  |
|  | Yearling | Male            | -100.0%                                    | +47.9%           | 2,187  |
|  |          | Female          | -98.5%                                     | +42.5%           | 2,116  |
|  | Adult    | Male            | +25.0%                                     | +46.7%           | 325  |
|  |          | Female          | +14.1%                                     | +44.6%           | 457  |
| Breeding (0–100%)  | Males    |                 | +27.5%                                     | +29.4%           | 28   |
|  | Females  | All age-classes | -100.0%                                    | +34.9%           | 2,024  |
|  |          | Juvenile        | +25.7%                                     | +29.0%           | 49   |
|  |          | Yearling        | +13.5%                                     | +34.9%           | 320  |
|  |          | Adult           | -93.7%                                     | +34.7%           | 1,925  |

<sup>a</sup> The sign indicates the direction of the variation (+, increase; -, decrease)

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**Fig 3. Impact of different parameters on wild boar population size according to the sensitivity tests.** Total decrease (impact) in the wild boar population size of the Collserola Natural Park, Spain, for each parameter tested. K, Hypothetical population threshold; Anthropogenic food resources availability; M, Mortality; B, Breeding; J, Juveniles; Y, Yearling; A, Adults.

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the most effective measures to control and reduce the CNP wild boar population. Therefore, HPT and juvenile and yearling mortality were the variables selected by the model and consequently defined as target values for the management strategies (Table 4).

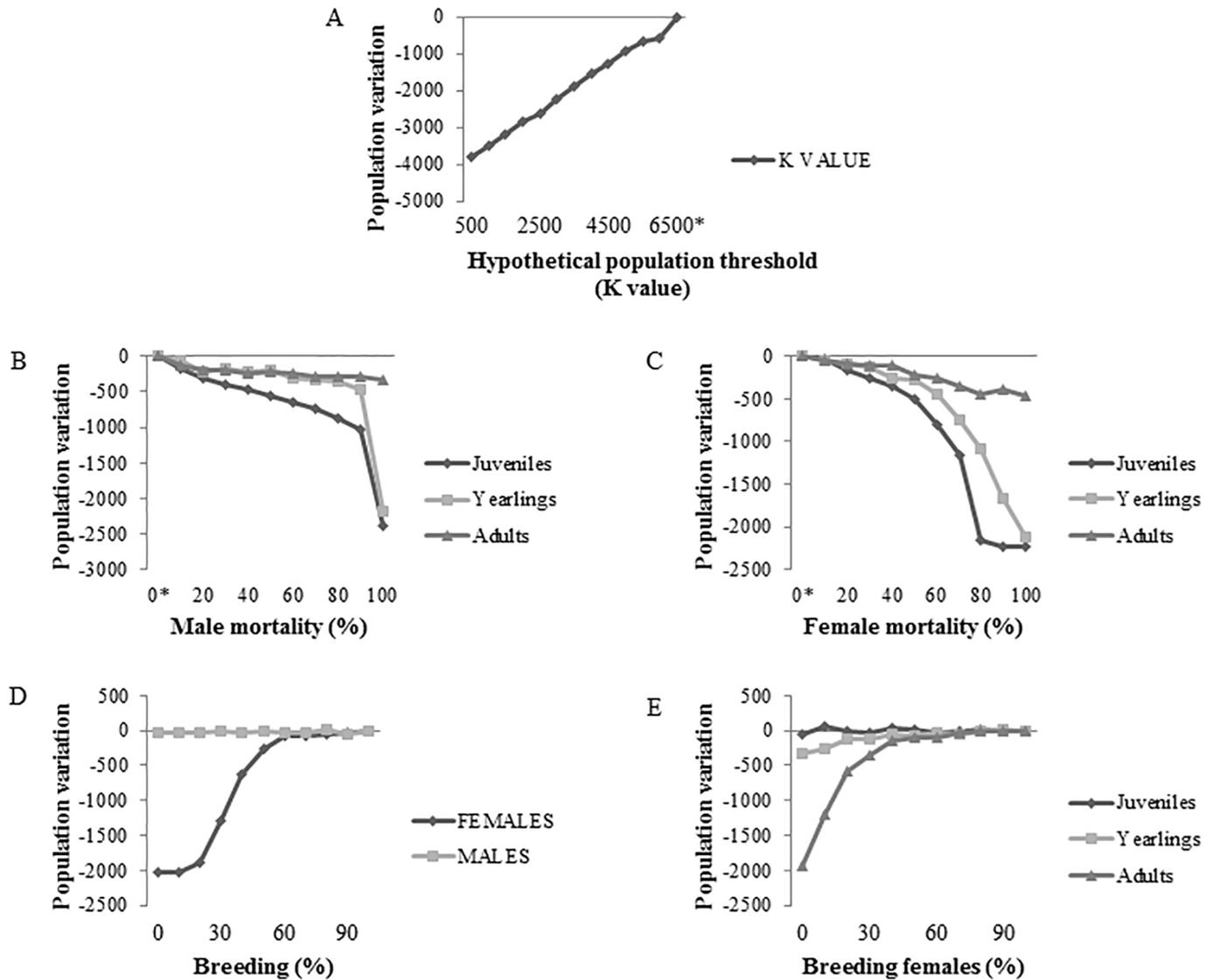
### Evaluation of management strategies

Decreasing the supplementary feeding had an 80% effectiveness to reach the target population value (fixed at 500 wild boar), with a 20% probability of decreasing the population a 58.6% (621 wild boar remaining) at the end of the modeled period for the idealistic decreasing rate option. The conservative decreasing rate option had an 86% effectiveness to reach the target population value, with a 14% probability of achieving a population decrease of 59.1% (614 wild boar remaining) at the end of the modeled period (Table 4, Fig 5A). The sensitivity test in the harvest value of juveniles and yearlings selected 240 individuals, 60 from each sex within each age category, as the most efficient and effective value for the selective harvest strategy (Fig 6). This strategy had 72% effectiveness of reaching the target population value, but also a probability of 28% of a 7.4% increase in population size (1,611 wild boar) at the end of the modeled period (Fig 5A).

When combining both strategies, the number of harvested wild boar necessary to control the population decreased (200 juveniles and yearling wild boar, 50 from each sex within each age category) while the effectiveness increased, achieving a 100% probability of reducing the population size below 500 wild boar by the end of the study period. The rate of decreasing supplementary feeding determined the time to reach this target population size, five years for the idealistic option and thirteen years for the conservative option (Table 4, Fig 5B).

### Discussion

Our models established the combination of a reduction of supplementary feeding resources and the selective harvest of juveniles and yearlings as the most effective and efficient measures to control the CNP wild boar population and revert the increasing trend. The observed annual increase in wild boar abundance fell within the previous interval reported by [52] (r: 0.211, 0.56 times lower) and [15] (r: 0.742, 1.99 times higher), and our predictive models pointed that



**Fig 4. Effect of different parameters on wild boar population size according to the sensitivity tests.** Wild boar population size of Collserola Natural Park, Spain, decrease for every 10% change of each of the parameters tested (A, Hypothetical population threshold: Anthropogenic food resources availability K value (Hypothetical population threshold: Anthropogenic food resources availability); B, male mortality; C, female mortality; D, breeding; E, breeding females). Breeding is the mean percentage of wild boar that breed in a given year (\*, reference value).

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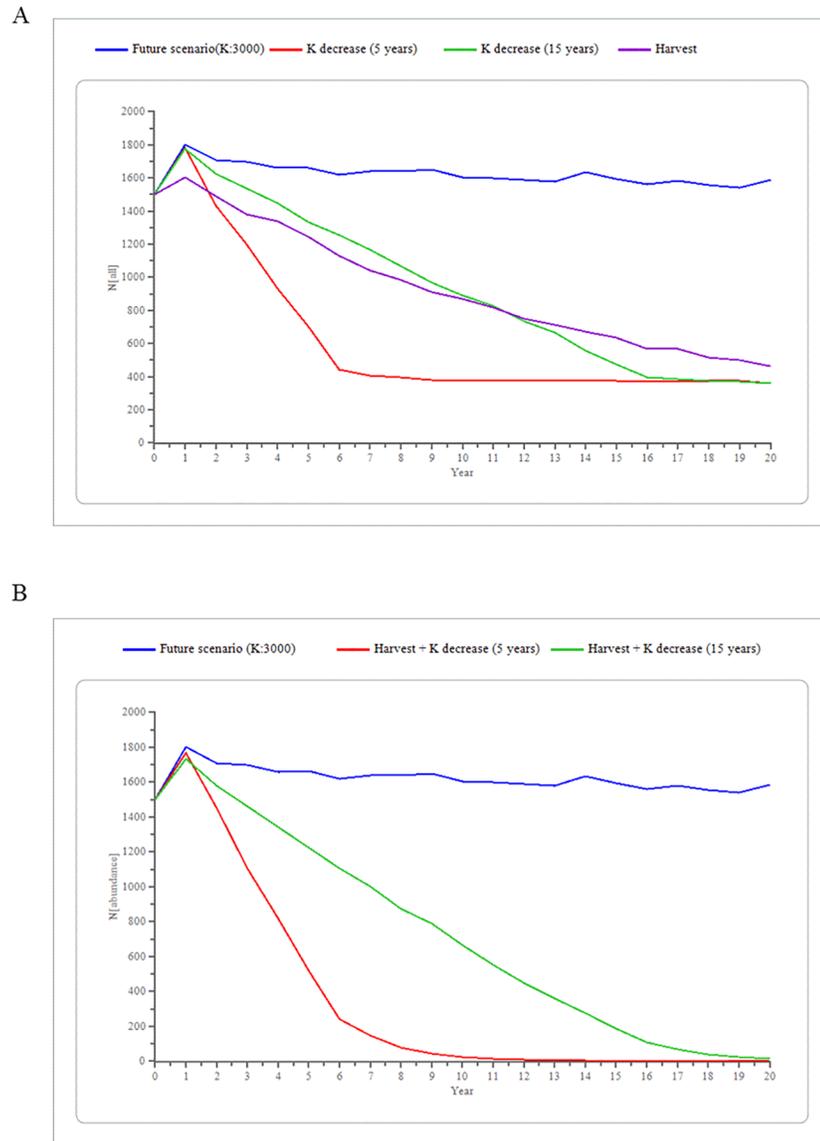
**Table 4. Evaluation of the management strategies assessed in the model.**

| Management strategy            | Effectiveness (success probability) | Years to reach target population size | Remaining abundance (N)            |
|--------------------------------|-------------------------------------|---------------------------------------|------------------------------------|
| Decrease supplementary feeding | 54 <sup>a</sup> -56 <sup>b</sup> %  | 6 <sup>a</sup> -15 <sup>b</sup>       | 626 <sup>a</sup> -636 <sup>b</sup> |
| Selective harvest              | 70%                                 | 20                                    | 1651                               |
| Combined                       | 100%                                | 5 <sup>a</sup> -10 <sup>b</sup>       | <501                               |

<sup>a</sup> Idealistic option (annual decrease of 15% during 5 years);

<sup>b</sup> Realistic option (annual decrease of 5% during 15 years).

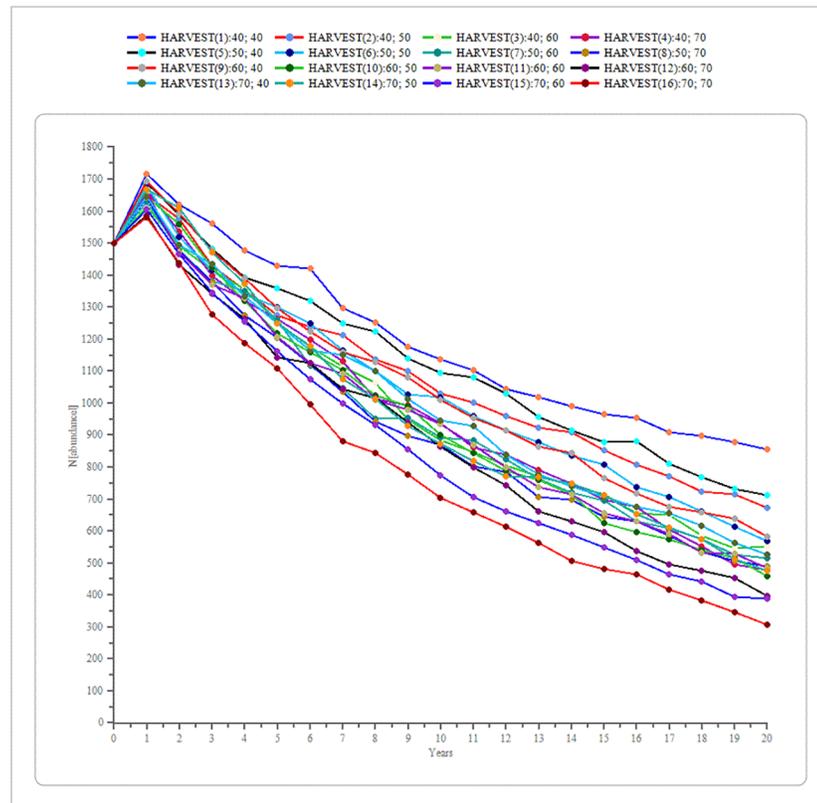
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**Fig 5. Predicted wild boar population trend under different management strategies.** Results of testing the management strategies for the wild boar population of Collserola Natural Park, Spain, in the future scenario show different effectiveness, was a) 80% for the idealistic option (annual decrease of 15% during 5 years), 86% for the realistic option (annual decrease of 5% during 15 years) for the decrease of anthropogenic food resources strategy and 72% for the Selective harvest strategy; and b) 100% for the Combined strategy.

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under the current conditions and management the CNP wild boar population will continue to increase. Since most of the demographic values used in this study (Table 2) fall within or were obtained from the previously reported intervals for other wild boar populations thriving in Mediterranean environments [36], the results and management applications obtained in our study could serve as a basis for other Mediterranean wild boar populations with supplementary feeding, either urban (e.g. rubbish, direct voluntary feeding, stray cat food) or agricultural (e.g. cereal, corn crops). However, since we used indices of relative abundance (hunting bags) producing high confidence intervals for wild boar population estimations (Table 1), our



**Fig 6. Effects of different harvest values.** Sensitivity test outcome showed the relationship between wild boar population size trend and the different harvest values, from 40 to 70 juveniles and yearlings of each sex in the Collserola Natural Park, Spain.

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models would gain accuracy by using more reliable wild boar abundance data, like those obtained through population counts.

The supplementary anthropogenic food resources available to wild boar in the peri-urban and urban areas surrounding and within the CNP has most probably increased CNP carrying capacity above the natural value [7,14]. Summer is the period with highest mortality of wild boar in Mediterranean populations due to the natural scarcity of food and water [43], but supplementary feeding, irrigated green areas and artificial fountains provide food, water and thermoregulation for wild boar, thus avoiding the natural constraints of foraging on demographic effect [52]. In the CNP population, the incidences in urban areas are mostly caused by juveniles and females with piglets in good nutritional conditions in summer [28], suggesting that the availability of anthropogenic resources in (peri-)urban areas compensate the aforementioned natural environmental constraints. This artificial food supply and the consequent reduction in mortality makes difficult the estimation of the real carrying capacity of CNP by direct methods.

Mediterranean wild boar populations consist predominantly of juveniles and yearlings, with high reproductive rates and high mortality in the first year of life [1]. Wild boar have one of the highest fecundity rate among ungulates under good conditions [53] and can even increase under strong hunting pressure, because of increased reproductive output of yearling females, which are recruited sooner and in a greater percentage [18,37]. Therefore, Mediterranean wild boar populations are characterized by intense responses to food availability and

weather conditions, resulting in sudden increases in numbers [39,44]. Under such conditions, generation time may be as low as two years, a value typically observed for rodents or passerine birds [18]. Population dynamics of wild boar population under favorable conditions seem rather typical for  $r$ , fast-life strategists or at an intermediate position along the capital–income continuum than for medium-sized ungulates [9,38, 49, 51,53,54]. Altogether, the supplementary food available and the capability of wild boar of exploiting these resources explain the increasing trend observed in the CNP wild boar population, and consequently the relevance of reducing such food resources to revert this trend.

The current hunting management strategy has not achieved a reduction in the CNP wild boar population increase, but maintains the CNP wild boar population approximately half (i.e. 1,500 individuals) of the HPT value (i.e. 3,000 individuals). Traditional battues focus on adult wild boar whose mortality has little if any impact on the demography of the CNP wild boar population, whereas our models point juveniles and yearlings as the age classes to target in order to achieve a significant reduction in the CNP wild boar population. The effect of yearling male mortality was low, but distinguishing male and female juvenile and yearling wild boar is rarely feasible when hunting Mediterranean bush environments. These results agree with previously reported results in other wild boar populations, where the sensitivity of juveniles and yearlings were higher under good environmental conditions [18,38,50], but are opposite to others where adult survival had the highest sensitivity in a growing population [15]. This higher effect of juvenile and yearling mortality on population dynamics is likely related to the increased offspring production, piglet survival and population recruitment due to the overabundance of anthropogenic resources in CNP and the AMB.

Decreasing the percentage of breeding females did not seem a feasible target for reducing the CNP wild boar population, since it would be necessary to restrain the percentage of adult breeding females below 30% in order to appreciate significant effects on the population size. Future approaches to fertility control achieved through feeding may be able to target a much higher proportion of the population for a given effort, thus making fertility control a feasible option in restricted areas such as urban or protected areas (i.e. National parks).

When assessing the most efficient and effective measures to reduce the CNP wild boar population selected by the models, decreasing CNP supplementary anthropogenic resources modified both HPT (K value in VORTEX model) and mortality rates for all age classes (being therefore less specific). On the other hand, selective harvest had a strong effect on the mortality rate of specific age classes. Considering each management strategy separately, decreasing supplementary anthropogenic food resources has the strongest total effect, whereas selective harvesting is more effective and easier to implement, although reducing juvenile and yearling population might be more challenging than reducing adult wild boar population. However, the combination of both strategies reached 100% of effectiveness in achieving the management objectives (Table 3) and decreased the number of harvested wild boar required to control the population growth.

The agreement between the modeled and the estimated wild boar population trend from 2000 to 2015 indicated that the model was at least one of the possible explanations and that the carrying capacity, mortality and breeding rates used were reasonable. Our study showed the utility of PVA models as a species control management tool, for indirectly determining carrying capacity through the analysis of past scenarios, predicting population trend, and testing and targeting the sensitivity of biological variables and management strategies. This allows to design efficient and effective management plans prior to undertaking any action, increasing the effectiveness of management efforts through saving money and resources under the usually limited budgets. Though the final evaluation of the application of the results will require budgeting of the management actions, this was beyond the objective of the present study. That

cost depends on the area and hence budget must be individually quantified for every particular context and management. PVA has also limitations, such as being usually focused on a single species, needing more data than other methods and, in many circumstances, the wide confidence limits of the estimates of extinction time produce meaningless results, unless used to compare the relative values of different management strategies [21,22].

## Conclusions

The combination of decreasing carrying capacity by reducing supplementary food and focusing the harvest effort on the demographically most relevant age categories (i.e., juveniles and yearlings) revealed as the most efficient management strategy to control an increasing wild boar population in a Mediterranean periurban environment with supplementary food over the natural resources. These strategies will probably be also the most efficient ones in other over supplemented increasing wild boar populations in similar situations, although studies should be carried out in a case by case basis in order to fine-tune the best management option and their specific efficacy and efficiency in each context.

Decreasing supplementary feeding involves natural, environmental and social factors. Management efforts should focus on (1) voluntary feeding control; (2) stray cat food; (3) waste collection; and (4) management of green areas in the CNP and its surroundings, including urban green spaces. Increasing night waits under special permits would allow targeting the vulnerable life stages, since they are more selective and efficient than traditional battues [55,56]. The capture of juveniles and yearlings wild boar using specially designed traps could also be an alternative option.

Our PVA allowed the prediction of the future trend of the CNP wild boar population under the current environmental conditions and management, validated by the agreement with the population trend observed in the past. Moreover, PVA also assessed the efficacy and efficiency of potential management strategies previously to their implementation, saving efforts and money by identifying those with more potential impact on the CNP wild boar population. This approach can be useful in other populations and scenarios not only for wild boar, but as a previous step before implementing management measures also for any other species.

## Supporting information

**S1 Table. Vortex functions.** Harvest and breeding functions used in the model of the Collserola Natural Park wild boar population.  
(PDF)

**S2 Table. Hunting data.** Wild boar captured, hunted or found dead from 2000 to 2015, used to calculate population and specific sex and age classes relative abundances and mortality rates.  
(XLSX)

**S1 Fig. Urban wild boar.** Wild boar population in the study area habituated to humans showing A) indirect and B) direct feeding from anthropogenic resources.  
(PDF)

**S2 Fig. Relationship between Hypothetical Population Threshold (HPT) and wild boar population trend.** Sensitivity test outcome of the Hypothetical Population Threshold (HPT): Supplementary feeding availability (K value in VORTEX model), showed a total variation in the Collserola Natural Park wild boar population size of 3,820 individuals and an effect of

9.96%. Each line represents the population projection for the different HPT values (from 500 to 6500, increasing by 500).

(PDF)

**S3 Fig. Relationship between mortality and wild boar population trend.** Sensitivity test outcome for the mortality rates of the wild boar population of Collserola Natural park (showed different values in variation in population size and effect for Juvenile a) males and b) females (2,000; 5.75%), Yearling c) males and d) females, and Adult e) males and f) females. Each line represents the population projection for the different mortality values (from 0% to 100%, increasing by 10%).

(PDF)

**S4 Fig. Relationship between fertility and wild boar population trend.** Sensitivity test outcome for the fertility rates showed different values in variation in the Collserola Natural Park wild boar population size and effect for a) males and b) females, c) Juvenile females, d) Yearling females, and e) Adult females. Each line represents the population projection for the different breeding values (from 0% to 100%, increasing by 10%).

(PDF)

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## Author Contributions

**Conceptualization:** Carlos González-Crespo, Emmanuel Serrano, José María López-Martín, Santiago Lavín, Jorge Ramón López-Olvera.

**Data curation:** Seán Cahill, Lluís Cabañeros, Joan Roldán.

**Formal analysis:** Carlos González-Crespo, Emmanuel Serrano, Seán Cahill, Raquel Castillo-Contreras, José María López-Martín, Jorge Ramón López-Olvera.

**Funding acquisition:** Santiago Lavín, Jorge Ramón López-Olvera.

**Investigation:** Carlos González-Crespo, Emmanuel Serrano, Raquel Castillo-Contreras, Jorge Ramón López-Olvera.

**Methodology:** Carlos González-Crespo, Emmanuel Serrano, Raquel Castillo-Contreras, José María López-Martín, Jorge Ramón López-Olvera.

**Supervision:** Emmanuel Serrano, Lluís Cabañeros, Santiago Lavín, Jorge Ramón López-Olvera.

**Writing – original draft:** Carlos González-Crespo, Jorge Ramón López-Olvera.

**Writing – review & editing:** Carlos González-Crespo, Emmanuel Serrano, Seán Cahill, Raquel Castillo-Contreras, Lluís Cabañeros, José María López-Martín, Santiago Lavín, Jorge Ramón López-Olvera.

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