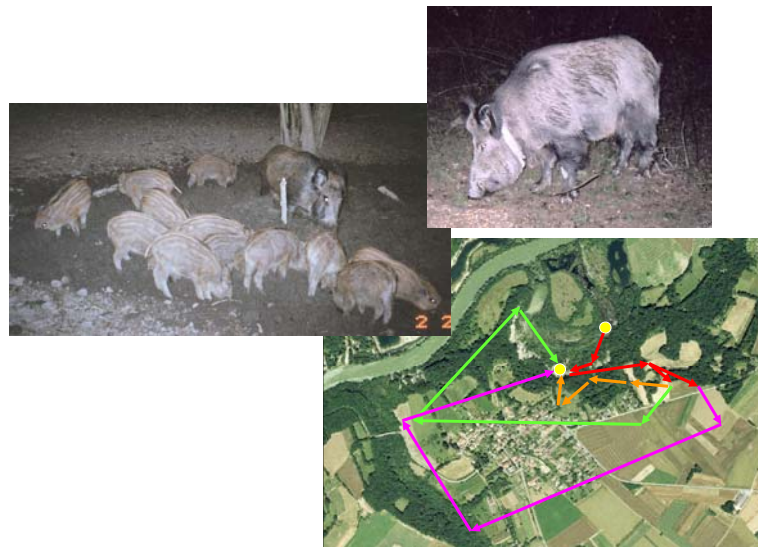


Population size, density and dynamics, and social organization of wild boar (*Sus scrofa*) in the Basin of Geneva



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Thesis presented the 26th November 2007 in presence of

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Population size, density and dynamics, and
social organization of wild boar (*Sus scrofa*)
in the Basin of Geneva

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ABSTRACT

Growing wildlife populations and their interactions with humans became important in the last decades, and raised concern about science-based management. Various intrinsic (sex, age, reproductive status) and extrinsic (habitat, climate, food resources, harvest) factors are likely to act upon a population at any considered scale, and therefore data should be collected over longer periods, as environmental conditions were shown to affect populations differently depending on sex and age structure, so as to help in management decisions. Given their adaptability to various environments, omnivorous diet and high fertility, the wild boar (*Sus scrofa*) has increased both its distribution range and local densities in the last decades, and adapted well where it had been introduced. As a consequence, conflicts with humans, mainly due to damages to agricultural crops, increased and required a lot of attention from wildlife managers. Increased damages and hunting bags were also recorded all over the Basin of Geneva from the end of the 20th century. Consequently, wildlife managers in the concerned administrative regions (Department Ain and Haute-Savoie and Cantons Vaud and Geneva) started a trans-border project on wild boar to gather new data and share their respective experiences in order to develop a concerted management of this particular species.

The present study is part of the aforementioned project, and aimed *i*) to adapt counting methods to estimate population size and density, *ii*) to assess the population dynamics and the effect of the management strategy, and *iii*) to describe the social organization of wild boar. The data concerning the first two aims were collected in the Canton of Geneva, while the last subject used data from the entire Basin. Field work provided most of the data using captures and marking of wild boars, radio-tracking and photo-trapping. Additional data on shot or killed individuals was provided by official game wardens and hunters.

Our study provided the following results: *i*) The densities recorded in the Canton of Geneva were among the highest reported in Europe, and wild boar proved to be able to find optimal environmental conditions even at a small scale and in a region characterized by small forests and intensive urbanization; *ii*) Current management appeared to be inappropriate to reduce population size, as the consequent application of the shooting rules favoured the survival of the older individuals. Given the favourable environmental conditions and the maintenance of the most productive individuals, the population appeared to be very dynamic and losses due to culling were rapidly compensated each year; *iii*) The social organization of wild boar was

dynamic and associations were evident during the day and more variable at night, in all type of groupings. Reported variations are likely to be influenced by kinship as well as environmental conditions.

RESUME

Le développement de la faune sauvage ainsi que l'augmentation de ses interactions avec les activités humaines observées durant les dernières décennies ont favorisé le développement d'une gestion fondée sur des données scientifiques. Etant donnée la diversité des facteurs intrinsèques (sexe, âge, reproduction) et extrinsèques (habitat, climat, ressources alimentaires, chasse) susceptibles d'agir sur une population à n'importe quelle échelle, la récolte de données devrait considérer ces facteurs et s'étendre sur le long terme, afin de fournir des applications utiles aux gestionnaires. Le sanglier (*Sus scrofa*) fait preuve d'une remarquable adaptabilité à des environnements variés, présente un régime omnivore et une fertilité élevée. Ainsi, les densités locales et l'aire de distribution de cette espèce ont augmentés au cours des dernières années, et le sanglier s'est également bien établi dans les zones où il fut introduit. En conséquence, les conflits avec l'homme, résultant principalement des dégâts aux cultures, ont retenus l'attention des gestionnaires. Un accroissement simultané des tableaux de chasse et des dégâts aux cultures a également été observé dans le bassin genevois dès la fin du 20^{ème} siècle. Afin de faire face à cette situation, les gestionnaires des régions concernées (les départements de l'Ain et de la Haute-Savoie et les cantons de Vaud et Genève) se sont associés dans un projet transfrontalier. Le but de cette collaboration étant de partager leurs expériences respectives et de collecter de nouvelles données, afin d'aboutir à une gestion concertée de l'espèce au niveau du bassin genevois.

Ce travail s'inscrit dans le cadre du projet transfrontalier, et visait *i*) à adapter des méthodes de dénombrement afin de déterminer la taille de la population et sa densité, *ii*) à comprendre la dynamique de population et l'effet de la gestion sur celle-ci, *iii*) et à décrire l'organisation sociale du sanglier dans le bassin genevois. Les données concernant les deux premiers sujets ont été récoltées principalement sur le canton de Genève, alors que le dernier sujet utilise des données couvrant tout le bassin. La capture, le marquage, le suivi télémétrique et les sessions de piègeage-photo réalisés sur le terrain constituent la principale source de données du présent travail. Les données additionnelles concernant les animaux tirés ou ayant périés proviennent des gardes faunes et des chasseurs.

Les résultats suivants ont été relevés : *i*) Les densités mesurées dans le canton de Genève sont parmi les plus élevées relevées en Europe. Le sanglier a donc su trouver des conditions environnementales favorable à son développement, même dans une région présentant des

surfaces boisées réduites et une urbanisation importante ; *ii*) La gestion actuelle se révèle inappropriée concernant la réduction des effectifs, étant donné que l'application actuelle des consignes de tir favorise la survie des animaux les plus âgées. L'effet conjoint de conditions favorables et du maintien des individus les plus productifs, en termes de reproduction, a favorisé l'établissement d'une population dynamique dans laquelle les pertes causées par les tirs de régulation sont facilement compensées d'une année à l'autre ; *iii*) Enfin, l'organisation sociale du sanglier s'est également avérée très dynamique, avec des associations importantes et stables de jour et beaucoup plus variables de nuit. Les variations observées sont probablement autant influencées par les liens de parenté que par des facteurs écologiques.

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INTRODUCTION

Many aspects of wildlife management have raised growing attention of scientists in the last decades, with respect to growing and expanding population, conflicts and interactions with human activity, sustainable harvest and conservation (eg. Bobek et al. 1991;1992). Wildlife populations are exposed to variable intra-population and environmental parameters, which often result in subtle mechanisms that require rigorous monitoring to be detected and understood (Milner et al. 2007). Demographic age and sex structure of any population is important to be assessed, as variations in population density and environmental conditions were shown to affect a population as a function of this structure (Coulson et al. 2001), even at a small scale (Coulson et al. 1999). The same characteristics apply in harvested populations as well, and their management requires therefore comparable science-based approach (Gordon et al. 2004), all the more these populations are exposed to numerous side effects which affect their dynamics, due to the selective removal of individuals (Milner et al. 2007). Ideally, harvest should reproduce natural survival patterns to minimize those side effects (Milner et al. 2007). In ungulates, adults usually display high and stable survival while juveniles tend to have lower and variable survival (Gaillard et al. 1998), and considering those differences and variations has been shown to implement management (Raithel et al. 2007). However survival patterns in harvested population are often different from those under natural conditions (Ginsberg and Milner-Gulland 1994, Solberg et al. 2000), as cultural aspects and hunting traditions also contribute to shape the composition of harvest bags (Milner et al. 2006). As an example of implication of cultural aspects, in red deer (*Cervus elaphus*) males are selectively more hunted than females, and therefore, female populations tend to become important. As an ecological consequence, the mortality and dispersal rates among males increase, and contribute even more to the male's scarcity. Consequently, even though males provide more appreciated trophies and thus contribute to important income, more females should be culled to turn the situation up (Clutton-Brock et al. 2002, Milner-Gulland et al. 2004). That said, side effects caused by harvest do not necessarily lead to population crashes, as the roles in the population dynamics of culled individuals can be taken over by the surviving ones. Thus, in moose (*Alces alces*), young males participated to reproduction instead of the killed adults and compensated their selective harvesting (Laurian et al. 2000), and subadult wild boar increased their participation to reproduction when harvest induced a lowered adult population (Massolo and Mazzoni della Stella 2006). Similarly, increasing wildlife stocks are not only linked to inappropriate harvest, but are likely to be influenced by decreasing food competition and

favourable weather conditions (Clutton-Brock et al. 2004) or reduced competition with livestock (Madhusudan 2004). Management decisions, in terms of a trade-off between sustainable harvest and efficient population control, can be encouraged by modelling approaches if the demographic structure is well known. Whatever the pursued aim might be, maintaining a population under its carrying capacity or maximizing harvest, the precision of the model is dependent on the accuracy of the data, and its outcome or feasibility might vary as a function of the harvest capacity (Hauser et al. 2006a, Hauser et al. 2007). However, monitoring a population might be time-consuming and costly (Hauser et al. 2006b), and gathering data on the demographic structure might not always be possible. As environmental factors play an important role in a species' ecology, indicators of ecological changes might provide a useful tool as well to assess population trends and set management issues (Morellet et al. 2007). Interactions between wildlife and human activities also raised problems in terms of damage to livestock (Woodroffe and Frank 2005, Woodroffe et al. 2005), agricultural crops (Goryńska 1981, Schley and Roper 2003) and natural environment (Power Bratton 1975, Clutton-Brock et al. 2004). Those conflicts can partly be solved by reducing the contact between wildlife and humans and by maintaining natural habitats (Mace and Waller 1998, Woodroffe et al. 2005). In other cases, harvest remains an efficient mean to control population size and reduce damages significantly (Geisser and Reyer 2004, Woodroffe and Frank 2005).

Global study : « Projet transfrontalier de marquage et suivis télémétriques de sangliers dans le bassin genevois »

During the last decade, the big game managers in the Basin of Geneva (Departments Ain and Haute-Savoie, and Cantons of Geneva and Vaud) had to face substantial increase of wild boar damage to agricultural crops, and regrouped to share their observations and experiences (Fig. 1). Issues about population trends and wild boar movements appeared to require focused and coordinated research, and raised a joint research program in 2002. One year later, a convention between the Hunters' Federation of Ain and Haute-Savoie and the Offices in charge of the fauna in the Cantons of Geneva and Vaud was signed, with the support of the French National Wildlife and Hunting Office (ONCFS; CNERA cervidés et sangliers) and the Swiss Federal Office for the Environment (OFEV, Programme Wildman).

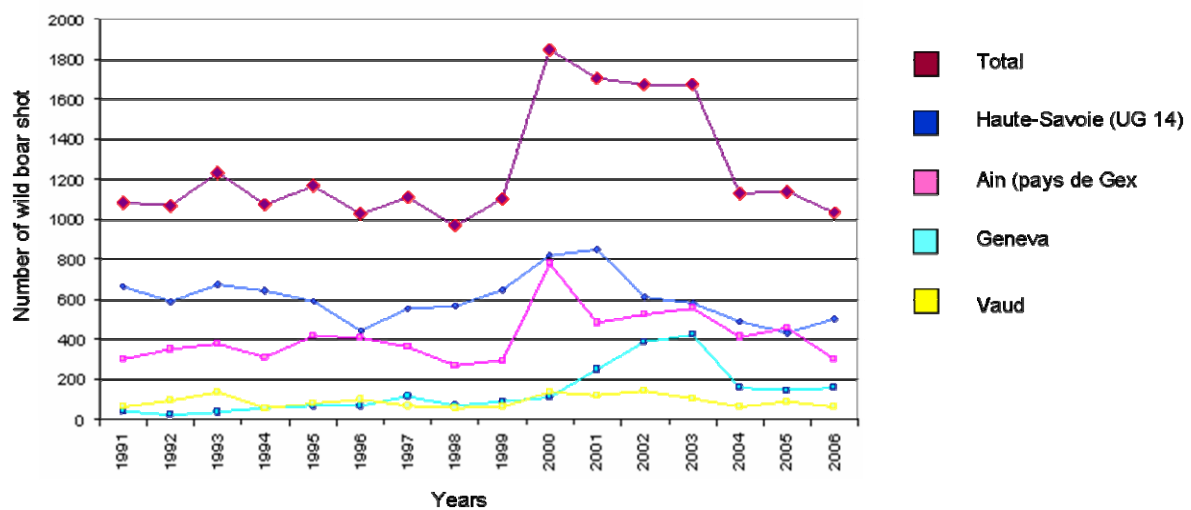


Figure 1: Number of wild boar shot in the study area from 1991 to 2006.

This convention was completed by a technical document which specified the applied methods, aims and hypotheses. Wild boar were captured in maize-baited life-traps, and marked with colour-coded and individually numbered ear-tags. Individuals were additionally fit with transmitters to enable radio-tracking. The main data consists therefore in capture-recaptures, radio-tracking locations and recoveries of shot animals. The research was focused on several purposes: 1) Spatial behaviour, 2) Diurnal resting places, 3) Group composition and stability, 4) Influence of prevention methods on spatial behaviour, 5) Population size estimates, 6) Influence of non-hunted areas on spatial behaviour, 7) Impact of urbanization, 8) Evaluation of applied methods and 9) Ecological factors as predictive indicators. In 2005, an intermediate report summarized the information of the first three years of the study and proposed guideline for the following years.

The field work has been coordinated and conducted by scientists (biologists, PhD and Ms students) in collaboration with game wardens, hunters, technicians and volunteers. Three Master thesis already investigated aspects of the demography and space use (Fattebert 2005) and diet and efficiency of supplemental feeding (Berger 2006). Less consequent reports have been written and were presented to the members of the project regularly, and a PhD thesis will investigate the effect of non-hunted areas on the spatial behaviour of wild boar.

The present PhD thesis has been divided in three chapters presented in a manuscript format, as they are or will be submitted for publication. All chapters have been written in collaboration with the two biologists which coordinated the scientific research in the global study; Dr. Eric Baubet and Claude Fischer.

Study organism

The wild boar (*Sus scrofa*) is probably the most widespread ungulate (*Artiodactyla*), as its native range extends over most of Eurasia, including North Africa's Atlas Mountains, from Portugal to Japan and Indonesia (Macdonald and Barrett 1995, Étienne 2003). The wild boar was carried to extinction on the British Islands, Ireland and Scandinavia in the last centuries. However in Britain and Sweden, wild boar farming became popular in the 20th century and wild populations established after successful escapes. Consequently, the wild boar is now again considered as part of these countries' fauna (Goulding 2001, Truvé 2004). Furthermore, this species has been successfully introduced in several regions around the world; *eg.* Northern America (Singer et al. 1981, Waithmann et al. 1999), South America (Herrero and Fernandez De Luco 2003), Australia (Heise-Pavlov and Heise-Pavlov 2003), Malaysia (Ickes 2001).



Figure 2: The distribution range of wild boar.

The wild boar has adapted to a wide variety of habitats, from semi-arid environment (Gabor et al. 1999) to tropical forests (Ickes 2001). Nevertheless, landscape structure and diversity were shown to affect their distribution, as the accessibility to water, food resources and shelters are determinant factors of habitat selection (Étienne 2003, Acevedo et al. 2006). Resting sites are preferably located in areas with dense cover and undergrowth to maximise the security (Cargnelutti et al. 1995). Although security remains important, habitat selection is also affected by food resources (Spitz and Janeau 1995). Wild boar are mainly nocturnal (Boitani et al. 1994, Cahill et al. 2003) but the diurnal activity can become gradually important in conditions of food shortage or little human disturbance (Russo et al. 1997).

Wild boar are opportunistic omnivores, as their diet is determined by the availability of various food types, including agricultural crops (Schley and Roper 2003). While adult males are solitary, females live in social family groups with overlapping generations (Kaminski et al. 2005). The breeding ecology is characterized by multiple litters (Servanty et al. 2007) and early onset of puberty (Mauget and Pépin 1991). The mean litter size and the participation of

females to reproduction varies along with environmental conditions (Fernandez-Llario and Mateos-Quesada 2005, Santos et al. 2006). Population densities were reported to vary from 10 to 0.01 individuals per km² in western Eurasia, and populations were expected to increase locally and expand their range in response to global warming (Melis et al. 2006).

Given these features, conflicts with humans became important in the last decades, and raised concern for the species management. However, as the wild boar is an appreciated game species and therefore represents an important source of income, its management has to be balanced against sustainable harvest (Hauser et al. 2007). Although damages can be reduced or limited efficiently with other methods (Calenge et al. 2004), the culling (by hunters or game wardens) still proved to be the most effective (Geisser and Reyer 2004). Additionally, hunting bags

still constitute an important source of data (Merli and Meriggi 2006). Hunting activities were reported to have a temporal effect on the spatial activity and habitat use, rather than on dispersal or home range (Sodeikat and Pohlmeier 2002). Nevertheless, hunting techniques have to be adapted to the local conditions (demography and habitat) as they will influence the management efficiency (Fernandez-Llario et al. 2003, Massolo and Mazzoni della Stella 2006).

Study area

The Basin of Geneva is at the far western tip of Switzerland and Lake Geneva (46°06' - 46°24' N, 5°54' - 6°10' E) with the city of Geneva in its centre. The Basin is delineated by wooded mountains that reach an elevation of 1,600 m. The Jura Mountains form the north-western boundaries along with the Vuache, and the Voirons and Salève form the south-eastern boundaries of the Basin (Fig. 4). The lowlands (between 350 and 600 masl) are a mosaic of cultivated land, scattered woods and extensive urbanisation, and host over 500,000 people within 680 km². Beneath the Rhône River, many smaller streams flow along the Basin. Extensive road networks constrain the movements of the local fauna. In the mountains, forests are dominated by beech (*Fagus sylvatica*), Silver fir (*Abies alba*) and Norway spruce (*Picea abies*) while the lowlands are dominated by deciduous oak stands (*Quercus sp.*) (Steiger



Figure 3: Adult male (top), adult female with piglets, juveniles (bottom).

1995, Delarze et al. 1998). In the lowlands, the climate is temperate with an average temperature of 9.8°C, varying from -1°C in January to 19°C in July. Annual precipitation averages 822 mm and is evenly spread throughout the year (<http://www.meteosuisse.ch>). The Basin of Geneva is spread over 2 countries, Switzerland and France, and 4 administrative sectors. On the French side, the Departments Ain and Haute-Savoie are separated by the Rhône River. On the Swiss side, the study area covers most of the Canton of Geneva, and the western tip of the Canton of Vaud.

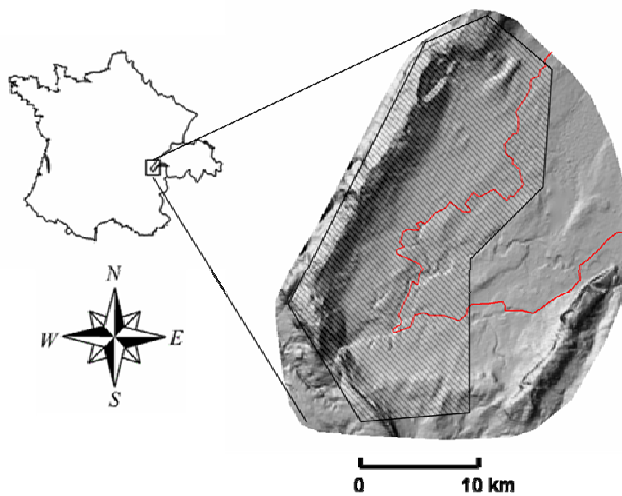


Figure 4: Location of the study area. Most of the research, especially captures and radio-tracking, were conducted in the hatched area. Red lines indicate the Swiss border.

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CHAPTER 1

Estimating wild boar (*Sus scrofa*) abundance and density using capture-resights in Canton of Geneva, Switzerland.

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Estimating wild boar (*Sus scrofa*) abundance and density using capture–resights in Canton of Geneva, Switzerland

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Abstract We estimated wild boar abundance and density using capture–resight methods in the western part of the Canton of Geneva (Switzerland) in the early summer from 2004 to 2006. Ear-tag numbers and transmitter frequencies enabled us to identify individuals during each of the counting sessions. We used resights generated by self-triggered camera traps as recaptures. Program Noremark provided Minta–Mangel and Bowden’s estimators to assess the size of the marked population. The minimum numbers of wild boars belonging to the unmarked population (juveniles and/or piglets) were added to the respective estimates to assess total population size. Over the 3 years, both estimators showed a stable population with a slight diminishing tendency. We used mean home range size determined by telemetry to assess the sampled areas and densities. Mean wild boar population densities calculated were 10.6 indi-

viduals/km²±0.8 standard deviation (SD) and 10.0 ind/km²±0.6 SD with both estimators, respectively, and are among the highest reported from Western Europe. Because of the low proportion of marked animals and, to a lesser extent, of technical failures, our estimates showed poor precision, although they displayed similar population trends compared to the culling bag statistics. Reported densities were consistent with the ecological conditions of the study area.

Keywords Noremark · Minta–Mangel · Bowden · Radio-tracking · Culling bag

Introduction

The population dynamics of a given species is known to be influenced by biological and ecological parameters (Coulson et al. 2001). Long-term data on density, age and sex structure, and ecological parameters enhance wildlife management (Clutton-Brock et al. 2004), but managers still need simpler data to allow a quick decision-making process (Hauser et al. 2006). Thus, population size and density estimates are commonly used as a basic indicator in wildlife management and conservation (Seber 1982; Hauser et al. 2007; Morley and van Aarde 2007). Estimates that depend on indirect indices of presence can be used to minimize interactions with the animals. However, these indices must be directly proportional to population density to enable comparison in space and time (Nichols 1992; Pollock et al. 2002), a condition rarely met in changing environmental conditions. Capture–mark–recapture (CMR) methods (Otis et al. 1978; Seber 1982; Pollock et al. 1990; Nichols 1992; Schwarz and Seber 1999; Pollock et al. 2002) are commonly used to estimate population size, although the trapping itself may bias the estimate. The sample size can

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be small if the trapping is not efficient, and probabilities of capture–recapture can vary among the population (Pollock et al. 1990; Nichols 1992; MacKenzie et al. 2005). To partially minimize the effects of trapping, the resight of an animal can be considered as its actual recapture (Minta and Mangel 1989; Nichols 1992; Bowden and Kufeld 1995; White 1996; Schwarz and Seber 1999). Capture–resight (CR) models either depend on direct reobservations [e.g., lion *Panthera leo* (Castley et al. 2002), brown bear *Ursus arctos* and black bear *U. amercianus* (Miller et al. 1997), coyote *Canis latrans* (Hein and Andelt 1995), or elephant *Loxodonta africana* (Morley and van Aarde 2007)] or pictures taken by self-triggered camera traps [e.g., grizzly bear *U. arctos horribilis* (Mace et al. 1994), lynx *Lynx lynx* (Zimmermann et al. 2005), jaguar *P. onca* (Silver et al. 2004), or tiger *P. tigris* (Karanth et al. 2004)]. Unambiguous natural marks, such as fur patterns (Karanth 1995; Karanth and Nichols 1998), are often used to identify the sighted animals and establish their capture history (Otis et al. 1978). In such cases, artificial marking is unnecessary.

Wild boar (*Sus scrofa* L., 1758) are well known to be difficult to count at an absolute level because of their mainly nocturnal activity and preference for wooded habitats (Boitani et al. 1994; Russo et al. 1997; Fattebert 2005) that limits observation. Consequently, most wild boar population size or density estimates have used relative indices of abundance rather than direct observations or counts. Most depend on hunting or culling statistics (Waithmann et al. 1999; Geisser and Reyer 2005; Acevedo et al. 2006; Melis et al. 2006; Merli and Meriggi 2006), catch per unit effort (Boitani et al. 1995b), or sampling of activity signs (Alpe 1995; Okarma et al. 1995; Massei et al. 1998). Few studies have used the statistical framework of CMR methods to estimate wild boar populations through live recapture (Andrzejewski and Jezierski 1978) or recoveries of hunted animals (Gabor et al. 1999). More recently, Fickel and Hohmann (2006) examined the use of genetics on hair and scat samples to identify wild boar. Only Sweitzer et al. (2000) used photographic resights of naturally marked wild pigs *S. scrofa* in California for CR analysis. However, individual recognition is not guaranteed in European free-ranging wild boar, which lack distinctive individual features. Considering this, animals have to be captured and marked, and capture histories of unmarked individuals will be missing. Consequently, estimators that only consider capture histories of marked animals should be used.

Wild boar populations have dramatically increased across Europe during the last decades (Sàez-Royuela and Telleria 1986; Boitani et al. 1995a; Schley et al. 1998; Fonseca et al. 2004; Klein et al. 2004; Geisser and Reyer 2005). As a consequence, crop damage is a growing problem, bringing concerns with respect to the control of boar numbers. As similar problems arose in the Basin of

Geneva, a cross-border project started in 2002 (Fischer et al. 2004b; Fattebert 2005). The aim of the project was to capture, mark, and radio-track wild boar, so as to improve the knowledge about the ecology of the species and its management at a biogeographically relevant basin scale. As a part of this project, we aimed to determine population size and density in the western part of the Canton of Geneva (Switzerland), where most of the damage occurs and the majority of wild boar is culled. We adapted CR methods to estimate the population size of free-living wild boar after the main farrowing period and before the beginning of the culling season. Then, we compared our estimates to the culling bag statistics, which was the only kind of data previously available in our study area to assess wild boar population trends. We go on to discuss the limits and reliability of our counting method and calculated densities.

Materials and methods

Study area

The Canton of Geneva, which lies entirely within the Basin of Geneva, is located at the western tip of Switzerland (Fig. 1). The Canton covers an area of 240 km² and hosts 400,000 people. Natural predators of wild boar are absent, and hunting was abolished after a public vote in 1974. The sample region is located in the western part of the canton in an area covering 66 km² (46°09.6′–46°13.7′N, 5°57.2′–6°03.9′E; Fig. 1). Elevation ranges from 350 to 470 m a.s.l. The climate is temperate with an average temperature of 9.8°C, varying from –1°C in January to 19°C in July. Annual precipitation averages 822 mm and is evenly spread throughout the year (<http://www.meteosuisse.ch>). Cultivated areas, mainly vineyards and cereal crops, cover 65% of the study area. Forests cover 20% of the area and are mainly distributed along the rivers or scattered in small patches, often not exceeding 1 ha in size. Deciduous oaks (*Quercus* sp.) are the dominant trees (Steiger 1995; Delarze et al. 1998) and might produce substantial amounts of mast in autumn and winter. Two main rivers, easily crossed by wild boar, pass through the area, the Rhône River (E–W) and the smaller Allondon River (N–S). The banks of the Allondon River are part of an active alluvial zone. Willows (*Salix* sp.), alders (*Alnus* sp.), and ash (*Fraxinus excelsior*) are present at the flooded areas and along the riverbanks (Delarze et al. 1998). Villages, roads, farms, and other buildings account for 15% of the surface.

Capture and marking

Animals were captured from 2002 to 2005 in live-traps baited with maize (Fischer et al. 2004b). All captured

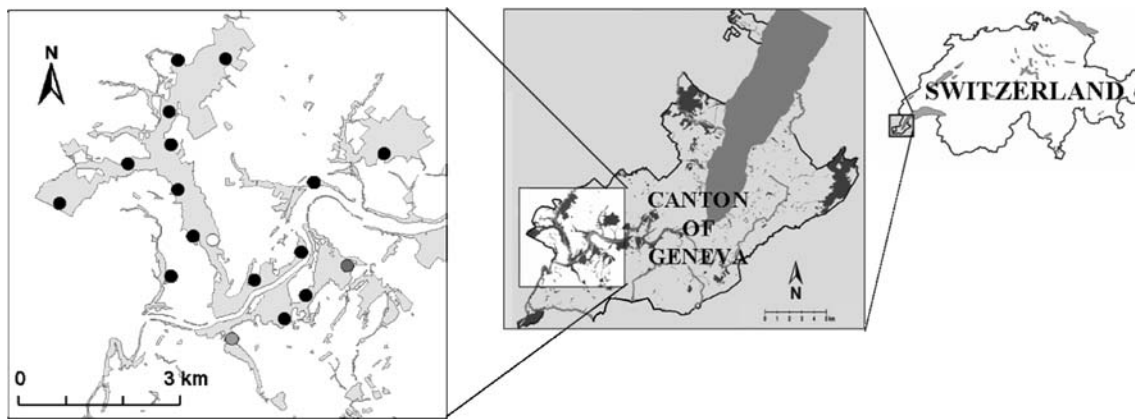


Fig. 1 Location of the Canton of Geneva and the study area. *Left map* Counting sites used throughout the study (*black spots*), only in 2004 (*dark gray spot*), in 2004 and 2005 (*gray spot*), and only in 2006

(*white spot*) are displayed. *Light gray patches* on the left map represent forests and wooded patches

animals were fitted with uniquely numbered yellow cattle ear-tags and assigned to one of four age categories according to their estimated weight and coat color. Piglets are striped coat, weighing less than 20 kg, and generally, up to 4 to 6 months old. Juveniles are reddish coat, weighing 20 to 40 kg, and generally, 6 to 12 months old. Subadults are black coat, weighing more than 40 kg, between 12–24 months old, looking smaller than adults. Adults are black or silver coat, looking big and heavy, and generally, weighing more than 60 kg (Dardaillon 1988; Fernandez-Llario and Carranza 2000; Santos et al. 2006). Fully-grown individuals were fitted with fixed radio-collars (ATS, USA). Other individuals were fitted with Televilt® transmitters (TVP Positioning AB, Sweden) adjusted in extensible collars developed by the ONCFS (Brandt et al. 2004) or ear transmitters (Biotrack®, UK). After handling, all were released at their capture site.

In 2004, only subadults and adults were marked with transmitters. Since 2005, to enlarge the marked fraction of the population, juveniles were also fitted with transmitters or special ear tags. These special tags (S05) were similar to the simple ear tags described above but with a stripe of red reflecting foil glued on it to allow identification. Thus, the marked population, i.e., all animals belonging to the same age classes as marked animals, considered in our counting sessions was made up of only subadults and adults in 2004, and juveniles, subadults, and adults in the two following years.

Resights

Resights were obtained through phototrapping sessions in early June in 2004, 2005, and 2006 for a period of four to six consecutive nights. Up to 18 different counting sites were used throughout the three counting sessions (Fig. 1). Most of the counting sites ($N=13$) were already used for trapping. However, no trapping was carried out at these sites during baiting and counting sessions. Other sites ($N=5$)

were selected according to presence indices and suitability for access and camera-trap installation. Before each session, the selected sites were baited with maize every second day for 1–2 weeks and checked for wild boar presence. During the counting sessions, all sites were checked and rebaited daily. All sites (except for two in 2004) were fitted with infrared motion-detecting cameras (CamTrakker®, CamTrak South, USA, and “Bandgenossenschaft Bern”, KORA, Switzerland). The minimum time delay between two successive photos was set to 20 min. Each wild boar on a photograph, either marked or unmarked, was considered as one sighting. In 2004, the two sites without camera traps were surveyed by observers at sunset. Time and kind of observation was noted, and this information was treated as if it had been generated by camera traps. To test the potential impact of sampling method variation, we calculated potential and effective sampling effort. Potential sampling effort considered all sites that were surveyed during a session and, so, could have produced sightings, multiplied by the total sampling nights. Effective sampling effort accounted for technical failures, thus, only considering the sites that really provided sightings.

For each counting session, we determined the number of marked boars (N_k) known to be present at the study area, i.e., the fraction of the marked population present. The presence of individuals with transmitters was checked by radio-tracking. S05-marked boars were eliminated from the marked population if (1) they were known to be dead or (2) they were subadult males at the time of the counting sessions, assuming that subadult males would have dispersed out of the study area (Truvé 2004). On the counting sites, individuals with transmitters were identified by radio tracking, whereas animals with S05 marks were identified visually.

We determined the number of marked individuals actually seen and identified on the counting sites (n_k), and the total number of sightings generated by marked (S_k) and unmarked animals (S_u).

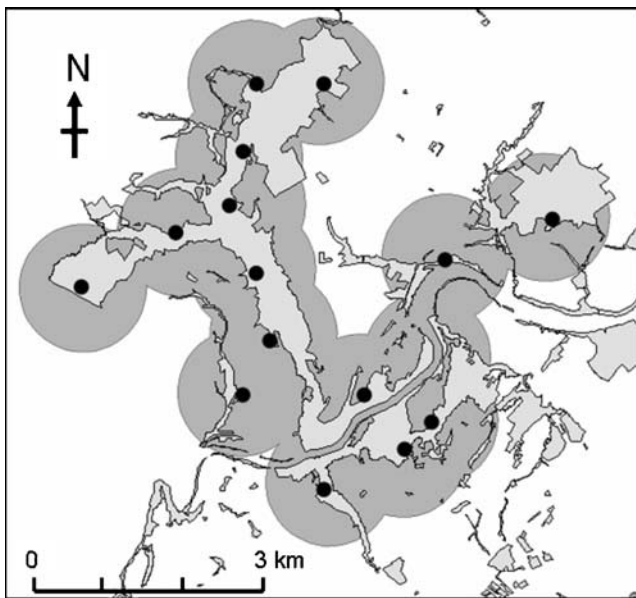


Fig. 2 Effectively sampled area in June 2005. Counting sites (*black spots*), forest patches (*light gray surfaces*), and total surface covered by merged buffers (*gray circles*)

Population size estimators

We used Minta and Mangel (MM, 1989) and Bowden's (BW; Bowden and Kufeld 1995) estimators to assess the size of the marked population (N). Basically, these estimators use the known sighting frequencies of marked animals to estimate the number of different unmarked animals that were sighted (for detailed methods, see Minta and Mangel 1989 and Bowden and Kufeld 1995). Both methods share the same general capture–resight assumptions for geographically and demographically closed free-ranging populations. Marked animals on initial captures are a random sample of the population, and both marked and unmarked animals have equal and independent probability of being sighted during the counting sessions. Both estimators require individual and proper identification of marked animals during sightings. Finally, both models allow a sample drawn with replacement (Seber 1982), so that marked animals might be seen more than once on a survey and

Table 1 Sampling effort realized during the different counting sessions

Session	June 2004	June 2005	June 2006
Date of session	14–18.06.2004	09–15.06.2005	29.05–03.06.2006
Counting nights (CN)	4	6	5
Counting sites monitored (CS)	17	16	16
By technicians	2	–	–
By camera traps	15	16	16
Camera-trap failures (CF)	–	2	3
Potential sampling effort (CN × CS)	68	96	80
Effective sampling effort (CN × (CS – CF))	68	84	65
Minimum time-span between two pictures (min)	20	20	20

admit variability in sighting frequencies of marked animals (Minta and Mangel 1989; Neal et al. 1993; Bowden and Kufeld 1995; White 1996). Concerning unmarked animals, only the sum of their sightings (S_{un}) needs to be known.

All calculations were run using the program Noremark (Neal et al. 1993; White 1996).

Total population size

To estimate the total population size (N_{tot}), we assessed the minimal size of the unmarked population, i.e., all animals belonging to the unmarked age-classes at each counting session. Thus, we added minimum numbers of juveniles and piglets (June 2004) or minimum number of piglets (June 2005–2006) to the CR estimates. These minimum numbers were determined as the number of different juveniles and/or piglets individually identified on the pictures taken through the counting sessions. To avoid double counting, particular attention was given to the following aspects: (1) timing of the observations, (2) morphological features of the animals, (3) group size, and (4) group composition (i.e., age classes).

Density

Wild boar density was assessed for each session as the total population size (N_{tot}), divided by the surface area that was assumed to be effectively sampled. This area varied slightly between the sessions according to changes in camera trap setups. To establish this area, each counting site was surrounded by a circular buffer (Sweitzer et al. 2000), which equalled the mean 95% fixed kernel home range observed in the study area (Fischer et al. 2004a). We defined the “effectively sampled area” as the total surface covered by the buffers without overlapping for each counting session (Fig. 2).

Culling bags

Wild boar are exclusively culled at night by official game wardens from July to February. Date and location of death, as well as the time spent in the field by the wardens, are

recorded among other information. The total number of shot animals on our study area was weighted by the daily culling effort (hours per day) to establish a Culling Index (*CInd*). The trends shown by the *CInd* were compared to our reported total population estimates (N_{tot}).

Results

In 2004, all sites but one (16 out of 17) were used by wild boar and provided sightings. In 2005 and 2006, an absence of sightings was recorded at two and three spots, respectively, although they were used by wild boar. However, neither potential ($\chi^2=4.84, df=2, p>0.05$) nor effective ($\chi^2=2.93, df=2, p>0.05$) sampling efforts differed significantly between the three counting sessions (Table 1).

At the time of the different counting sessions, 12, 20, and 17 boars were marked, whereas 5, 6, and 7 of these individuals were resighted at least once during each session, respectively. Marked animals were seen one to three times in the 2004 survey, two to four times in the 2005 survey, and five to ten times in the 2006 survey. The overall proportion of resighted marked animals (n_k/N_k) did not differ significantly between sessions ($\chi^2=0.41, df=2, p>0.05$). There was no significant difference in the total sightings of marked ($S_k, 04-05; \chi^2=2.28, df=2, p>0.05$) and unmarked ($S_u, 04-05; \chi^2=0.46, df=2, p>0.05$) individuals between June 2004 and June 2005, whereas there was a significant increase in both values in June 2006 ($S_k, 05-06; \chi^2=11.57, df=1, p<0.01; S_u, 05-06; \chi^2=73.22, df=1, p<0.01$; Table 2).

The Minta–Mangel estimator gave stable estimates for June 2004 and June 2005 ($N=188$) and a decrease in June 2006 ($N=148$). Bowden’s estimator showed a slight increase of estimated population size from June 2004 ($N=164$) to June 2005 ($N=177$) and a decrease in June 2006 ($N=138$). Both estimators indicate a decreasing tendency over the 3 years of survey. For both estimators, 95% confidence intervals (CIs) were narrowest in 2006. Significantly more piglets were counted in 2006 than in 2005 ($\chi^2=13.2, df=1, p<0.01$). When compared to each other, both estimators provided similar N_{tot} in each counting session, with no significant difference (2004, $\chi^2=1.01$; 2005, $\chi^2=0.25$; 2006, $\chi^2=0.20, df=1, p>0.05$). For any estimator, differences in N_{tot} over the three sessions were not significant (MM, $\chi^2=5.49$; BW, $\chi^2=3.01, df=2, p>0.05$) (Table 2). Thus, the total population appears to be quite stable over the three counting sessions. However, a slight decreasing tendency can be observed between the first two sessions (Fig. 3). Despite a comparable culling effort over the three culling periods, the number of shot wild boars diminished from 2004 to 2005, which resulted in a significant decrease of the *CInd* ($\chi^2=6.01, df=2, p<0.05$; Table 3). Thus, a decrease in population size between the first two culling seasons seems reasonable,

Table 2 Results overview for resights, marked population, and total population estimates, using Minta–Mangel and Bowden’s estimators, and associated 95% CI

	Marked population						Total population size (N_{tot})		
	Marked individuals located in the study area (N_k)	Marked individuals resighted (n_k)	Proportion of resighted marked individuals (n_k/N_k)	Total sightings of marked individuals (S_k)	Total sightings of unmarked individuals (S_u)	Estimation of population size (N)		95% CI	
June 2004 Minta–Mangel Bowden	12	5	0.42	10	148	188	156–227	110	298
June 2005 Minta–Mangel Bowden	20	6	0.3	18	160	164	78–345	110	274
June 2006 Minta–Mangel Bowden	17	7	0.41	45	354	177	160–242	60	248
						148	95–332	60	237
						148	124–182	107	255
						138	78–246	107	245

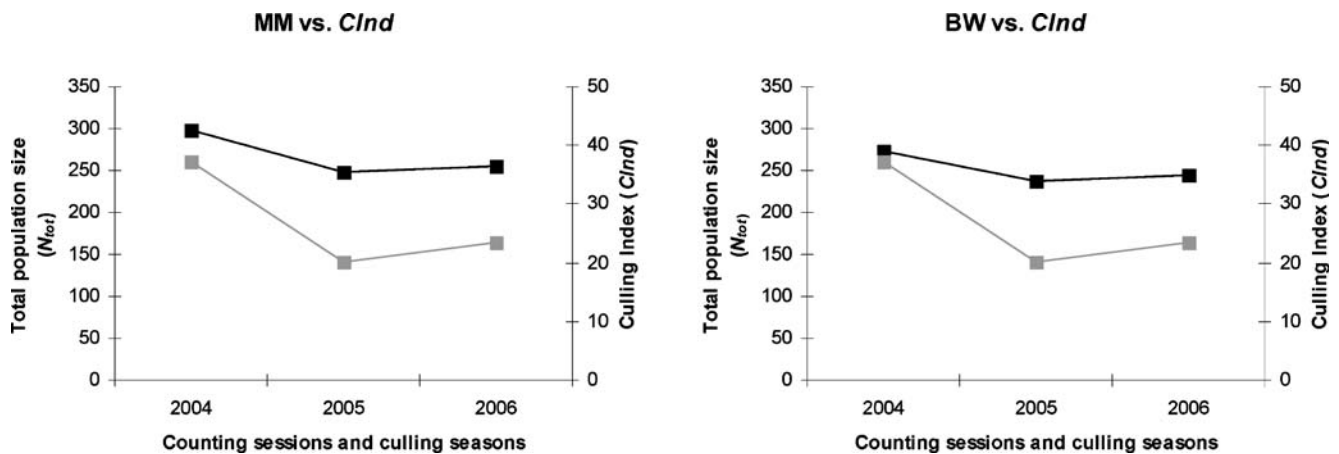


Fig. 3 Total population size estimates (N_{tot}) with both Minta–Mangel (*MM*; left) and Bowden’s (*BW*; right) estimators compared to the Culling Index (*CInd*). Squares and lines indicate N_{tot} ; gray squares and lines indicate *CInd*

whereas the population remains stable afterwards. When compared together, *CInd* and total population estimates displayed similar trends (Fig. 3).

The sampling areas did not vary significantly over the sessions ($\chi^2=0.11$, $df=2$, $p>0.05$). Densities displayed the same tendencies as those reported for the total population estimates (Table 4). Overall, considering MM and BW total population estimates, mean population density was 10.6 ± 0.8 SD individuals/km² with 95% CI ranging from 8.7 to 12.8 and 10.0 ± 0.6 SD individuals/km² with 95% CI ranging from 6.2 to 17.4, respectively.

Discussion

Population size estimators

Several assumptions needed to be fulfilled to apply the selected estimators. As we had some evidence of migrations into as well as out of the study area through mark recoveries, we assumed these migrations to be balanced and not to significantly act upon local densities. Radio tracking indicated that wild boar were mostly sedentary (Fischer et al. 2004b), and additionally, none of the radio-tracked individuals left the study area during the sessions. Thus, given the restricted duration of each counting session, we assumed the population to be closed geographically and demographically over these periods. Furthermore, significant recruitment because of births was also unlikely in the early summer, as most of the farrows occurred between December and May in the study area, with a marked minimum in the summer (Fattebert 2005). Transmitters and S05 ear tags allowed proper identification of all resighted individuals. Multiple recaptures of marked individuals indicated that ear tags remained consistently on the animals during their lifetime (Fischer, personal communication). Trapping and marking animals can influence their subsequent recapture probabili-

ties, especially if both capture and recapture methods are the same (Seber 1970, 1982), and Burnham and Overton (1979) suggested changing methods. Although we baited both cage traps and camera traps with maize, we expect the trapping techniques to differ enough to reduce bias because of trap response. The flashing of the cameras did not disturb the animals, as they stayed on the same spot for 1 h or more. Fournier et al. (1995) used spotlights to identify animals before trapping and made the same observations. Furthermore, Sweitzer et al. (2000) did not notice any significant difference in sighting rates of tagged and untagged animals in California. Sighting rates were also similar between age classes. Morley and van Aarde (2007) assessed several mark–resight methods with an elephant population in dense woodlands. They concluded that Bowden’s estimator provided the most realistic estimates and performed best with aggregated breeding herds. These findings suggest that this estimator might also be efficiently applied to other species living in forests and within social groups, e.g., wild boar (Kaminski et al. 2005). Regarding the narrower CI obtained with MM, Neal et al. (1993) showed that CI coverage performed poorly (i.e., is too narrow) for this estimator. Despite improvements brought to MM (Gardner and Mangel 1996), Neal et al. (1993) and White and Shenk (2001) suggested the use of Bowden’s estimator to be preferred. Even so, we thought it was useful to consider both methods, as no other relevant population estimates, except culling bags, were available in our study area.

Population estimates

Variation in the sampling methods did not significantly affect resights over the three sessions. Thus, both estimators provided similar and comparable estimates of a stable population over the three consecutive counting sessions, although a slight decreasing tendency was apparent. However, the precision of any CMR estimate depends on

Table 3 Culling bag statistics of the study area (DNP; Wildlife and Fishery Department, Geneva)

Culling season	Total wild boar shot in the study area (N_c)	Total culling effort (h)	Culling period (days)	Daily culling effort (h/day)	Culling index (N_c /daily culling effort)
2004	189	1,233	243	5.1	37.2
2005	116	1,396	243	5.7	20.2
2006	118	1,222	243	5.0	23.5

the proportion of marked animals in the sampled population (Seber 1982). Our estimated proportion of marked animals (N_k/N) was only about 10% of the total population, which is quite low compared to the 47 and 67% obtained with wild pigs by Sweitzer et al. (2000). Thus, our study may only provide raw estimates with poor precision. Because wild boar lacks unambiguous natural marks, determining minimal numbers of juveniles and/or piglets is difficult and does not contribute to increase precision. To increase accuracy, marking should be extended to more animals of all age classes. Some camera traps in 2005 and 2006 did not work, and because footprints and daily consumption of maize attested wild boar presence on these sites, some animals are likely to have been overlooked.

Sightings of tagged and untagged animals were significantly higher in 2006 than in the two previous sessions, leading to narrower 95% CIs. Neither variation in the sampling effort nor in the amount of maize used for baiting between the sessions is thought to explain these variations. More likely, the increased sightings are linked to the time setting of this last session, as it was held 2 weeks earlier than the previous ones. Wild boar were possibly less attracted to the less ripe surrounding crop fields and spent more time in the forest, consequently increasing their probability to feed on maize at the counting sites. Radio-tracking data collected around the time of the counts lends support to this idea. The same factors might also have contributed to the increased number of piglets counted in 2006. Reduced food competition because of a significant population decrease could also have allowed the animals to spend more time on the camera sites. However, we assume this to be unlikely regarding our stable estimates. Never-

theless, the significant increase of sightings in 2006 led to narrower CIs and, so, to higher precision. Morley and van Aarde (2007) showed that precision of both the estimates and the 95% CI provided by Bowden's estimator increase with increased sampling effort. Consequently, counting sessions should be held over a longer period of time to provide more sightings and, preferably, in mid-spring, to optimize attraction of the counting sites. Still, the length of the counting session should be defined so as to satisfy the assumption for a closed population.

Nevertheless, as culling effort is known with precision and is comparable among the considered culling seasons, we can use this information to assess the suitability of our methods. Despite aforementioned factors that reduced precision, our estimates showed the same patterns as the culling bags. Considering this, these CR methods might describe reasonably well wild boar population trends in our study area. As far as marking and sampling efforts are standardized over several counting sessions, CR methods are thought to be a useful and quite simple tool to estimate the abundance of wild boar populations. Still, in our study area, the effect of the culling strategy has to be assessed, as we believe it to be the most important factor to influence wild boar mortality and variations in population size.

Densities

Despite differences in sampled areas and sampling methods, the densities found in the present study are among the highest reported in Western Europe (Melis et al. 2006; Table 5). Comparable densities were found in areas that provide favorable conditions for the wild boar. Habitat

Table 4 Wild boar densities for each year of survey and both estimators, and associated 95% CI

Session	Estimator	Sampling area (km ²)	Total population (N_{tot})	Density (N_{tot}/km^2)	95% CI
June 2004	Minta–Mangel	26.2	298	11.4	10.1–12.8
	Bowden	26.2	274	10.5	7.2–17.4
June 2005	Minta–Mangel	25.2	248	9.8	8.7–12.0
	Bowden	25.2	237	9.4	6.2–15.6
June 2006	Minta–Mangel	23.9	255	10.7	9.7–12.1
	Bowden	23.9	245	10.3	7.7–14.8

Sampling areas correspond to the total merged buffer area surrounding the counting spots

Table 5 Reported wild boar densities from different studies

Country	Location	Sampled surface (km ²)	Sampled surface assessed by relocations and/or radio-tracking	Potential habitat	Density (individual/km ²)	Method	Source
Switzerland Italy	Canton Geneva Tuscany	23.9–26.2	Yes	Oak-hornbeam forests	10.6/10.0	Capture–resight	This study
		96.72	No	Deciduous oak and chestnuts forests	12	Drive counts	Massolo and Mazzoni della Stella (2006)
Spain Italy	Doñana National Park Tuscany	–	No	Marshes, dune shrubs and forests	10	–	Fernandez-Llario (1996)
		48.40	No	Oak and chestnuts forests with patches of crop fields	9.8	Catch per unit effort	Boitani et al. (1995b)
Italy	Northern Apennines	7.7–42.1	No	Mixed and deciduous forest.	1.5 to 6.5	Drive counts	Merli and Meriggi (2006)
Spain	Monfrague	–	No	Perennial oak stands with dense shrub undergrowth	3.5	–	Fernandez-Llario et al. (2004)
Italy	Maremma National Park	70	No	Mediterranean scrubland	3	–	Massei et al. (1997)
France	Camargue	10.47	No	Marshes, scrub and grassland, surrounded by cultivated farmland	2.7	–	Dardaillon (1986)
France	Grésigne	36	No	Oak and chestnuts forests with patches of crop fields and vineyards	2.5	–	Spitz and Janeau (1990)
Italy	Genoa Apennines	59.56	No	Hills and mid-range mountains	1.7	Drive census	Marsan et al. (1995)
USA	California	–	Yes	Oak woodlands, coastal sage scrub shrubs and riparian areas	0.7 to 3.8 ^a	Capture–resight	Switzer et al. (2000)
USA	Santa Catalina Island	60	Yes	Patches of oak woodlands, coastal sage scrub and grassland	21 to 34 ^b	Capture-recapture	Baber and Coblenz (1986)
Malaysia	Pasoh Forest Reserve	25	No	Lowland dipterocarp rain forests	47/27 ^a	Line transects	Ickes (2001)

^aDensity of wild pigs (*S. scrofa*)^bDensity of feral pigs (*S. scrofa*)

quality and diversity, especially at a small geographical scale, provide rich food availability all year round and favorable bedding sites (Acevedo et al. 2006; Merli and Meriggi 2006). Food availability also affects the reproductive success of wild boar, as this factor largely explains variation in population size between years (Massolo and Mazzoni della Stella 2006), as well as the birth distribution (Santos et al. 2006). Even if hunting can efficiently reduce population size (Geisser and Reyer 2004), it can also contribute to favor the regeneration of a hunted population (Fernandez-Llario et al. 2003; Massolo and Mazzoni della Stella 2006). Therefore, hunting might not be the most important factor to explain density variations as similar population densities are reported in hunted (Dardaillon 1986; Boitani et al. 1995b) and non-hunted (Fernandez-Llario 1996; Massei et al. 1997) areas. More likely, patchy distribution and changing availability of resources contribute to lower (Spitz and Janeau 1990; Marsan et al. 1995; Fernandez-Llario et al. 2004) or fluctuating (Sweitzer et al. 2000; Merli and Meriggi 2006) densities. Geographic confinement (Baber and Coblentz 1986), absence of predators, and abundant year-round food supply (Ickes 2001) can lead to extreme densities not yet reported in the native range of the wild boar in Europe. The climatic parameters, especially mild winters, should be favorable for the wild boar in our study area. The diversified habitat constituted by patches of oak forests, wetland, and cultivated areas provide good year-round feeding conditions and suitable resting sites. Moreover, as densities remained rather constant over the duration of the study, we think the ecological conditions to be suitable enough to allow the population to compensate the losses caused by culling. Therefore, we assume our density estimates to be representative for the situation in our study area.

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CHAPTER 2

Wild boar (*Sus scrofa*) management and its effects on survival parameters in Canton Geneva, Switzerland

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Keywords : culling, distribution of births, management, recovery analysis, survival, *Sus scrofa*, Switzerland, wild boar.

Abstract

In wildlife management, population control is often a trade-off between sustainable harvest and maintaining the damage to agricultural crops at an acceptable level. In the Canton of Geneva, Switzerland, hunting was abolished in 1974 and wild boar (*Sus scrofa*) have subsequently only been culled by game wardens. We used data from culling bags from 2003 to 2006 to assess the breeding potential and the structure and dynamics of the harvested population. We used marked individuals to estimate survival parameters using a recovery analysis. Weight gain was fast in both sexes during the first two years of life, and juvenile females frequently participated in reproduction. Births occurred year round but with a peak during the spring. The population sex-ratio did not significantly vary over the four culling seasons, but the proportion of juveniles in the culling bags significantly increased while the culling efficiency significantly decreased. The recovery analysis showed that different age-classes were affected in contrasted ways by culling. Survival was lowest in juveniles ($S_{\text{juveniles}} = 0.46$), intermediate in subadults ($S_{\text{subadults}} = 0.66$) and highest in adults ($S_{\text{adults}} = 0.92$), and differed from most other areas where wild boar are hunted. Our results suggest that the current culling protocol was inadequate to reduce population size, but in fact contributed to fluctuations in population size. We propose improving the management regime by shooting more individuals, especially subadults and adult females, and to focus the effort in autumn, to avoid shooting females with dependant piglets.

Introduction

As a consequence of growing wildlife populations and increasing conflicts with humans, wildlife management has received sustained attention in the last decades (eg. Bobek et al. 1991;1992, Woodroffe and Frank 2005, Woodroffe et al. 2005). In harvested populations, management decisions are often a trade-off between sustainable harvest, as an important source of income, and efficient population control to limit wildlife damage (Hauser et al. 2007). These trade-offs have been researched in details in ungulates, and is easiest with long-term individual-based data (Laurian et al. 2000, Clutton-Brock et al. 2002, Milner-Gulland et al. 2004). Collecting long time-series on the structure and density of a population, and on the environmental factors associated with population dynamics have helped to establish models, with good predictive power even at small spatial scales (Coulson et al. 1999, Coulson et al. 2001). Models which allow reliable predictions might limit the need for supplemental and costly monitoring (Hauser et al. 2006b). Recovery models using marked animals are often used to assess survival and recovery rates in harvested populations (Lebreton et al. 1992, Catchpole et al. 1995).

Long-term data are often missing on wild boar (*Sus scrofa*) or are of poor quality, and survival rates are rarely estimated by recovery analysis (Toïgo et al., ONCFS, unpublished data). Moretti (1995b) and Neet (1995) used hunting data to estimate survival and to develop population models, and Jezierski (1977) used known fate of marked individuals to estimate survival parameters. In most cases, game bag analysis is used to characterize parameters like age structure (Fernandez-Llario and Mateos-Quesada 2003), growth rate (Pépin et al. 1987) or reproductive status (Fonseca et al. 2004). Additionally, several authors have discussed the effects of hunting effort and hunting techniques on population dynamics (Debernardi et al. 1995, Fernandez-Llario et al. 2003, Merli and Meriggi 2006).

The distribution of wild boar has expanded over the last decades (Sàez-Royuela and Telleria 1986, Mitchell-Jones et al. 1999). Their high fertility (Servanty et al. 2007) and omnivorous diet (Schley and Roper 2003) mean that under favourable environmental conditions they can rapidly increase in density (Geisser and Reyer 2005, Melis et al. 2006). Natural mortality (i.e. not related to human activity) is a function of harsh climatic conditions (Okarma et al. 1995, Massei et al. 1997), or predation by wolves (*Canis lupus*) (Mattioli et al. 1995, Ansorge et al. 2006), but mainly affects the youngest individuals. Culling has proved to be the most successful means to control population size, and to reduce habitat damage (Sweitzer et al. 2000, Fernandez-Llario et al. 2003, Geisser and Reyer 2004).

In Switzerland, wild boar are well established although their distribution is still expanding (Hausser 1995, Moretti 1995a). According to the yearly harvest statistics of the Federal Office for the Environment, hunting bags showed a marked increase since 1990 (www.bafu.admin.ch). Hunting is practised throughout the country, with the exception of Canton Geneva where it was abolished by public vote in 1974. Wildlife populations are controlled, and culled, by the official game wardens since. Thus, recoveries of culled animals are guaranteed and reliable data can be recorded over an extended period. As a part of a wild boar trans-border project conducted in the Basin of Geneva (Fischer et al. 2004), we analysed culling bags in the Canton Geneva. We used these data to assess the breeding potential of the population. As the reproductive status of shot females was not systematically investigated, we focused our attention on mass gain, to assess the participation of juveniles to reproduction (Mauget and Pépin 1991), and the distribution of births. We analysed the structure and evolution of the harvested population, as well as the culling efficiency, and computed survival rates using recoveries of marked individuals. The effectiveness of the current management is discussed and improvements are proposed.

Study area

The Canton of Geneva is located at the western tip of Switzerland. The Canton covers an area of 240 km² and hosts 400,000 people. The sample region is located in the western part of the canton in an area covering 66 km² (46°09.6'–46°13.7'N, 5°57.2'–6°03.9'E; Fig.1).

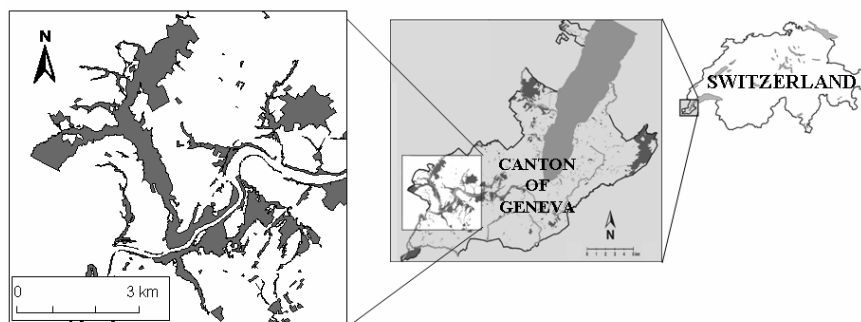


Fig.1. Location of the study area within the Canton of Geneva.

Natural predators of wild boar are absent. Elevation ranges from 350 to 470 m asl. The climate is temperate with an average temperature of 9.8°C, varying from -1°C in January to 19°C in July. Annual precipitation averages 822 mm and is evenly spread throughout the year (<http://www.meteosuisse.ch>). Cultivated areas, mainly vineyards and cereal crops, cover 65% of the study area. Forests cover 20% of the area and are mainly distributed along the rivers, or

scattered in small patches, often not exceeding 1 ha in size. Deciduous oaks (*Quercus sp.*) are the dominant trees (Steiger 1995, Delarze et al. 1998), and might produce substantial amounts of acorn mast in autumn and winter. Two main rivers, easily crossed by wild boar, pass through the area; the Rhône River (E-W) and the smaller Allondon River (N-S). The banks of the Allondon River are part of an active alluvial zone. Willows (*Salix sp.*), alders (*Alnus sp.*) and ash (*Fraxinus excelsior*) are present at the flooded areas and along the riverbanks (Delarze et al. 1998). Villages, roads, farms and other buildings account for 15% of the surface.

Material and methods

Culling strategy

Wild boar are tracked using light amplifiers and shot at night in open areas and on the forests edges, from July to February. When shooting, the following instructions have to be observed: (1) leading or lactating sows are not shot, (2) orphaned piglets have to be tracked and shot, (3) big solitary males are not shot, as far as they don't cause important damage, (4) all wounded animals have to be recovered, (5) all remaining animals can be shot, although in general, the smaller individuals within a group are preferentially shot. Each shot individual has to be reported, along with data on the date and localization of death, sex, weight and age. Age was determined by tooth eruption (Matschke 1967, Baubet et al. 1994). This shooting protocol was consistently applied from 2003 onwards. All individuals were assigned to three age-classes; juveniles (<1 year), subadults (1-2 years) and adults (>2 years). Whenever possible, individuals were assigned to one of the following age-categories; 4, 5, 6, 7-11, 12-14, 14-18, 19-23 and > 24 months old. As culling seasons usually overlap two calendar years, we will only refer to the first year of each culling season (i.e. culling season 2003-2004 is the 2003 season). We analysed culling bags from 2003 to 2006.

Breeding potential

To assess the breeding potential of the population, we analysed body weight development, growth rates and the distribution of births. We used the weight of animals up to 21 months old to determine body weight development. We calculated mean weight \pm SD for males and females within each age-category. Growth rate was calculated for juveniles up to 11 months by dividing weight at death by age and was reported as mean growth rate \pm SD (g/day).

We estimated the birth dates of all shot individuals by assigning them the median of the age-category in which they were in (e.g. we considered animals aged 7 to 11 months to be 9 months old). Additionally, we used date of death of gestating females to determine the birth dates of their litter. Considering a gestation period of 115 days, we measured the length of foetuses (cm) and determined the age of the foetuses (F_a) in days using Bouloire's formula (Henry 1968, Bouloire and Vassant 1989); $F_a = (\text{foetus length} * 4) + 17$. We used these data pooled across all four study years to calculate the relative birth frequencies for each month.

Culling bag statistics

To assess the outcome of the culling strategy, we recorded the number of wild boar shot in our study area in each year. Sex ratio (M:F), and frequencies and relative frequencies of age-classes were reported for each culling season. Variations in sample size between analyses are due to missing sex or age data. We determined the culling effort (C_e ; (h/day)) for each culling season, as the relation between the total of hours spent in the field for culling purpose divided by the number of days culling is applied (*i.e.* 243 days from July to February). We calculated the culling efficiency in each year by dividing the total number of animals shot by the related culling effort.

Survival parameters

To assess wild boar survival rates (S) on our study area, we analysed recoveries of culled animals. We ran a recovery analysis using *Seber* parameterization (Seber 1970, Anderson et al. 1985, Catchpole et al. 1995) in Program MARK (White and Burnham 1999). Capture and marking methods have been previously described in Fischer *et al.* (2004). All captured animals were fitted with individually numbered cattle ear-tags. Captures mostly took place in spring and early summer. From 2002 to 2005, 122 wild boar were marked (85 juveniles; 37 subadults). We grouped our capture-recovery data into four events, each of which spanning one year. As culling ended in February and captures began afterwards, each event spanned from March to February. Thus, we had four consecutive capture and recovery events (March 2002 - February 2003, March 2003 - February 2004, March 2004 - February 2005 and March 2005 - February 2006). We classified individuals into two groups (*i*) those marked as juveniles and (*ii*) those marked as subadults. According to the applied culling strategy, we tested the following null hypotheses; (*i*) survival is constant with age and (*ii*) survival is constant over time. Seven different models were specified. The most parameterized model

incorporated full time- and age-class-dependence in S and recovery rates (r) in both groups (model $S(g*t)r(g*t)$). In all other models, r (i.e. the probability for a marked individual to be recovered and reported after shooting) was equal and constant in both groups, as all shot animals have to be reported. For these models, r was referred to $r(\cdot)$ in model notation. First, to assess differences in S among age classes, we compared three models, without time effect; (1) survival is constant among age-classes (model $S(\cdot)r(\cdot)$), (2) survival is equal between juveniles and subadults but different in adults (model $S(2a-\cdot)r(\cdot)$) and (3) survival is different in each of the three age-classes (model $S(3a-\cdot/\cdot)r(\cdot)$). Second, we added time dependence on the survival parameters of the most parsimonious model to look for possible year to year variation within a specific age class. Thus, three more models were specified; (1) time-dependence of juvenile survival (model $S(3a-t/\cdot)r(\cdot)$), (2) time-dependence of juvenile and subadult survival (model $S(3a-t/t/\cdot)r(\cdot)$) and (3) time-dependence of all three age classes (model $S(3a-t/t/t)r(\cdot)$). To determine the most parsimonious model (i.e. the model providing the best description of the data), we used Akaike's information criterion (AIC; see (Burnham and Anderson 2002)). The model with the lowest AIC was retained.

Statistical analysis

Differences body weight development as a function of sex and age class were tested using Student's t-test, as well as differences in birth distributions. We applied the sequential Bonferroni technique (Rice 1989) to correct the α levels for multiple comparisons of sex-ratios by Chi-square tests: $P_i \leq \alpha / (1 + k - i)$ (for k tests). In our case, considering the five sex-ratios, the new threshold was: $\alpha'_{0,05} = 0,05/5 = 0,01$. Differences in culling efficiency were tested with a Chi-square test, while frequencies of age classes in the culling bag have been compared by Chi-square test for k -independent samples (Siegel and Castellan 1988). All the analyses were carried out by using SPSS 12.0 software for Windows, apart from the survival analyses which was done in MARK (White and Burnham 1999).

Results

Body weight development was similar in males and females ($n = 351$) excepted for the 16 months olds (Student's t -test; $t = -2,525$; $df = 50$; $p = 0,015$), even though males tend to become heavier than females during their second year. All individuals exceeded 40 kg at the end of their first year and reached nearly 70 kg by the end of their second year (Fig. 2). Mean growth rate (\pm SD) in juveniles was 151.5 ± 57.5 g/day.

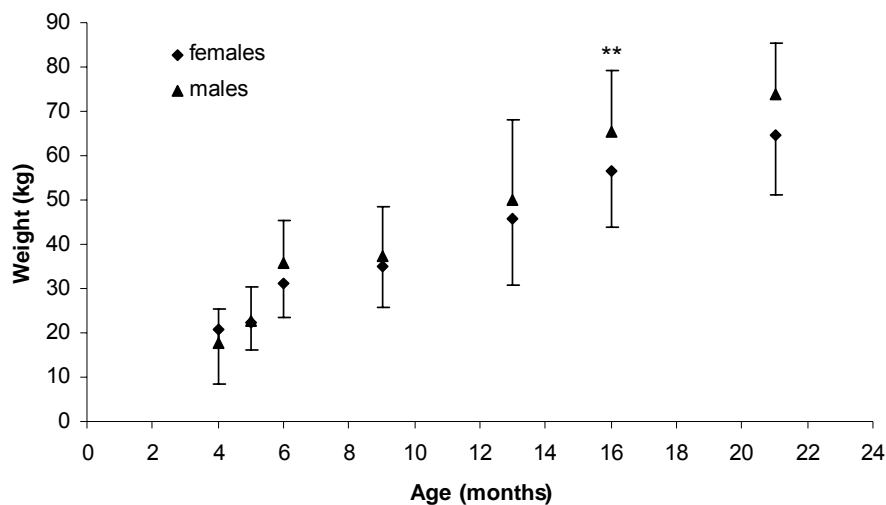


Fig. 2. Mean body weight \pm SD in relation with age and sex. To avoid overlapping, only positive SD are reported in males and negative SD in females. Significant differences are highlighted by crosses.

Births ($n = 547$) are distributed all year round, with a marked increase in winter (December to February) and a peak in spring (March to May; Fig. 3). Forty-six percent of the birth occurred in spring, twenty-five percent during winter and the remaining twenty-nine percent were evenly spread throughout summer and autumn. Significantly more births were recorded in spring ($t = 12.45$, $df = 7$, $p < 0.001$) and winter ($t = 5.99$, $df = 7$, $p = 0.001$) than in summer-autumn. The difference between spring and winter was also significant ($t = -6.57$, $df = 4$, $p = 0.003$).

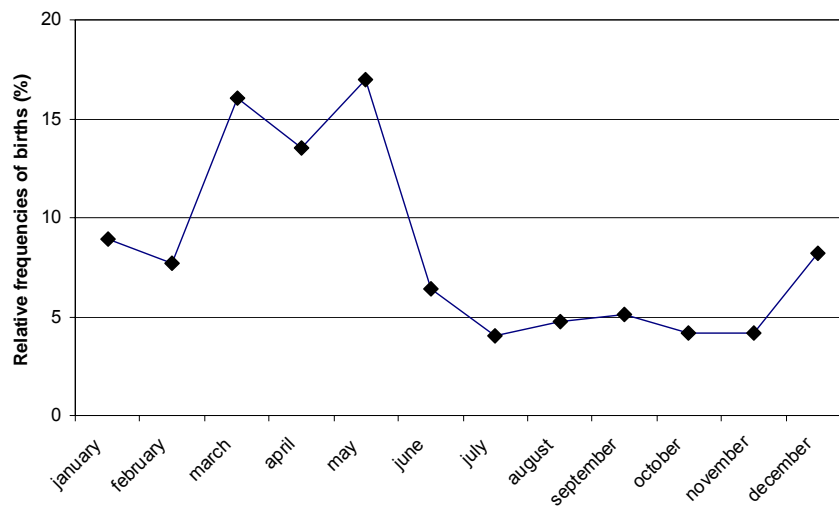


Fig. 3. Monthly distribution of births ($n = 547$).

Overall, sex-ratio was balanced and did not vary significantly over the years ($\chi^2 = 3.95$, $df = 1$, $P_1: 0.0468 > 0.01$). The culling effort reached 7.8 h/day in 2003, and stabilized around 5 h/day in the following seasons (Table 1).

Table 1. Total number of males and females shot on the study area and associated sex ratios (M:F) and culling efforts.

Culling season	M	F	M:F	Culling effort (C_e) (h/day)
2003	164	202	1:1.23	7.8
2004	85	104	1:1.22	5.1
2005	61	55	1:0.90	5.7
2006	56	59	1:1.05	5.0
Total	366	420	1:1.14	

The number of wild boar shot in the study area decreased from 366 in 2003 to 115 in 2005 and remained stable between 2005 and 2006. The marked decrease in culling efficiency appeared to be significant ($\chi^2 = 14.96$, $df = 3$, $p < 0.01$) (Fig. 4).

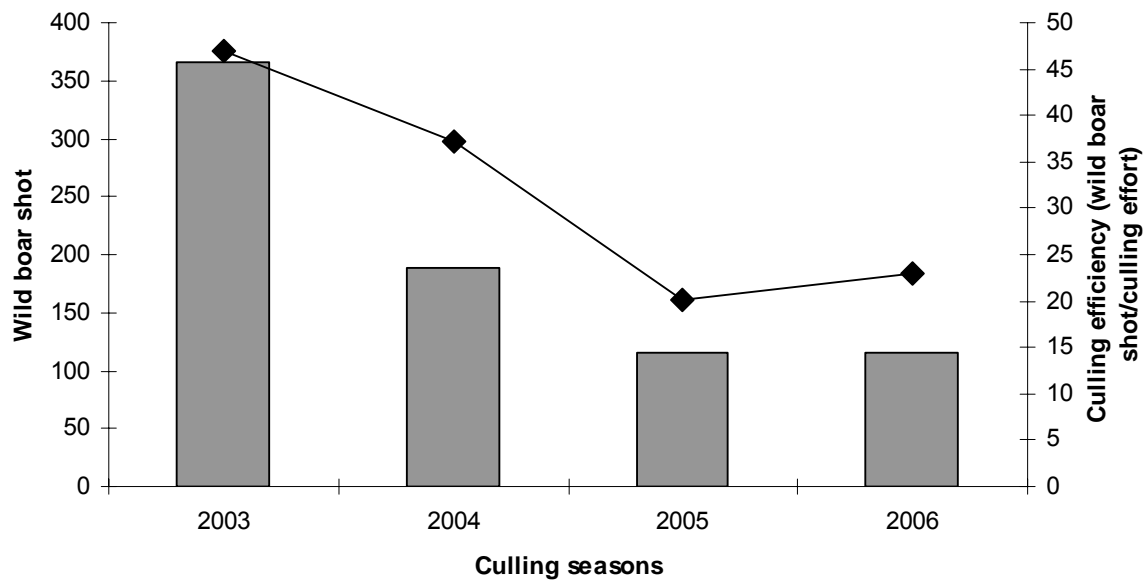


Fig.4. Total number of wild boar shot in the study area (grey boxes) and associated culling efficiency (black lines and squares).

Considering the shot animals of determined age ($n = 674$), changes in the proportion of juveniles in the culling bag were significant ($\chi^2 = 15.05$, $df = 3$, $p < 0.01$; Table 3). Juveniles made up 63% of the culling bag in 2003 and 83% in 2006, at the expense of both subadults and adults, the latter accounting for less than 10% of the culling bag (Fig. 5).

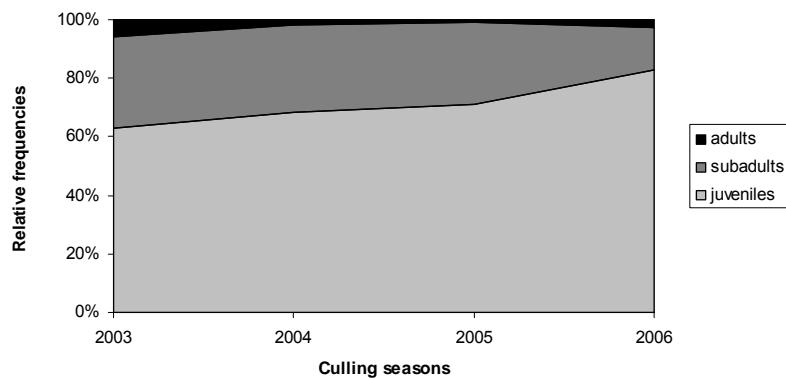


Fig. 5. Relative frequencies of juveniles, subadults and adults in the culling bags, calculated from all shot animals of determined age ($n = 674$).

Among all tested models, the most parameterized one (model $S(g^*t)r(g^*t)$) had least support based on AICc. Considering differences in survival among age-classes, the model with 3 age-classes had greater support in the data than models with 2 age-classes or no age-structure. Model $S(3a-././.)r(.)$ also showed the lowest deviance (Table 2). Thus, we can accept that there are differences in survival between juveniles, subadults and adults, and reject the first null hypothesis. Adding time-dependence to the 3 age-class models decreased their fit (Table 2).

As there is no evidence for differences in survival among years, the second null hypothesis is accepted. In other words, culling was applied consistently through the years of survey, and selective shooting induced different survival rates among age-classes.

Therefore, juveniles experienced the lowest survival, as less than half of them lived through the culling ($S_{\text{juveniles}} = 0.47$). Moreover, two third of the subadults ($S_{\text{subadults}} = 0.66$) and more than 90% of the adults ($S_{\text{adults}} = 0.92$) survived each culling season.

Table 2. Tested models to calculate the survival of wild boar in Canton Geneva (see text for the model notation). Number of parameters considered in the different models, and associated AICc (Akaike Information Criterion), Δ AICc (difference in AICc between each tested model and the most parsimonious model), AICc weights and model likelihood (AICc weight of any considered model divided by the AICc weight of the most parsimonious model). The most parsimonious model (showing the lowest AICc and highest AICc weight) was retained.

Models	Number of		Model		
	Parameters	AICc	Δ AICc	AICc Weight	Likelihood
$S(3a-.l.l.)r(.)^a$	5	235.40	0.00	0.5761	1.0000
$S(2a-.l.)r(.)$	4	237.28	1.88	0.2253	0.3911
$S(.)r(.)$	2	237.99	2.59	0.1575	0.2734
$S(3a-t.l.)r(.)$	8	241.11	5.71	0.0331	0.0575
$S(3a-t/t.)r(.)$	10	244.38	8.98	0.0064	0.0111
$S(3a-t/t.)r(.)$	12	248.32	12.93	0.0009	0.0016
$S(g*t)r(g*t)$	14	249.76	14.37	0.0004	0.0007

^a The most parsimonious model accounted for different survival between age-classes although without time-dependence, and constant recovery in all age-classes without time-dependence.

Discussion

In natural conditions, survival among wild boar is low in the first years of life and higher in older animals (Jeziński 1977). Our reported survivals tend to reproduce this general pattern, despite the culling. Moreover, as only the juveniles exhibit low survival, compared to animals up to 3 years (Jeziński 1977), conditions in the Canton Geneva might be more favourable than they were in Poland. In hunted areas juvenile survival is higher, usually around 70% and both subadult and adult survival is around 30% (Fruziński and Labudzki 2002). In Switzerland the shooting of wild boar is not restricted to any age-class and survival rates of juveniles varied between 55% and 78% and were higher than in older age-classes (Moretti 1995b, Neet 1995). According to the same authors, the main culling effort was focused on subadults or adults and this reduced their survival to about 20% in each case. Toïgo et al. (Carole Toïgo, Office National de la Chasse et de la Faune Sauvage, France, unpublished data) estimated the survival of wild boar in an intensively hunted population in North-Eastern France. Over a period of twenty years, all individuals experienced a survival rate below 50% ($S < 0.5$). In our study area, survival rates displayed an opposite trend, as juveniles experienced the lowest survival, subadults survived at 66% and adults were mainly unaffected by the culling as their survival reached 92%. In this latter case, the survival is even higher than the natural survival of 0.86 reported by Toïgo et al. (ONCFS, unpublished data). Thus, on average, adults are mainly unaffected by culling in our study area. Considering the absence of natural predators and the favourable environmental conditions, natural mortality might kill only a few piglets in their first months of life (Nahlik and Sandor 2003). Even if some individuals do succumb to traffic, these few losses are unlikely to substantially influence our calculated rates. Consequently we consider culling to be the factor which most strongly influences survival.

The breeding biology of wild boar has been shown to be influenced by environmental conditions (Santos et al. 2006), and hunting techniques (Fernandez-Llario et al. 2003), and hence population dynamics are also affected by both factors (Massolo and Mazzoni della Stella 2006). The growth rate recorded in our study area was higher than the average reported for piglets aged 0.5 to 6 months by Gaillard et al. (1992), although similar values were also reported in this study and in the one by Spitz et al. (1990). Wild boar displayed faster body weight development as juveniles than as subadults, with differences between sexes appearing during the second year. These differences are likely to be related to the females' investment in reproduction leading to a lowered weight increase in their second year of life compared to

males, and to a slower growth phase in winter months (Pépin et al. 1987, Spitz et al. 1990). Although we observed such differences, we only found the one between males and females in the 16 months age category to be significant. The smaller sample size in older age-classes and the width of age-classes (spanning up to four months) might also have added some variance to our data set, and therefore weakened the statistical test. Additionally, the wide distribution of births in our study area might also have weakened our analysis, as individuals born in early spring fed more efficiently until winter than those born in summer or autumn. Given the importance of maternal investment, variations in food resources do not significantly affect the development of weight in juveniles (Pépin et al. 1987). In wild boar, the onset of puberty is related to a minimal weight of 30-35 kg, and first breeding is possible at less than 12 months in optimal feeding conditions (Mauget and Pépin 1991). As all individuals weigh between 35 and 45 kg by the end of their first year of life, juveniles can potentially participate to the reproduction in our study area. Even if the breeding status of females was not systematically checked, we had some evidence of pregnant juvenile females which tend to support our findings (Hebeisen et al., unpublished data). The contribution of breeding juvenile females varies with ecological conditions and can be locally important (Gaillard et al. 1993, Fruzinski and Labudzki 2002). In any wild boar population, adult females usually display the highest litter sizes and greatest participation to reproduction (Santos et al. 2006). Additionally, high survival among adult females is likely to have an indirect impact on reproduction, as subadult females are more likely to reproduce if they were born from adult ones (Kaminski et al. 2005). Finally, it has been reported that both litter size and participation of females to reproduction increase in favourable ecological conditions (Massei et al. 1996, Fernandez-Llario and Mateos-Quesada 2005). The observed distribution of births is similar to other studies (Boitani et al. 1995, Durio et al. 1995, Moretti 1995b) and emphasizes favorable environmental conditions. Regarding our data, we assume the breeding potential of our population can compensate for the losses due to culling quite rapidly, as it had already been reported from other studies (Marsan et al. 1995, Fernandez-Llario et al. 2003, Massolo and Mazzoni della Stella 2006).

The first culling season we considered coincided with the highest culling effort and the greatest efficiency. Consequently, more individuals from all age-classes were shot, and the decreased bag in 2004 probably reflected a decreased breeding population. Fattebert (2005) additionally showed that in 2003, the effort significantly affected subadult females which are known to contribute efficiently to the recruitment (Massolo and Mazzoni della Stella 2006).

Although some individuals might have learned to avoid open areas, and so kept safe from shooting, the decreased bags and culling efficiency are probably more related to the consistent application of the shooting protocol. The high survival among adults insured important yearly recruitment, which consumed most of the effort. Given the wide distribution of births, lactating sows are present at any time of the year, thus limiting shooting possibilities, and important body weight development lessened the distinction between subadults and adults. Thus, the game wardens gradually concentrated their effort on juveniles so as to avoid trouble shootings, and neglected older individuals. Knowing the demographic structure of a population is key in harvest decisions and outcomes (Getz and Haight 1989), and allows targeting of the most productive individuals, if one wants to reduce population size (Hauser et al. 2006a). Ironically, the high survival of subadults and mainly adults would favour maximized harvest by maintaining the breeding population (Hauser et al. 2007), and the risk of population and damage increase is even favoured. Population estimates showed stable abundance from 2004 to 2006 and densities around 10 individuals per km² in our study area (Hebeisen et al.) and tend to support our interpretation. Despite these facts, damages could be greatly limited and might only partly reflect population trends, as most of them affected vineyards and electrical fences proved to protect them efficiently (Domaine Nature et Paysage, Geneva, pers. comm.). Therefore, the culling effort should be increased towards subadult and especially adult individuals, as their mortality rapidly affect population size (Andrzejewski and Jezierski 1978, Bieber and Ruf 2005, Servanty 2007), and effort should be maximized in autumn. Piglets are weaned at the age of 3 to 4 months (Macdonald and Barrett 1995, Étienne 2003), and as the main farrowing period lasts from March to May, lactating females should be scarce at this period. Moreover, presence of mixed groups of adults and subadults at this time of the year (Dardaillon 1988) should make the identification of individuals easier on open fields. Our personal observations showed that the spatial behaviour of wild boar is mostly unaffected by the nocturnal culling, as was already observed in daytime hunted areas (Sodeikat and Pohlmeier 2003).

Given their omnivorous diet (Schley and Roper 2003), wild boar show little food competition with other herbivorous ungulates, and therefore react differently to environmental changes (Madhusudan 2004). Notwithstanding, collecting data on sex and age structure (Coulson et al. 2001) or ungulate-habitat interactions (Morellet et al. 2007) proved to enhance the decision-making process in ungulates management (Clutton-Brock et al. 2004, Gordon et al. 2004) and the maintaining of mortality close to its natural level (Milner et al. 2007). Therefore, the same

monitoring processes should also be favoured in wild boar management, as their complex population dynamics require consistent monitoring (Hauser et al. 2006b).

Given their adaptability, wild boar populations should be monitored regularly to obtain both quantitative and qualitative data on their dynamics. In our case, most of the shooting effort was targeted towards the youngest individuals and contributed to maintain a very dynamic population in which the losses were rapidly compensated. The current management strategy for wild boar failed to decrease the population size significantly. We therefore advise to increase the shooting effort on adult females, and recommend considering qualitative hunting bags to set up wild boar management.

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CHAPTER 3

Social organization of wild boar (*Sus scrofa*) in the Basin of Geneva

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Abstract

Wild boar live in matrilineal family groups of overlapping generations of related females. Associations between family groups due to shared home ranges and resources can lead to bigger groups, usually known as sounders. We used diurnal and nocturnal radio locations of 35 individuals spread in 10 different groups to describe the social organization within and between family groups. We computed a social affinity index and measured the distance between two individuals once they were separated to assess the importance of associations and their spacing, respectively. Social affinity was highest during the day, among juveniles and subadults and within family groups. Associations of all kind were strongly weakened during the night, as nocturnal activity was randomly done in association with other individuals or alone, but animals usually shared a common range. Sounders appeared to have a more dynamic organization, as several family groups were shown to share common resting sites and to split at night, and fission-fusion patterns between family groups were frequently observed. Variations in grouping patterns at all levels of organisation (individual, family group and sounders) are possibly influenced by several factors such as kinship, distribution and quality of resources and breeding conditions. Kinship and favourable resources are likely to favour the cohesion within a family group and interactions between them. Given the strong association of individuals in a family group and the variable interaction in sounders, orphaned individuals might be able to build independent groups or associate with other family groups. Therefore hunting activities might not disrupt the social organisation significantly.

Introduction

A major purpose in the study of mammalian societies is to understand the way species characteristics and environmental parameters may affect the relations between individuals and hence social organization (Crook et al. 1976). In most polygynous mammals, males tend to disperse while female offspring tend to remain in their natal group and to be philopatric (Greenwood 1980). However, mainly to avoid inbreeding, female transfer between groups can be observed if the timing of their first reproduction is anterior to the mean residence time of males (Clutton-Brock 1989). Male-biased dispersal often results in matrilineal social systems (Christal et al. 1998, Charif et al. 2005, Kaminski et al. 2005). Those matrilineal systems are maintained by philopatry and display important genetic relatedness (Mathews and Porter 1993).

As in other Suidae (*Phacochoerus aethiopicus*; Somers et al. 1995), the typical social organization for wild boar (*Sus scrofa*) is matrilineal and characterized by family groups with overlapping generations of females (Kaminski et al. 2005). Those groups can be maintained over several years by simultaneous farrowing of females (multi-family groups; Nakatani and Ono 1995). The majority of males disperse over longer distances between the ages of ten to sixteen months, while only few females disperse, and when doing so, tend to stay relatively close to their natal range (Truvé and Lemel 2003, Truvé 2004). Although the basic social unit consists of the mother and her litter (mother family; Frädrieh 1974), family groups display continuous variations in size and composition following the sexual cycle of the species. Pregnant females become independent shortly before giving births and rejoin related individuals, mostly other females and their previous litter, a few weeks afterwards. Therefore, groups become progressively more important in summer and autumn, following the breeding and growing period, and reach maximal size during the rut, when adult males join the groups (Dardaillon 1988, Braza and Alvarez 1989, Fernandez-Llario et al. 1996).

If genetic relatedness has been shown to play an important role in the maintenance of associations (Gabor et al. 1999, Kaminski et al. 2005), other factors such as philopatry and spatial ontogeny might also contribute to shape the socio-spatial organization (Spitz 1992). Juveniles become gradually more independent from their mother and siblings and tend to explore areas outside their post-natal range (Cousse et al. 1994, Cousse et al. 1995). The subadult stage is characterized by important exploration, triggered by dispersion and temporary or definite separation of females from their mother (Spitz and Janeau 1990, Kaminski et al. 2005). Adult females display great fidelity to a restricted number of resting

sites and select habitats which maximize both security and food resources to insure the rearing of their litter (Janeau et al. 1995b, Spitz and Janeau 1995). Moreover, home ranges of adults females overlap considerably (Boitani et al. 1994) due to the similarity of their movement patterns (Janeau et al. 1995a). These features contribute to stabilize the population in space and to the presence of stable groups of breeding age females and their offspring that share a common range. These groups have been defined as sounders (Gabor et al. 1999) and might be made of non-random sub-groups.

As a matter of fact, the social organization appears to be very dynamic, but little has been done so far to assess the effect of hunting activities on this organization. Although hunting activities might affect the spatial use of wild boar (Maillard and Fournier 1995), effects are mainly measured in terms of temporal changes in home range utilization (Sodeikat and Pohlmeier 2003), and orphaned juveniles and subadults have been reported to constitute independent and stable groups (Spitz 1992, Rosell et al. 2004). Notwithstanding, the concept of a leading sow, guiding a group and determining its activity, is still widespread and has important influence in the species' management. The shooting of such individuals is thought to have a major disrupting impact on the coordination of spatial activity, and hence on the distribution of damage. Additionally, the social organization has been studied using only nocturnal observations (Dardaillon 1988), diurnal radio-locations (Kaminski et al. 2005), or with pooled diurnal and nocturnal locations (Gabor et al. 1999). However, diurnal and nocturnal behaviour are driven by different interests who might also influence the social organization. Wild boar usually display nocturnal activity related to the search for food and displacement between feeding and resting places (Spitz and Janeau 1995, Cahill et al. 2003) and rest during the day, selecting the most secure habitat (Cargnelutti et al. 1995).

In this paper, we considered diurnal and nocturnal radio locations separately to assess variations in associations between individuals. We aimed to characterise the grouping patterns of juvenile, subadult and adult wild boar, considering their social affinity and their spacing once they are separated. In a second step, we focused our attention on the socio-spatial organization of several family groups throughout the Basin of Geneva. The potential influence of resource distribution, kinship and socio-spatial ontogeny on the dynamic of groups is discussed. Finally, we discussed the potential impact of the shooting of adult individuals on the social organization in respect to group stability.

Study area

The Basin of Geneva is at the far western tip of Switzerland and Lake Geneva ($46^{\circ}06' - 46^{\circ}24' \text{ N}$, $5^{\circ}54' - 6^{\circ}10' \text{ E}$), and is surrounded by wooded mountains that reach an elevation of 1,600 m (Fig.1). The lowlands (between 350 and 600 masl) are a mosaic of cultivated land, scattered woods and extensive urbanisation, and host over 500,000 people within 680 km^2 . In the mountains, forests are dominated by beech (*Fagus sylvatica*), Silver fir (*Abies alba*) and Norway spruce (*Picea abies*) while the lowlands are dominated by deciduous oak stands (*Quercus sp.*) (Steiger 1995, Delarze et al. 1998). The climate is temperate with an average temperature of 9.8°C , varying from -1°C in January to 19°C in July. Annual precipitation averages 822 mm and is evenly spread throughout the year (<http://www.meteosuisse.ch>). The study area can be divided in three sectors according to the size and shape of wooded areas. Moreover, significant differences in wild boar home ranges have been reported between these sectors (Fischer et al. 2004a).

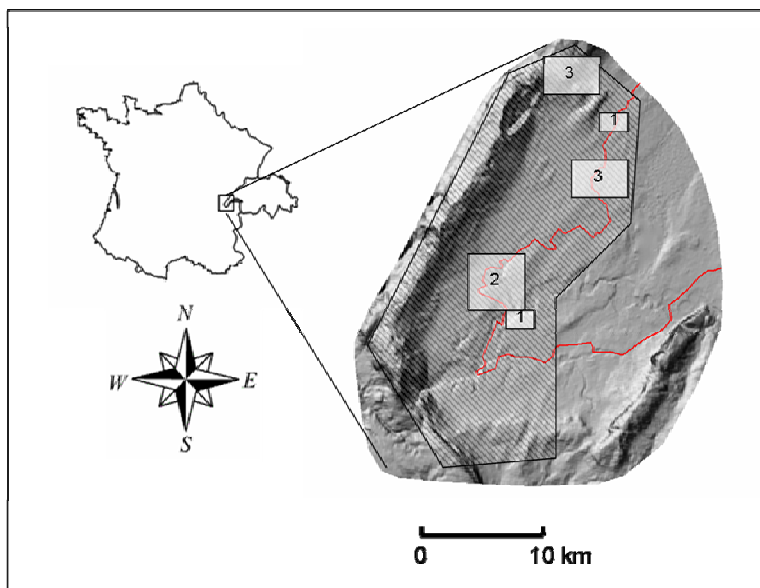


Figure 1. Location of the study area. The hatched surface is the global study area, light grey polygons stand for the considered sectors, the black line indicates the Swiss border.

Sector 1 comprises two marsh- and wetland areas with dense cover located in the lowlands: the Moulin-de-Vert (MdV) and the Marais de Versoix (VxVD). Both wooded areas do not exceed 150 ha in size and are surrounded by cultivated areas of cereal crops, mainly wheat and maize. Some parts of both areas are natural reserves thus with few human disturbance. Sector 2 is also part of the lowlands, but forests are larger than in sector 1 and mainly located along the major rivers (Rhône and Allondon). Wooded areas are surrounded by cereal crops and vineyard. Sector 3 comprises the Bois de Versoix (VxGE) in the lowlands and Vesancy at

the slopes of the Jura Mountains. Forests with sparse undergrowth cover larger areas than in the previous sectors. Forests are surrounded by cereal crops, grassland and pastures.

Material and methods

Capture and marking

Animals were captured from 2002 to 2005 in live-traps baited with maize (Fischer et al. 2004b). All captured animals were assigned to one of three age classes according to their estimated or effective weight and coat colour. Juveniles: stripped or reddish coat, weighing up to 40 kg, from 0 to 12 months old. Subadults: black coat, weighing more than 40 kg, between 12-24 months old. Adults: black or silver coat, looking big and heavy, generally weighing more than 60 kg (Dardaillon 1988, Fernandez-Llario and Carranza 2000, Santos et al. 2006). The age was further controlled by tooth eruption (Matschke 1967, Baubet et al. 1994) when those animals were shot and by following their capture history. All radio-tracked juveniles were already weaned at the time of capture. Each animal was assigned to a code, according to age-class and sex, *e.g.* AF1 for Adult Female 1. Whenever possible, at least two individuals per capture were fitted with transmitters. Fully-grown individuals were fitted with fixed radio-collars (ATS, Inc., USA). Other individuals were fitted with Televilt[®] transmitters (TVP Positioning AB, Sweden) adjusted in extensible collars developed by the ONCFS (Brandt et al. 2004), or ear-transmitters (Biotrack[®], Ltd., UK). After handling, all were released at their capture site.

Radiotracking

For the present study, we focused our tracking effort on two types of individuals. First, individuals of all age-classes captured simultaneously and suppose to be closely related and therefore to be part of a same family group. Secondly, subadults and adult females captured and marked during a same period on a common sector and sharing a common home range and therefore supposed to be part of a same sounder. Details of tracking groups (TG) are given in table 1. Animals were located by triangulation, using Sika (Biotrack Ltd, UK) and TRX-2000S (Wildlife Materials Inc., USA) receivers connected to a hand-held Yagi antenna. The accuracy of the locations was estimated with an error polygon size of 1 ha during night-time and 0.25 ha during the day (Hebeisen et al., unpublished data). Each individual was located at daytime two to three times a week, and before and after each night sessions. Night sessions started before sunset and lasted until sunrise. During these night sessions, all individuals

within a TG were located within 1 to 1.5 hours intervals. As far as we could not clearly differentiate the positions between two individuals by triangulation, those individuals were considered to be together.

Social affinity and mean distance between individuals

We treated day and night locations separately. Within each TG we calculated the distance between two individuals in each common time-interval for all possible dyads. To characterize the social association between members of a same TG (Ginsberg and Young 1992) we determined the social affinity (S) of each dyad using the following formula (Lazo 1994):

$$S = N_{A,B}/\min(N_A, N_B)$$

Where $N_{A,B}$ is the number of combined locations of individuals A and B , N_A is the number of locations of individual A , and N_B is the number of locations of individual B . A combined location was considered when the distance between both members of a dyad was equal or inferior to 50 m. Thus, index takes values between 0 (no combined locations for a dyad) and 1 (members of the dyad were always located together). For TG4 and TG5, which included at least one adult sow or a sow with piglets, we used S values to build cluster trees using UPGMA linkage (Sneath and Sokal 1973).

To assess the spatial features of separations, we calculated the Mean Distance Between Individuals (MDBI) for each dyad using all locations that were not combined.

Movement patterns

To characterise the movement patterns of individuals within a TG we used the classification proposed by Janeau et al. (1995a, 1995b) assuming that within a social group, all individuals usually perform the same kind of movement pattern at a given day (Spitz 1992). For each animal we used the data from night sessions and their respective daytime locations (before and after the sessions). We calculated the maximum distance from departure point and the distance between two consecutive resting places to attribute each session to one of the five defined patterns; “Stay”, “Stay and rest nearby”, “Loop”, “Ranging and return” and “Ranging widely” (Fig. 2).

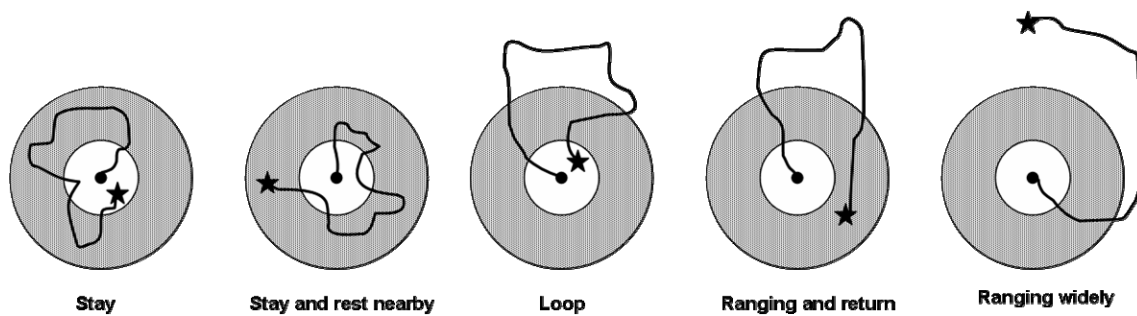


Figure 2. Movement patterns of wild boar (the radius of the small circle = 500 m; the radius of the large circle = 1,000 m; Janeau et al. 1995a).

Data analysis

We treated day and night locations separately. To assess differences in tracking effort, we compared average number of radio-locations per individual between age classes. We compared S and MDBI values pooled among age-classes and reported means \pm standard error (SE). This analysis should highlight the general patterns of associations among individuals. Additionally, we completed the analysis by focusing on four TG (4; 5; 9; 10) which included at least one adult sow or one sow with piglets, to assess association patterns within and between family groups. For these groups we reported S and MDBI values (mean \pm SE), S -cluster trees (only for TG 4 and 5) and movement patterns. To assess differences in S and MDBI we used Student's t -test, or Chi-square test for 2x2 contingency table for small samples (TG4 and TG5). Differences in average number of radio-locations and movement patterns were tested using Chi-square test for k -independent samples (Siegel and Castellan 1988). Significance level was set at $p = 0.05$. All statistical analyses were carried out on SPSS 12.0 software for Windows.

Results

Overall, 35 (6 males and 29 females) wild boar spread in 10 different TG were tracked for one to seven months, until they get shot or lost their transmitters, from 2003 to 2006 (Table 1). The tracking effort did not vary significantly between age classes ($\chi^2 = 1.78$, $df = 2$, $p > 0.05$), and averaged 94 locations per individual. The missing night-dyad in the table is due to an absence of night location in this particular case.

Table 1. Composition of tracking groups. Individuals on a same line were captured together. Concerning individuals, the first letter stands for age class (Juveniles, Subadults or Aadults), the second for sex (Female or Male).

Tracking group (TG)	Individuals	Date of capture	Sector	Tracking period	Notes
1	JF1, JF2, JF3, JM1	01.12.2005	2	winter 2005-2006	
2	JF4, JF5, JF6, JM2, JM3	12.10.2005	2	autumn/winter 2005-2006	
3	JF7, JM4, JM5	28.05.2006	1	summer 2006	
4	SF1, SF2	01.04.2003	1	summer /autumn 2003	with 6 piglets
	SF3, SF4	17.06.2003			
	SF5	13.05.2003			
5	SF6	10.05.2005	3	summer 2006	with 11 piglets
	SF7	04.04.2005			
	AF3, AF4	10.05.2005			
	AF5	11.04.2005			
6	SF8, SF9	20.05.2005	1	summer 2005	
	SF10	23.03.2005			
7	SF11, SF12, SM1	01.02.2005	2	winter/spring 2005	
8	SF13, SF14, SF15	01.07.2003	2	summer/autumn 2003	
9	AF1, AF2	13.06.2006	1	summer/autumn 2006	with 12 piglets
10	AF6, AF7	01.04.2004	3	throughout autumn 2005	AF6 was gestating

Social affinity and spacing

Considering social affinity, juveniles displayed the highest values ($S_{\text{day}} = 0.83 \pm 0.06$, $S_{\text{night}} = 0.56 \pm 0.06$), followed by subadults ($S_{\text{day}} = 0.73 \pm 0.03$, $S_{\text{night}} = 0.44 \pm 0.07$) and adults ($S_{\text{day}} = 0.46 \pm 0.16$, $S_{\text{night}} = 0.38 \pm 0.11$). Differences between day and night were significant in juveniles ($t = 3.08$, $df = 36$, $p = 0.004$) and subadults ($t = 3.69$, $df = 37$, $p = 0.001$), both age-classes displaying higher affinity at day. When S values are compared between age-classes, juveniles ($t = 2.57$, $df = 22$, $p = 0.017$) and subadults ($t = 2.67$, $df = 23$, $p = 0.014$) displayed significantly higher affinity than adults at daytime (Fig. 3). The variations in S values at night were not significant; therefore the mean S at night was of 0.49 ± 0.04 , *i.e.* members of a dyad spent around 50% of their time together. The MDBI were lower in juveniles (MDBI_{day} = 243 m \pm 49, MDBI_{night} = 588 m \pm 167) than subadults (MDBI_{day} = 518 m \pm 51, MDBI_{night} = 851 m \pm 267) and adults (MDBI_{day} = 601 m \pm 250, MDBI_{night} = 573 m \pm 226). However differences were only significant at daytime between juveniles and subadults ($t = -3.91$, $df = 37$, $p < 0.001$) and juveniles and adults ($t = -2.39$, $df = 22$, $p = 0.026$) (Fig. 3). Thus, when both individuals of a dyad were separated at night the MDBI averaged 730 m \pm 141.

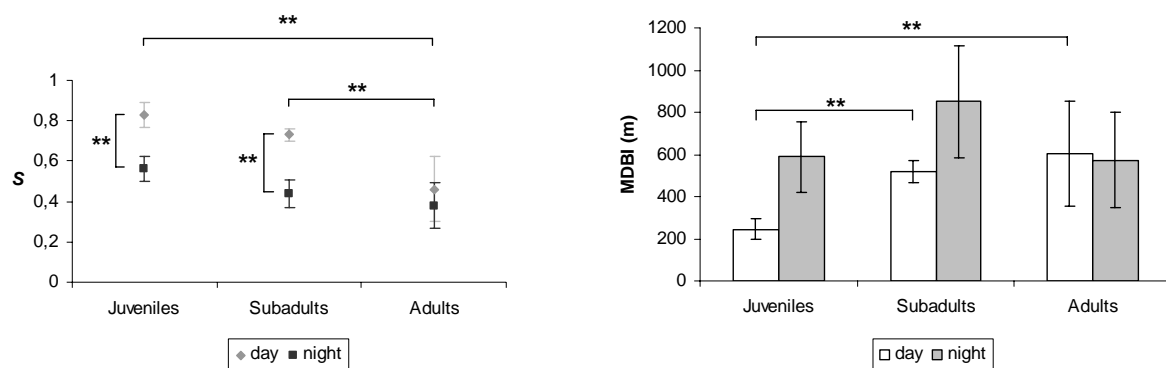


Figure 3. Social affinity (S ; left) and Mean Distance Between Individuals (MDBI; right) in each age-class, reported as mean \pm SD. Lines and crosses indicate significant differences.

Group stability

Individuals in TG 4 and TG5 displayed higher social affinity during the day than at night (Fig. 4). However, this difference was only significant in TG4 ($t = 4.15$, $df = 18$, $p = 0.001$), where $S_{\text{day}} = 0.69 \pm 0.03$ and $S_{\text{night}} = 0.30 \pm 0.09$. No significant differences were found in MDBI, by this means individuals of these groups were separated by 454 m \pm 34 each time they were not located together (Fig. 4).

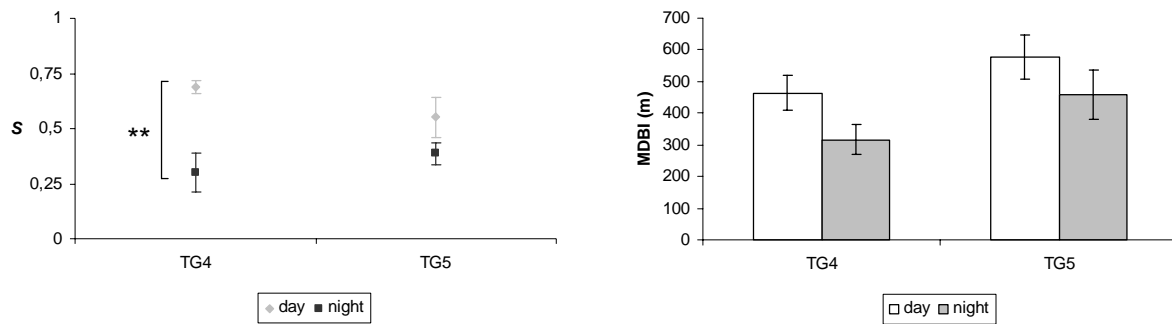


Figure 4. Social affinity (S ; left) and Mean Distance Between Individuals (MDBI; right) in tracking groups 4 and 5, reported as mean \pm SE. Lines and crosses indicate significant differences.

In TG4, two stable clusters made of SF1-SF2 and SF3-SF4 showed comparable associations at day and night, while SF5 was associated to both of them about 60% of time at day but less than 20% during the night. Associations between the first two clusters were strongly weakened at night. Consequently, we considered TG4 to be made of three distinct and stable groups (SF1-SF2; SF3-SF4; SF5) which were strongly associated during the day but split during the night (Fig. 4). In TG5, SF6-SF7 and AF3-AF4 formed two distinct clusters. Within each cluster individuals were more often associated at day, even if they spent more than 50% of time together at any time. AF5 was mostly associated to AF3-AF4 at day but showed the weakest association to all other individuals at night. AF3-AF4 were preferably associated to the two subadults at night. As a result, we considered TG5 to be made of three groups as well (SF6-SF7; AF3-AF4; AF5). However the associations within and between those groups appeared to be more dynamic than in TG4 (Fig. 5).

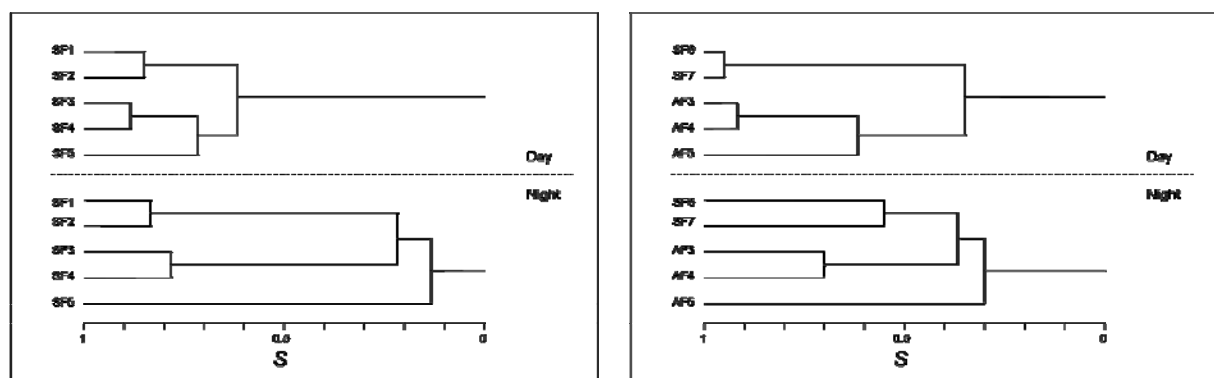


Figure 5. UPGMA-cluster trees using social affinity (S); TG4 (left) and TG5 (right).

The movement patterns used by both tracking groups were significantly different ($\chi^2 = 14.68$, $df = 4$, $p < 0.05$). Beneath the pattern “Stay”, which was preferred in both groups, the

individuals of TG4 mainly used the pattern “Loop” (27%), while those in TG5 mainly used patterns that implied changes in resting sites and/or movements over longer distances (Fig. 6).

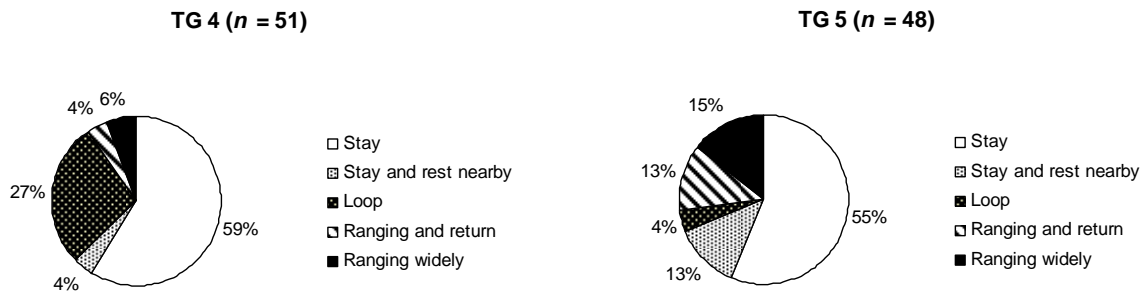


Figure 6. Movement patterns used by individuals of Tracking group 4 (left) and Tracking group 5 (right).

Although AF1 and AF2, forming TG9, were located more often together at night ($S_{\text{day}} = 0.18$ and $S_{\text{night}} = 0.45$) this difference was not significant ($\chi^2 = 2.68$, $df = 1$, $p > 0.05$). The MDBI did not show significant variations between day and night and averaged $220 \text{ m} \pm 28$, but was significantly lower compared to TG4 and TG5 ($t = -2.90$, $df = 4$, $p = 0.044$). Considering the movement patterns ($N = 16$), individuals of TG9 used only three patterns; “Stay” (68%), “Loop” (19%) and “Stay and rest nearby” (13%).

Both adult females in TG10 were captured together, but were seldom located together ($S_{\text{day}} = 0.02$ and $S_{\text{night}} = 0.08$) and separated by an average distance of $1360 \text{ m} \pm 113$ at any time. The MDBI was significantly higher compared to TG4 and TG5 ($t = 9.67$, $df = 4$, $p = 0.01$). All five movement patterns were evenly used in this group ($N = 22$), as the patterns “Stay and rest nearby”, “Loop” and “Ranging widely” accounted for 22% each, and the patterns “Stay” and “Ranging and return” for 17%.

Discussion

Grouping patterns in wild boar appeared to be most obvious during their diurnal resting phase, as social affinities were more important at day independently of the considered groups; family groups or sounders. The importance of diurnal resting sites has already been stressed by several authors as they are selected to maximize security (Cargnelutti et al. 1995, Fernandez-Llario 2004) and influence the daily movement patterns of individuals, especially of adults females (Janeau et al. 1995b), and hence their socio-spatial organization. Our results confirm these findings and suggest that this resource might as well contribute to the maintenance of social units. Despite that juveniles tend to become progressively more independent (Cousse et al. 1994), strong associations and contacts are maintained between individuals both in terms of social affinity and spacing. The lessened distance separating juveniles might indicate selection of few but secure resting areas by family groups with juveniles and the tendency to use only a restricted part of the mother's range (Spitz 1992). Separations can be due the exploration of juveniles outside their native range (Cousse et al. 1995), or to temporal segregation between two related litters. Spitz (1992) stated that subadults tend to use distinct resting places apart from their relatives. Contrary to this study, subadults appeared to maintain close association at day in our study area. Although most of the subadult females stay with their mother, those that segregate might also remain associated to build novel and independent groups (Dardaillon 1988, Kaminski et al. 2005). Considering their social affinity and spacing, adult females meet regularly on resting sites and tend to use similar areas, in accordance with other studies (Boitani et al. 1994, Gabor et al. 1999). Overall, the importance of diurnal associations within a family group, reflected by associations in juveniles and subadults, seemed to be more important than associations between family groups, reflected by associations between adults. Important diurnal associations are also maintained up to the subadult stage.

Although the spacing remains rather constant and comparable at any time and therefore support the use of a common range, associations between individuals were significantly weakened at night. As a consequence, nocturnal associations are maintained in terms of spatial distribution rather than social contacts. In all age-classes, individuals are as likely to be found with relatives, siblings or members of their family group, as to be found separated from them. Foraging is an important nocturnal activity (Cahill et al. 2003) and might be collective, depending on the distribution of resources and population densities (Spitz 1992). In our study area, food resources are available all year round in sufficient quantities (Comte 2005, Berger

2006) and might therefore not be a limiting factor, thus creating little competition. Moreover, population density can be as high as 10 ind./km² (Hebeisen et al.). If these features are likely to allow collective feeding, they can also contribute to decrease associations as individuals might as well find their food on their own or in smaller groups. Additionally, subadults preferably feed on open areas that provide rich food and females with their litter tend to use more dense and secure areas (Spitz and Janeau 1995). These different strategies might also contribute to weaken associations between individuals.

If individuals of a family group are typically relatives (Spitz 1992, Kaminski et al. 2005), associations between family groups, *i.e.* sounders, are thought to reflect both kinship and sharing of a common range (Boitani et al. 1994, Gabor et al. 1999). Associations should therefore be marked in the former and more variable in the latter groupings. As all individuals of TG4, TG5, TG9 and TG10 shared a common range and associated non-randomly, we can consider these groups as sounders. The stable clusters indicate that at least three family groups constituted the TG4 sounder. The social affinity within these family groups remained comparable at any time, but the different family groups tended to share optimal resting sites and to forage separately at night. TG4 and TG9 lived in sectors providing comparable resources; spatially restricted but dense cover, surrounded by fields. However, both females in TG9 associated less often in time, especially at day, but spatial association was evident. Two factors are likely to explain these variations. As their piglets were not weaned, both females tended to maintain a certain territoriality at resting sites, and as population density was lower than in the area where the sounder TG4 lived, encounters are less frequent (Spitz 1992). The distribution of resources strongly affected their movement patterns, which were characterized by high fidelity to resting places and short nocturnal displacement due to close connexion to the surrounding fields. Therefore good environmental conditions are likely to favour interactions between family groups and to stabilize spatial organization of sounders. The socio-spatial organization of the sounder made of TG5 appeared to be more dynamic, and the 5 individuals, probably spread in 3 family groups, appeared to be located together in around 50% of the cases at any time. However, during the day, strong associations were maintained within family groups, but family groups tended to use distinct resting sites. At night, both associations, within and between family groups, are weakened. Variations in the structure of diurnal and nocturnal cluster trees indicate that exchanges between family groups were frequent, attesting the fission-fusion dynamic already reported by Gabor et al. (1999). The broader distribution of resources (resting places and food) encountered by this sounder

implied more frequent changes in resting sites and longer movements than for the previous two sounders, therefore contributing to a more dynamic organization. Despite that the two adult females of TG10 living on the mountain slopes were captured together, they were only rarely relocated together. Visual observations confirmed that both females constituted independent family groups with their respective litter. Limited resources, mostly food in this case, are thought to make the association too costly to prevail.

Kinship is thought to play an important role in the social organization of family groups, given the persistence of mother-daughter associations, but also of sounders, as segregating females usually belong to the same litter and female groups tend to agglomerate (Spitz 1992, Janeau et al. 1995b, Kaminski et al. 2005). Gabor et al. (1999) showed that even if most individuals of a sounder were genetically related, some of them were not, as a consequence of fission-fusion dynamics between sounders, and dispersal of subadults (Truvé and Lemel 2003). In African elephants (*Loxodonta africana*) individuals usually live in stable family groups of adult females and their dependant offspring that might share common home-ranges with other family groups, and therefore form clans, without being necessarily genetically related (Charif et al. 2005). However, fission and fusion events within those clans happened more frequently between related groups (Archie et al. 2006). Even though Asian elephants (*Elephas maximus*) are organized in similar family groups with overlapping home ranges, associations and transfers between those groups have not been reported (Fernando and Lande 2000). Female and immature sperm whales (*Physeter macrocephalus*) live in stable, and partially matrilineal, social units. Social units are maintained when two or more social units move together, but exchanges between social units are also observed (Christal et al. 1998, Christal and Whitehead 2001). Considering the aforementioned examples, we assume kinship to be more important to maintain interactions within family groups than between them. Nevertheless, kinship might also favour fission-fusion patterns within sounders, thus allowing related individuals to tolerate each other and to share common resources, such as resting or feeding sites. However, our results showed that distribution and quality of resources might also contribute to influence the social organization of wild boar, and that associations of adult females might not necessarily be maintained.

If nocturnal activity seems to be coordinated within a family group, there is no evidence of coordination within sounders, as they rather split or exhibit important fission-fusion activity in accordance to resource distribution. Thus, the shooting of adult individuals is unlikely to modify the nocturnal socio-spatial behaviour of a sounder. As associations were stronger

within family groups and activities appeared to be coordinated, members of a family group might rapidly learn to find optimal resources. However, our data showed that nocturnal activity can as well be made in association with relatives as alone, even as juveniles. As individuals within a family group tend to associate randomly at night, the loss of individuals due to culling might not affect this pattern significantly. Moreover, the strong associations which are maintained in both weaned juveniles and subadults would probably last over the loss of the mother, as already mentioned by other authors (Spitz 1992, Rossel et al. 2006). Either way, nocturnal activity and consecutive damage are certainly more dependent on factors such as population density and distribution of resources than on social organization.

Acknowledgments

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SUMMARY & CONCLUSION

Summary

Chapter one

In the first chapter, we exposed the limitations about the estimation of wild boar abundance, presented the applied methods and results, and discussed their consistency. The estimation of wild boar abundance is constrained by several species' characteristics such as nocturnal activity, preference for habitats with important cover, absence of natural marks that would allow individual identification and dynamic grouping patterns. We applied a modified capture-mark-recapture method to cope with these features. Wild boar were trapped in cages and marked using individual ear-tags and/or radio-transmitters, which enabled their further identification. Recaptures were performed using motion-detecting camera-traps set on maize-baited spots. We used two estimators operating with resights (direct observations or pictures) to assess population size: Minta-Mangel estimator and Bowden's estimator. Both allow multiple sightings of individuals and only marked individuals have to be identified. The sampled surface used to estimate the density was determined using the actual home range size reported in our study area.

Camera-traps proved to be suitable to observe wild boar, as their flashing did not disturb the animals. Total population estimates were stable over the three years of survey and in accordance with the reported culling bags. However, our estimates showed poor precision regarding the wide confidence intervals. This lack of precision is mainly due to insufficient marking and variations in the timing of the counting sessions rather than to technical failures. Indeed, as the marking was not initially intended for counting purpose, younger individuals were neglected. Thus, we estimated their number and added it to the capture-resight estimates, as we could not apply the estimators on these individuals. Moreover, the number of marked individuals appeared to be low considering our total population. Finally, as we held our sessions in early June, the agricultural crops certainly attracted an important part of the population, marked and unmarked, outside of the forests and maintained them away from the counting spots. If both the capture-resight method and the estimators seem very promising to estimate wild boar population size, marking should be extended to all age-classes and sessions

should be planned so as to maximize the attraction of the baited sites. Nevertheless, the densities we reported are among the highest reported from Europe, both in hunted and non-hunted areas, and reflect the favourable environmental conditions of our study area. Our results stress the importance to consider the local spatial behaviour of wild boar as well as habitat features when determining densities.

Chapter two

In the second chapter, we used culling data to assess the effect and efficiency of the applied management in Canton Geneva. If science-based management is improved by long-term studies that investigate sex and age structure of a population in relation with environmental factors, this kind of data is mostly missing in wild boar, and the analyse of harvest data is preferred. As hunting was abolished in the Canton of Geneva, the wild boar population is exclusively controlled and monitored by official game wardens. This particular situation allowed us to use consistent data recorded on the culled individuals. First, we determined growth rates, body weight development and the distribution of births, as these data give information on the reproductive potential of the population. Second, we assessed the structure of the harvested population and the culling efficiency. Finally, we used the marked individuals to determine the effect of the culling strategy on survival parameters among the different age-classes.

The reproductive potential was likely to be important, as the considered indicators reflected the favourable conditions in our study area. Reported growth rates consistently allowed important body weight development, juvenile females to participate to reproduction and subadult females to continue to gain weight. Although the main farrowing period was in spring, births were distributed all year round. The culling efficiency decreased over the years of survey, in terms of quantity (less individuals shot) and quality (increased proportion of juveniles), as a consequence of both application of the shooting protocol and the species' ecology. As game wardens have to avoid shooting leading or lactating sows and solitary adult males, adults experienced a high survival. As a consequence, the most productive individuals, in terms of breeding potential, were maintained in the population, and certainly contributed to compensate the losses caused by the shooting. Given their important body development, individuals grow big rapidly, and differentiation from adults is hindered. Thus, subadults also displayed high survival and probably participated actively to reproduction. Given these features, the main culling effort affected the juveniles, which experienced the lowest survival,

as a consequence of their numerical importance and unproblematic identification. Even if the environmental conditions are already likely to favour the population dynamic, the current shooting regime contributed to maintain a dynamic and numerous population, rather than to induce a population decrease. That said, it appeared important to restrict the culling to the only lactating females with dependant piglets, and to increase the effort on the bigger individuals especially in autumn when lactating sows are scarce.

Chapter three

In the third chapter, we used diurnal and nocturnal radio-locations of wild boar simultaneously tracked on a common area to assess their social organization and grouping patterns. These “tracking groups” were regularly located at daytime and intensively tracked during the night. All individuals of a single “tracking group” were located within time intervals of 1 to 1.5 hours. For each location, we calculated the distance between two individuals for each possible dyad. We used these locations to calculate a social affinity index between individuals as a function of combined locations (two individuals at the same place and time). Additionally, we assessed the spatial separation between individuals calculating the mean distance between individuals for all non-combined locations. We also used the social affinity to establish UPGMA-cluster trees for some tracking groups including at least one adult female or a female with piglets. We used our data to assess the strength and variations of associations and spacing between individuals in family groups and sounders at day and night. Overall, associations between individuals were more marked during the day, and therefore on the diurnal resting places, than during the night. Juveniles and subadults associated for more than 70% of time at day. Adults associated around 50% at any time. These results are conditioned by the specific requirements of each age-class. However, they stress the importance of resting sites in the species’ requirements. Relations within family groups are important, but family groups tend to meet randomly, given that adult females share about 50% of their time. Moreover, associations are weakened at night and are similar in all age categories. The good quality of food resources is thought to limit competition and therefore individuals are probably equally able to feed on their own as in association with other individuals. If the socio-spatial interactions in the considered sounders certainly reflected breeding conditions of some individuals, environmental factors such as suitable resting places and food resources also contributed to explain the plasticity among reported associations. In areas with optimal resting places and sufficient food in the vicinity, sounders were

characterized by the similar movement patterns, close association in space and/time at the resting places, and lowered associations at night. Some individuals maintained close association at any time and were therefore considered to belong to a same family groups, even if their kinship still has to be defined. In areas where resources (shelter and food) are of poorer quality or more evenly spread, associations were more variable at any time of the day, when both grouping levels, sounders and family groups, were considered. Variations in daily and nightly structure of associations displayed fission-fusion type of interaction within and between family groups. Family groups can be reduced to one female and her offspring and rarely meet with other groups in case of unfavourable environmental resources, possibly reflecting a strategy that minimizes competition. Even if the genetic affiliation between individuals is unknown, we have reasons to think that social organization in wild boar is very dynamic, and driven by environmental factors as well as by kinship, and that the latter might be more important in the cohesion of family groups than in sounders. Finally, as cohesion is important in related individuals but interactions are still variable at night, we suppose that culling will have little effect on the social organization as a whole, and likewise on the spatial distribution of damages.

Conclusion

As we already discussed it in the introduction, wild boar have limited requirements to establish in a given area. Among those, the most important resources are resting sites and food. If the world-wide distribution of the species attests its adaptability, our limited study also contributes to stress this features once more. Even in fragmented landscapes with restricted wooded areas and important human activity, wild boar can be found at very high density, benefiting from various factors such as food supply in form of agricultural crops or mild climate. Natural conditions are likely to set the basic framework of the species' population dynamics, and have to be considered to set management goals. However, it is also very important to monitor the outcome and efficiency of the applied management. In our study, the high density of the population was certainly influenced by field conditions, but management was not adapted to the situation and rather contributed to maintain a dynamic population.

Given the subtle mechanisms resulting from interactions between environmental conditions, the species ecology, in terms of population dynamics and social organization (as showed in the present study), science-based management makes sense. It can contribute to adapt methods to the species particularities, to analyse data more deeply with appropriate tools, to assess its efficiency and point out critical points which have to be revised. As a consequence, the gathering of qualitative data on culled animals, such as sex, weight, age and reproductive status, should be favoured by the official wildlife offices in complement to the usually assessed quantitative data.

Although differences in hunting systems can be considerable from one administrative region to the other (table 1), in terms of traditions, rules, techniques and decisional framework, and joint management might be difficult, wildlife management has to be considered and analysed as one of the ecological parameters acting on a given species.

Table 1: Harvest rules, techniques and limitations in the study area.

County	Culling periode	Day	Hunting	Technique	Limitations
Geneva	July to February	all days	abolished in 1974	Nocturnal culling by official game wardens	Sows with depending piglets, leading sows and adult males (whithout important damage) are not shot
Vaud	September October November to January February	mon-tue-thu-fri mon-tue-thu-fri mon-tue-thu-fri-sat	classical hunting	single hunts or battues of up to 18 hunters	Sows with depending piglets are not shot, hunting is maintained with snow cover, no restrictions in weight and numbers only with important densities, weight is limited
Ain	August September to January until 20th December until 20th January	mon-wed-thu-sat-sun week-ends + holidays week-ends + holidays	classical hunting	battues with minimum 5 hunters single hunts or battues organized by the local hunter associations battues with minimum 10 hunters battues with minimum 10 hunters	only in fields and with important damage no restrictions, harvest cotes for each communal association are discussed in commissions. Only animals < 50 kg can be shot in January. snow depth < 15 cm snow depth < 15 cm --> only in case of important damage and with official authorization
Haute-Savoie	August September to Januaray	mon-tue-thu-sat-sun and holidays	classical hunting	battues single hunts or battues	only in fields and with important damage Sows with depending piglets are not shot, hunting days and restricted weights are defined in each administartive sector, hunting with snow cover is not allowed in all sectors

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