UNIVERSITY OF SASSARI

DISSERTATION OF THE DEGREE OF PHD SCHOOL
IN NATURAL SCIENCE
UNIVERSITY OF SASSARI, 2010
XXII CYCLE

BEHAVIOURAL ECOLOGY OF WILD BOAR (*Sus scrofa*) IN AN APENNINE ENVIRONMENT

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FIRST PART*: GROWTH POPULATION PARAMETERS*

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INTRODUCTION

During last decades throughout Europe wild ungulate populations are experiencing simultaneous geographical and demographic expansion (Acevedo et al., 2005). This phenomena mainly act thanks to the changing modes of agricultural production and also to the depopulation of rural areas increased availability of fodder, the disappearance of the larger predators and also the hunting plans introduced. The demographic variation of ungulate populations have a consequent different impact on human activities.

The adopted measures, concerning wild species, try to regulate the presence of animals on the territories. Laws are addressed to species safeguard in one side and, on the other hand, to their containment, in order to avoid too much competition between them and human activities. The Bern Convention concerns the conservation of wildlife and the natural environment in Europe. In this case are taken appropriate measures to protect wild fauna species, as well as their natural habitats. However the same law provides for possible exceptions to this strict protection obligation to prevent serious damage to crops or livestock. The Directive on “Fauna, Flora, Habitats”, 92/43/CEE, concerns the conservation of natural habitats and the wild fauna and flora species present in these habitats, and is aimed at ensuring the preservation of biological diversity and the maintenance of a positive state of conservation of natural habitats and wild fauna and flora species of Community interest. Also in this case this law provides for derogation from strict protection as to prevent damage to crops, livestock, forests, fisheries, water or any other types of property.

The law that regulate the argument struggle between different needs. The one of specie conservation and, on the other hand, human activities. Among these it is clear an hostile situation: in one side agricultural activities, who take part of its would like the total absence of any damaging animal. On the other hand there is hunting activities world. This is constitute both from hunters and from complementary productive activities. Hunters are often stimulated by deep traditions and by social relationship, that goes beyond the simple capture moment. Furthermore hunting needs to be based on scientific monitoring that ensures sustainable harvests and it needs to be regulated by policies that address the timing, location and methods of hunting, as well as the distribution of benefits to all stakeholders. The satisfactory of needs so opposite is not simple and an imbalance in one sense or the other, could cause direct effects on animal populations and social conflicts.

The trade-off between reproduction and survival is a core concept of life history strategies. Because ungulates have strongly age-structured populations and markedly iteroparous life histories, different vital rates may respond differently to various limiting factors. Adult survival has a low yearly variability and a high potential impact on population growth rate, while juvenile survival has a high yearly variability and a low potential impact on population growth rate (Eberhardt, 2002; Gaillard et al., 1998). Juvenile survival, which determines recruitment, is highly sensitive to limiting factors. Ungulate females such as bighorn sheep *Ovis canadensis* (Festa-Bianchet et al., 1998), mountain goat *Oreamnus americanus* (Festa-Bianchet and Coté, 2008) or reindeer *Rangifer tarandus* (Cameron and Du Toit, 2005), tend to skip reproduction when in poor conditions so to maximize their own survival (Gaillard and Yoccoz, 2003).

Understanding species-specific responses to habitat variables should be an important precursor of conservation and management programs. Ecological and behavioural attributes can play an important role when attempting to predict interspecific differences in responses to habitat factors. To understand fully their effects and interactions and the relative influences of ungulates, is important to understand factors controlling population growth, animals distribution and behaviour.

Most animals use the same areas repeatedly over time, hence animal movements are often defined using the home range concept, where the home range is the area used by an animal over a given time interval (Burt, 1943; White and Garrott, 1990). Home range is characterized typically with descriptors of its size, shape and structure (Kenward, 2001). Patterns influencing home ranges are associated with basic aspects of animal life history. Consequently home ranges are determined by temporal, spatial, and individual level processes. Ecological factors such as density, food availability, weather generally or predation and human disturbance account for most of variation in the dynamics of ungulate populations (Acevedo et al., 2008; Gaillard et al., 2000; Jeppesen, 1987), often in interaction with phenotypic differences such as sex , age (Cederlund and Sand, 1992), social status or mating system (Sandell and Liberg, 1992).

It seems that differences between sexes in their spatial dynamics are regulated by two hypothesis one that relates to energetic needs only (Harestad and Bunnell, 1979) and the other concerning mating systems (Clutton-Brock, 1989). In polygynous species, males have two constraints, the female distribution and the distribution of other male competitors, while females have only one, resource distribution. Animals in highly productive areas are able to meet their resource needs using smaller areas than those inhabiting less productive areas. The space use of ungulates is determined by spatial distribution and seasonal variation in food quality and availability (Festa-Bianchet, 1988; Owen-Smith, 1994; Tufto et al., 1996) and agricultural lands were often an important component of wildlife spatial behaviour. Corn provided for food from emergence through harvest and for cover throughout the growing season (McIvor and Conover, 1994; Nixon et al., 1991; Wolf and Conover, 2003). After corn harvest, home range sizes increased and centre locations shifted deeper into permanent cover, and other feeding areas (Nixon et al., 1991). Osborn and Jenks (1998) have noticed, that white-tailed deer density was twice higher in areas with access to agricultural land, suggesting that these fields are important feeding sites. Food intake often decline during winter season and apart from reducing food availability, climate conditions could affect ungulates movements. In Alpine ibex, for example, it has been demonstrate that the high snow cover reduce female movements in winter and in summer with high temperatures females increase their ranges (Grignolio et al., 2004).

Studies of habitat selection provide information in fact on environmental characteristics needed by animals, essential knowledge for the development of wildlife management and conservation policies. Habitat heterogeneity is an important feature because different habitat types has different and complementary resources. Predation risk is an important factor influencing the habitat choice of ungulates (Brown, 1999; Lima, 1998). Human harvest can affect the density of ungulates, not only by direct removal of individuals and avoidance behaviour but also through reduced fitness (Frid, 1997). Female moose (*Alces alces*) (Edwards, 1983), caribou (*Rangifer tarandus*) (Bergerud et al., 1984; Heard et al., 1996), and bighorn sheep (*Ovis canadensis*) (Festa-Bianchet, 1988) all selected home ranges with habitats that provided security from predators and disturbance at the expense of forage quality. On the other hand, males of the same species selected home ranges searching for an abundance of high-quality forage inspite of security.

In area exposed to human disturbance ungulates may use different habitats depending on the time of the day (Loft and Kie, 1988; Mann and Putman, 1989). The main protection system against predators seemed to be the choice of bed-site, constituted by high vegetation and canopy cover (Alldredge et al., 1991; Linnell et al., 1999; Rachlow and Bowyer, 1998). Apart from spatial modification in case of disturbance, ungulates could also react with different activity responses, for example Ciuti et al. (2008) shown in mouflon (*Ovis orientalis musimon*) how females with fawns react faster to a disturb, increasing their flight response.

Wild boar population proliferation in Europe it has been one of the mayor causes of farming damages. This situation prejudiced relationship between hunters and farmers. Landowners are not helpful to grant fruition of territories for hunting activities. Furthermore farmers and hunters have different wishes: farmers would like the species extermination to stop crop damages, while hunters would like an expansion of the species to increase their hunting activity.

In many countries, wild boar population numbers have increased dramatically during the past three decades (Apollonio et al., 1988; Gerard et al., 1991; Saez-Royuela and Telleria, 1986; Schley et al., 1998). Wild boar can reach very high densities in many places where they are established and this has been attributed to the adaptable breeding biology (Saez-Royuela and Telleria, 1987). It is a highly polytocous species, pirmiparity might occur at a younger age than other European ungulates (Gaillard et al., 1993) and in the favourable years it s possible to have two breeding seasons. An important feature of wild boar is the high plasticity and adaptability to different ecological situations, as climate conditions, predation, hunting pressure. Reproductive features, such as birth period and litter size, are known to vary with latitude (Saez-Royuela and Telleria, 1987), and also drought conditions are able to shape the reproduction parameters (Fernàndez-Llario and Carranza, 2000). Very few research on reproduction and fertility were performed on this species, particularly in Italy. For this reason, the main goal of the ***First Part*** of this thesis was to define the reproductive features of an Italian wild boar population **(Chapter 1)**. I analyzed the influence of biological and ecological characteristics on reproductive status and fertility. The aim of the research was to understand the growth capacity of the population and make comparison with other studies performed in Europe.

An other aspect that promote the great species expansion is the omnivorous diet. Main items in wild boar diet always belong to the most abundant and most easily accessible food source for the period of the year. In the Mediterranean region, the abundant crop of wood fruits (acorn, chestnut, beech) is the wild boar’s main source of food from September to June, while in Summer, when natural foods were limited, they could searching for agricultural crops. Because of that any locally abundant food source is often exploited, and conflicts with humans have resulted from this behaviour. Food availability together with snow depth and temperatures are considered the limiting factors for wild boar, able to shape their spatial behaviour (Calenge et al., 2002; Keuling et al., 2008; Meriggi and Sacchi, 1991; Singer et al., 1981). In the ***Second Part*** of the thesis I analyzed the influence of biological and ecological characteristics in shaping wild boar spatial behaviour. In particular, I considered the influence on movements of different variables, such as individual features, weather conditions, population density and food resources availability. The habitat selection analyses could be useful to clarify the relationship between populations and vegetation typologies and to define the habitat requirements of wild boars. Therefore I performed the habitat selection to understand which environments were preferred by wild boars in different seasons **(Chapter 2)**. In the **Annex 1** I present a paper, concerning the habitat selection of Alpine ibex, in which was used the same analysis methodology.

Subsequently I examined a specific aspect of spatial behaviour, looking at the importance of water presence in the biology of the specie subject of this study. The water is considered a factor affecting the wild boar survival (Caley, 1993; Massei et al., 1997), in fact wild boar lack sweat glands or other efficient physiological cooling mechanism. Other works shown that wild boar seek the cool moist forests with an abundance of wallows especially during hot days (Howe et al., 1981). Furthermore nest sites were always located in close proximity to water (Fernàndez-Llario, 1996). I performed a research specifically addressed to the influence of water in the environment on spatial behaviour of wild boars **(Chapter 3)**.

In this study area, the wild boar is the main prey of predators, wolves and red foxes (Donaggio et al., 2009, submitted). Furthermore the hunting impact was very intensive, almost 9.6 hunted boar/100ha. Predation and intensive hunting pressure could cause modification in the wild boar spatial behaviour. The disturbance could bring out modification of range size, previous study shown an increase of home range size during hunting season (Baubet et al., 1998; Calenge et al., 2002). In this chapter I investigate the anti-predator strategies adopted by wild boar, checking on the use of refuge areas to avoid predation and human disturbance **(Chapter 4)**.

REFERENCES

Acevedo P, Delibes-Mateos M, Escudero MA, Vicente J, Marco J, Gortazar C. 2005. Environmental constraints in the colonization sequence of roe deer (Capreolus capreolus Linnaeus, 1758) across the Iberian Mountains, Spain. Journal of Biogeography 32:1671–1680.

Acevedo P, Ruiz-Fons F, Vincente J, Reyes-Garcia AR, Alzaga V, Gortazar C. 2008. Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. Journal of Zoology 276:37-47.

Alldredge AW, Deblinger RD, Peterson J. 1991. Birth and Fawn Bed Site Selection by Pronghorns in a Sagebrush-Steppe Community. Journal of Wildlife Management 55(2):222-227.

Apollonio M, Randi E, Toso S. 1988. The systematics of th wild boar (*Sus scrofa* L.) in Italy. Boll Zool 3:213-221.

Baubet E, Brandt S, Touzeau C. 1998. Effet de la chasse sur les stratégies d'occupation de l'espace des sangliers (Sus Scrofa). Analyses préliminaires. Gibier Faune Sauvage, Game Wildl 15:655-658.

Bergerud AT, Jakimchukz RD, Carruthers DR. 1984. The Buffalo of the North: Caribou (*Rangifer tarandus*) and Human Developments. Arctic 37(1):7-22.

Brown JS. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. Evolutionary Ecology Research 1:49-71.

Burt WH. 1943. Territoriality and home ranges as applied to mammals. Journal of Mammalogy 24:346-352.

Calenge C, Maillard D, Vassant J, Brandt S. 2002. Summer and hunting season home ranges of wild boar (*Sus scrofa*) in two habitats in France. Game Wildl Sci 19:281–301.

Caley P. 1993. Population dynamics of feral pigs (Sus scrofa) in a Tropical riverine habitat complex. Wildlife Research 20:625-636.

Cameron EZ, Du Toit JT. 2005. Social influences on vigilance behaviour in giraffes *Giraffa camelopardalis*. Animal Behaviour 69:1337-1344.

Cederlund NG, Sand HK. 1992. Dispersal of subadult moose (*Alces alces*) in a non migratory population. Canadian Journal of Zoology 70:1309-1314.

Ciuti S, Pipia A, Ghiandai F, Grignolio S, Apollonio M. 2008. The key role of lamb presence in affecting flight response in Sardinian mouflon (*Ovis orientalis musimon*). Behavioural Processes 77:408-412.

Clutton-Brock TH. 1989. Mammalian mating systems. Proc R Soc Lond B 236:339-372.

Donaggio E, Cappai N, Bernardi M, Gazzola A, Apollonio M. 2009, submitted. The predation impact on a wild ungulate community by two sympatric predators: red fox and wolf.

Eberhardt LL. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841–2854.

Edwards J. 1983. Diet shifts in moose due to predator avoidance. Oecologia 60:185–189.

Fernàndez-Llario P. 1996. Ecología del jabalí en Doñana: parámetros reproductivos e impacto ambiental: University of Extremadura.

Fernàndez-Llario P, Carranza J. 2000. Reproductive performance of the wild boar in a Mediterranean ecosystem under drought condition. Ethology Ecology & Evolution 12:335-343.

Festa-Bianchet M. 1988. Seasonal range selection in bighorn sheep:conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75(4):580-586.

Festa-Bianchet M, Coté SD. 2008. Mountain Goats: Ecology, Behavior and Conservation of anAlpineUngulate. Washington, DC: Island Press.

Festa-Bianchet M, Gaillard JM, Jorgenson JT. 1998. Mass- and Density-Dependent Reproductive Success and Reproductive Costs in a Capital Breeder. The American Naturalist 152(3):367-379.

Frid A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. Animal Behaviour 53:799-808.

Gaillard J-M, Yoccoz NG. 2003. Temporal Variation in Survival of Mammals: A Case of Environmental Canalization? Ecology 84(12):3294-3306.

Gaillard JM, Brandt S, Jullien JM. 1993. Body weight effect on reproduction of young wild boar (*Sus scrofa*) females: a comparative analysis. Folia Zoologica 42:204–212.

Gaillard JM, Festa-Bianchet M, Yoccoz NG. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Tree 13(2):58-63.

Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annu Rev Ecol Syst 31:367-393.

Gerard JF, Cargnelutti B, Spitz F, Valet G, Sardin T. 1991. Habitat use of wild boar in a French agroecosystem from late winter to early summer. Acta Theriologica 36:119-129.

Grignolio S, Rossi I, Parrini F, Bassano B, Apollonio M. 2004. Seasonal variations of spatial behaviour in female Alpine ibex (*Capra ibex ibex*) in relation to climatic conditions and age. Ethology Ecology & Evolution 16(3):255-264.

Harestad A, Bunnell FL. 1979. Home range and body weight—a reevaluation. Ecology 60:389-402.

Heard DC, Williams TM, Melton DA. 1996. The relationship between food intake and predation risk in migratory caribou and implications to caribou and wolf population dynamics. Rangifer 9:37-44.

Howe T, Singer FJ, Ackerman BB. 1981. Forage relationship of European wild boar invading Northern hardwood forest. The Journal of Wildlife Management 45:748-754.

Jeppesen JL. 1987. Impact of human disturbance on home range size, movements and activity of red deer (Cervus elaphus) in a Danish environment. Dan Rev Game Biol 13(2):1-38.

Kenward RE. 2001. A Manual for Wildlife Radiotracking. London: Academic Press.

Keuling O, Stier N, Roth M. 2008. Commuting, shifting or remaining? Different spatial utilisation patterns of wild boar Sus scrofa L. in forest and field crops during summer. Mammalian Biology.

Lima SL. 1998. Nonlethal effects in the ecology of predator - prey interactions - what are the ecological effects of anti-predator decision making? . Bioscience 48:25-34.

Linnell JDC, Nijhuis P, Teurlings I, Andersen R. 1999. Selection of bed-sites by roe deer *Capreolus capreolus* fawns in a boreal forest landscape. Wildlife Biology 5:225-231.

Loft ER, Kie JG. 1988. Comparison of pellet-group and radio triangulation methods for assessing deer habitat use. Journal of Wildlife Management 53(3):524-527.

Mann JCE, Putman RJ. 1989. Patterns of habitat use and activity in British populations of sika deer of contrasting environments. Acta Theriologica 34:83-96.

Massei G, Genov P, Staines BW, Gorman ML. 1997. Mortality of wild boar, *Sus scrofa*, in a Mediterranean area in relation to sex and age. Journal of Zoology, London 242:394-400.

McIvor DE, Conover MR. 1994. Perceptions of farmers and non-farmers toward management of problem wildlife. Wildlife Society Bulletin 22(212-219).

Mech LD, Fritts SH, Wagner D. 1995. Minnesota wolf dispersal to Wisconsin and Michigan. Am Midl Nat 133:368–370.

Meriggi A, Sacchi O. Habitat selection by Wild Boars in Northern Apennines (N-Italy); 1991. p 435-438.

Mladenoff DJ, Sickley TA, Wydeven AP. 1999. Predicting gray wolf landscape recolonization: Logistic regression models vs newfield data. Ecol Appl 9:37-44.

Nixon CM, Hansen LP, Brewer PA, Chelsvig JE. 1991. Ecology of White-Tailed Deer in an Intensively Farmed Region of Illinois. Wildlife Monograph 118:3-77.

Osborn RG, Jenks JA. 1998. Assessing dietary quality of white-tailed deer using fecal indices: effects of supplemental feeding and area. Journal of Mammalogy 79:437-447.

Owen-Smith NR. 1994. Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. Ecology 75:1050-1062.

Rachlow JL, Bowyer RT. 1998. Habitat selection by Dall’s sheep (Ovis dalli): maternal trade-off. Journal of Zoology, London 245:457-465.

Saez-Royuela C, Telleria JL. 1986. The increased population of the Wild Boar (*Sus scrofa* L.) in Europe Mammal Review 16(2):97-101.

Saez-Royuela CJ, Telleria JL. 1987. Reproductive trends of the wild boar (*Sus scrofa*) in Spain. Folia Zoologica 36(1):21-25.

Sandell M, Liberg O. 1992. Roamers and stayers: a model on male mating tactics and mating systems. American Naturalist 139:177-189.

Schley L, Krier A, Wagner M, Roper TJ. 1998. Changes in the wild boar Sus scrofa population in Luxembourg during the period 1946 to 1996. Bull Soc Nat luxemb 99:77-85.

Servanty S, Gaillard J-M, Allainé D, Brandt S, Baubet E, Johnson AK. 2007. Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. Behavioral Ecology 18:427–432.

Singer FJ, Otto DK, Tipton AR, Hable CP. 1981. Home ranges, movements, and habitat use of European Wild Boar in Tennessee. Journal of Wildlife Management 45(2):343-353.

Sodeikat G, Pohlmeyer K. 2001. Temporary home range modifications of wild boar family groups (*Sus scrofa* L.) caused by drive hunts in Lower Saxony (Germany). European Journal of Wildlife Research 48:161-166.

Tufto J, Andersen R, Linnel J. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology 65:715-724.

White GC, Garrott RA. 1990. Analysis of wildlife radio-tracking data. San Diego. London: Academic Press.

Wolf T, Conover MR. 2003. Feral pigs and the environment: an annotated bibliography. Berryman Institute Publication 21, Utah State University, Logan; Mississippi State University, Starkville.

FIRST PART

Growth population parameters

Chapter 1

Factors affecting fertility and reproduction in wild boar (*Sus scrofa*) in a mountainous environment

FACTORS AFFECTING FERTILITY AND REPRODUCTION IN WILD BOAR (*Sus scrofa*) IN A MOUNTAINOUS ENVIRONMENT

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ABSTRACT

Identify which factors influence the growth of a wild population is crucial to apply a correct management. In this paper we analyzed the variation in fertility and reproduction in wild boar (*Sus scrofa*) females, using shot animals collected in three hunting seasons. Wild boar females had to reach a threshold body weight of 35 Kg before breeding, moreover pregnant females were heavier than not pregnant. The pregnancy status seemed to be affected by chestnut availability of the previous year and by climate condition of the spring before the hunting season. The litter size ranged from 1 to 9 with a mean of 4.74 ± 0.115, and was affected by female age class, in fact subadult females had smaller litter size than females. The analysis of foetuses condition shown a difference between years and an improvement of foetuses condition with the increase of mother condition and litter size. The peak of birth was located from February to April, generally adult females bred before subadult ones. In second sample year we observed a general births anticipation and subadult females bred before adult ones The low body weight threshold, the high litter size and the plasticity in breeding and births period, in comparison with other ungulate species, were typical features of a population with a low life expectancy because of an high hunting pressure.

INTRODUCTION

Different biological and ecological features may affect the reproductive biology of many ungulates species and in literature is possible to find several examples of their effect on vital rates (Clutton-Brock and Iason, 1986; May and Rubesnstein, 1985). In ungulates, for example, body mass is a good proxy for individual performance (Clutton-Brock, 1991). As a general rule, the heaviest individuals survive better at all ages (Gaillard et al., 1997; Gaillard et al., 2000a) and, starting earlier in life, they produce a larger number of offspring than lighter conspecifics (Hewison and Gaillard, 1996). Female age may affect the timing of reproduction (Langvatn et al., 2004).Generally female performances could also be driven by climatic conditions, through their impact on food resources (Gaillard et al., 1997; Gaillard et al., 1992; Green et al., 1989; Langvatn et al., 2004; Pettorelli et al., 2001). Quantity and seasonality of food may have a strong impact on dynamics of ungulate populations. It influences ovulation and conception rates, neonatal mortality, age at first reproduction and number of offspring per birth event, and the moment when females reach the condition threshold and the peak of food availability for offspring (Clutton-Brock and Albon, 1989; Hardy, 1996; Langvatn et al., 1996).

The wild boar (*Sus scrofa*) is a large, polygynous mammal that can reach very high densities and with a significant reproductive effort. It has a high reproductive capacity based on the relatively short gestation period and the high mean litter size, whereas most other similar-sized ungulates produce singletons. Some studies conducted in Mediterranean basin (France, Spain, Italy) shown a mean litter size higher than 4 (Mauget, 1972; Pedone et al., 1991; Saez-Royuela and Telleria, 1987; Servanty et al., 2007), while an average of 5 foetuses/litter in Central and Eastern Europe (Ahmad et al., 1995; Briedermann, 1971; Dzieciolowski, 1991; Servanty et al., 2007). The birth weight of the piglets is slightly more than 1 kg each (Fernàndez-Llario et al., 1999). Females wild boar can give birth for the first time at a younger age (1 year of age, Mauget 1981) than other similar-sized ungulates.

The wild boar reproductive performance is affected by heavy snowfall and low temperatures in populations located in areas were the harshest season is winter. In other areas, as the Mediterranean one, summer may be the most extreme season (Massei et al., 1996). It is underlined that in dry years, the only females that usually breed are those that have completed their corporal development, while in rainy years, the percentage of pregnant adult females increases and litter size are larger (Fernàndez-Llario and Mateos-Quesada, 2005). Previous studies have shown that the sexual maturity in wild boar females strongly depends on resource availability, especially on acorn mast, that is the main food item of wild boars but a typical pulsed resource (Ostfeld and Keesing, 2000). The fluctuations from year to year of this resource may induce large variation in females reproduction and thereby in population growth rate. The greater the production of acorns, the earlier births and the higher birth synchrony occur (Ostfeld and Keesing, 2000). Some research showed a relationship between habitats with abundant food and the number of pregnant females (Massei et al., 1996; Saez-Royuela and Telleria, 1987). Climate characteristics and food availability contribute to body mass increase and body mass plays a fundamental role in shaping variation in life-history traits. The individual body mass is a determinant of litter size and primiparity age.

Wild boar has been considered an highly adaptable species, with adaptable feeding and reproductive behaviour. Very sparse are knowledge about reproduction and fertility of wild boar in Italy. This research was conducted in a mountainous area, in which wild boar was subject to a really strong hunting pressure, consequently the wild boar population had a short generation time. For a correct management of critical wild population, as the wild boar, it is important to kwon the potential growth of the population, for this reason we aimed to describe the reproductive pattern in this wild boar population. We analyzed the pregnancy status of females looking for biological features that could affect it, considering the age and body mass threshold. We studied the effect of female biological features on litters, considering both litter size and foetal conditions. We regarded the birth period and biological features that could affect its temporal placing. Finally we evaluated whether ecological characteristics were related to females and foetuses characteristics.

METHODS

Study area - The study area was located on the Tuscan slope of the Apennine Mountains, in the Arezzo Province, Italy (43°48’N, 11°49’E). It had a surface of 11000 ha and an altitude ranging from 300 m to 1414 m a.s.l.. The territories of 7 wild boars hunting teams surrounded a protected area (Oasi “Alpe di Catenaia” OAC) which had an area of 2730 ha where hunting was strictly forbidden (Figure 1).

***Figure 1**: Study area. Territories of 7 hunting teams, surrounding the OAC (in grey).*

The cover areas was very extended, over than 80 % of the study area. Deciduous woods were constituted by chestnut (*Castanea sativa*), beech (*Fagus sylvatica*) and turkey oak (*Quercus cerris*). Coniferous woods were composed of black pine (*Pinus nigra*), white fir (*Abies alba*), and Douglas fir (*Pseudotsuga menziesii*). Undergrowth vegetation showed species like broom (*Cytisus scoparius*), fern (*Pteridium aquilinum*), bramble (*Rubus spp*.), juniper (*Juniperus spp*.), hawthorn (*Crataegus spp.*), wild rose (*Rosa spp*.), and blackthorn (*Prunus spinosa*).

The ungulate species most represented in the study area were wild boar (*Sus scrofa*) and roe deer (*Capreolus capreolus*).

The climate was continental with an high humidity rate, hot and dry summers (from June to August we found highest temperatures and lowest rainfalls), and cold and rainy winters (in October and December we found maximum rainfalls). Snow could fell from October to April with a maximum from January to March when the temperatures were low.

In the study area wild boar hunting period ranged from September to January and could vary in presence of high crop damages. The shooting technique was drive hunts with a large number of dogs and 25-50 hunters with dogs and permitted the harvesting of males and females of each age class. Hunting days were three per week: Wednesday, Saturday and Sunday. In this study area the hunting activity was really intensive (9.6 hunted boars/100 ha).

Methods - Data were collected during 3 hunting seasons (2006-2007, 2007-2008, 2008-2009), from September to January. During all hunting days, trained hunters gathered lower jaws of all boars and reproductive tracts of all females and also culled day and location of shooting, sex and weight of each animal shot. Every week we collected all samples of the seven hunting teams and then we analyzed all at the laboratory.

In laboratory the age of all animals was estimate by eruption and consumption of teeth (Boitani and Mattei, 1992; Genov et al., 1991; Massei and Toso, 1993). Animals were then grouped on the basis of age in three different age class: piglets (< 12 months of age), subadults (1-2 years old), adults (> 2 years old). After age estimation pregnant females' lower jaws were boiled to remove fat and muscles and then measured with an electronic calliper (Borletti, mod.CDJAAB30). Three characters of mandibles were measured: the length of symphysis (LS), the length from the angle to anterior-most point of symphysis (LAS) and the length from the condyle to anterior-most point of symphysis (LCS) (Figure 2).

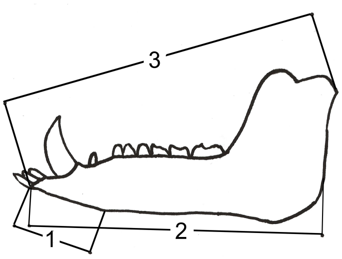

Figure 2. *Lower jaw's measurements: 1 = LS length of symphysis; 2 = LAS length from the angle to anterior-most point of symphysis; 3 = LCS length from the condyle to anterior-most point of symphysis.*

Looking for foetuses or corpora lutea in ovaries we determined if females were pregnant or not (N = 995). Uteri were dissected and embryos or foetuses were counted, weighted, measured (total length foetuses TLF) and, when possible, sexed. All foetuses too small to be identified by eye (N=41), have been sexed using genetic markers co-amplifying a fragment of the Y chromosome (SRY gene, Richard et al. 1994) and a portion of mitochondrial DNA (cytochrome B gene) using universal primers L14841 and H15149 (Koecher et al., 1989). Total genomic DNA was extracted by using commercial kit GenElute Mammalian Genomic DNA miniprep (Sigma-Aldrich, St.Louis, Missouri) and kept at –20°C. Each polymerase chain reaction (PCR) was performed in a 10-μL reaction volume, containing 3 μL of DNA solution, 0.5 U of Taq DNA polymerase (Euroclone, Siziano, Italy), 1 x PCR buffer (Euroclone), 3.0 mM $MgCl_2$, 100 μM of each dNTP and 2 pmol of each primer. The amplification profile was set up with an initial step of denaturation at 95 °C for 3 min, followed by 35 cycles of 92 °C for 40 s, Ta (58-55°C) for 60 s, and 72 °C for 40 s. A further extension step of 72 °C for 10 min concluded the reaction. PCR-amplified fragment were visualized in a 2% agarose electrophoresis gel. Males resulted in a double band, one for the SRY fragment and another for the mtDNA positive control, while females showed the latter band only.

Temperature, precipitation and snow cover data were collected by 4 weather stations located in and around the study area by CFS (Corpo Forestale dello Stato) (Figure 3).

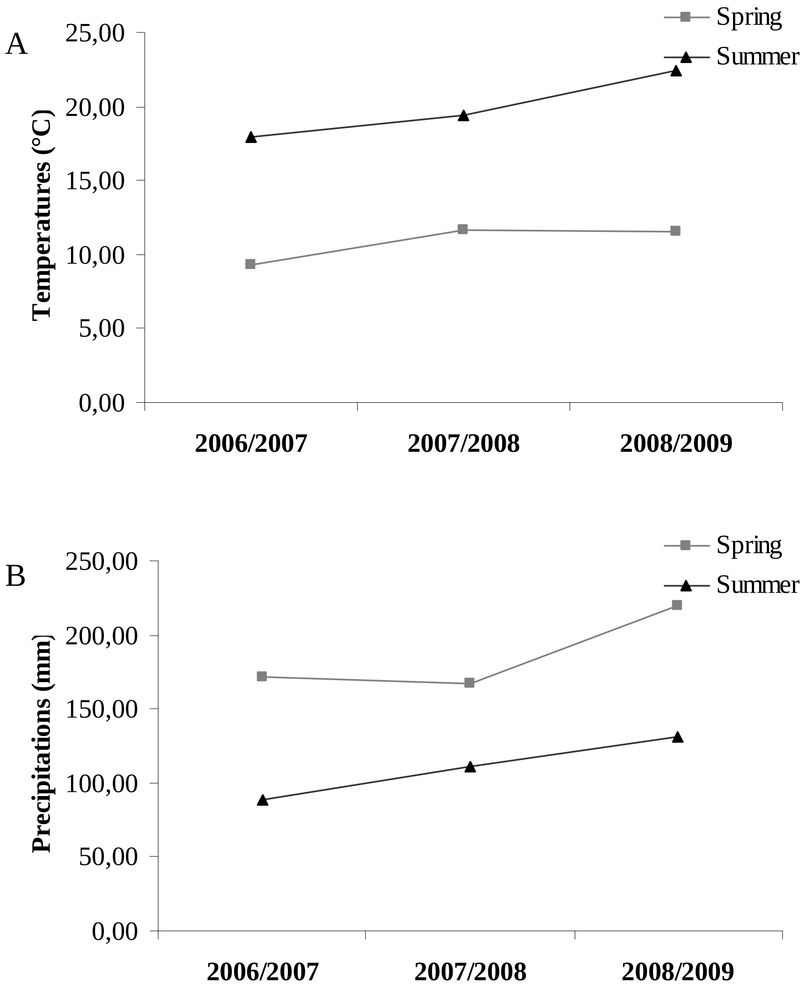

***Figure 3**: Meteorological features in Spring and Summer in different years. A represents temperatures (°C), while B represents precipitations (mm).*

The National Institute of Forestry (Arezzo) reported annual deciduous production evaluated as seeds density (MG/ha) of chestnut (*Castanea sativa*), Turkey oak (*Quercus cerris*), beech (*Fagus sylvatica*) (Figure 4). The fruits calculation was periodically performed, every fifteen days, in autumn and winter period, using collection traps of 50x50 cm, systematically distributed in all OAC. This method allowed to carefully estimate the yearly seeds production.

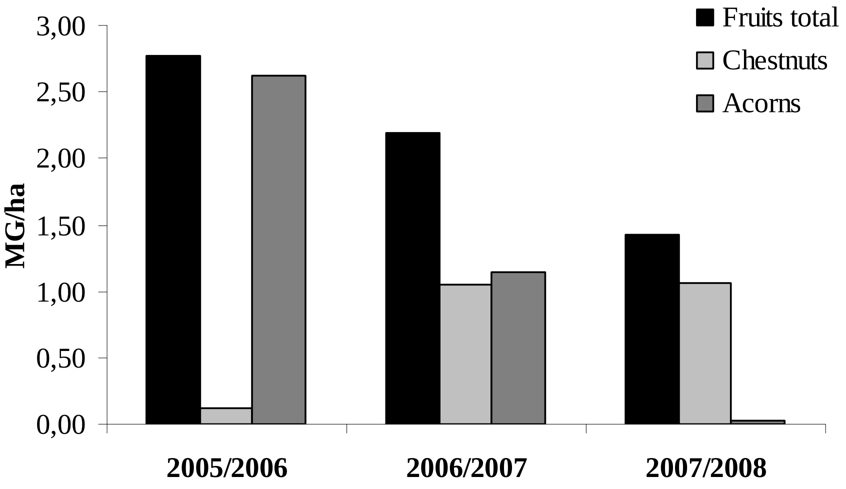

Figure 4*: Fruits production (MG/ha) in OAC.*

Data analysis – Considering females lower jaws measures, in some cases we couldn’t collect all three dimensions because of lower jaws breakage. Therefore we verified the correlation (Pearson Correlation) between all measurements, to establish if we could use only the one we had the grater sample size.

For each female of which we collected lower jaws measurements, we calculate the Body Mass Index (BMI) as the ratio between female body weight and the square lower jaws measure (Hwang et al., 2005; Jakob et al., 1996; Moya-Laraño et al., 2008). The same BMI was calculate for foetuses, using foetuses body weight and their total length. This index allowed us to quantify the maternal and foetuses conditions.

Time of gestation was estimated from the average weight of foetuses in the litter, using the Hugget and Widdas formula (1951), applied by Vericad (1994) also in wild boars:

$$t = \frac{3\sqrt{\text{Weight}} + 24.1}{0.097}$$

The determination of time of gestation permitted us to evaluate the foetuses age and, consequently, the expected date of birth, in the case in which the foetus would be born. Birth dates were therefore determined using mother's day of death, foetuses age and a gestation period of 120 days (Abaigair et al., 1994; Mauget, 1972).

In order to compare birth periods in different years we calculate the days of delay from December 1st of every year, asserting that none piglets could born before this date.

We calculated the Gaussen Index (GI) as the amount of precipitation minus twice the mean temperature (Dajoz, 1973) (Figure 5). The GI is a measure of the water available for vegetation (Dajoz, 1973), and has been previously related to ungulate performance (Gaillard et al., 1997; Garel et al., 2004).

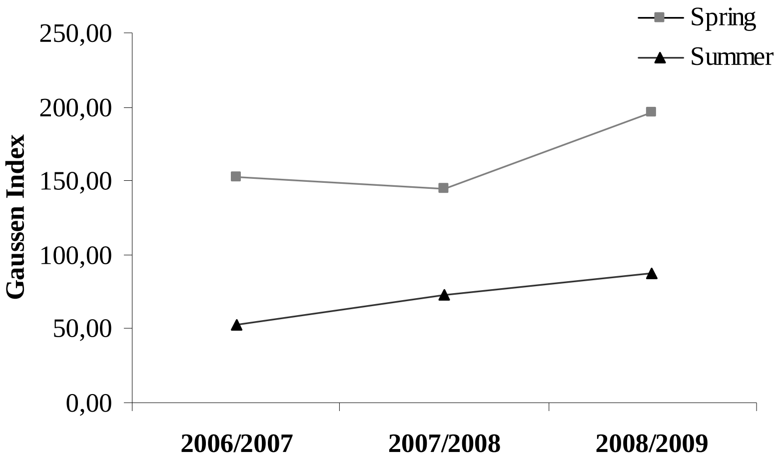

***Figure 5**: Gaussen Index in Spring and Summer of different years.*

To checked the different body weight in pregnant and not pregnant females with an independent samples t-test. In order to analyze the pregnancy status we fitted a logistic regression, considering the pregnancy status as the binomial dependent variable (0 = not pregnant, 1 = pregnant). In the logistic regression we should excluded body weight from the model, because its it is correlated with other independent variables. Therefore we considered the females age class, quantity of chestnut the year before the hunting season and the GI of the spring just before hunting season as independent variables. A forward stepwise (likelihood ratio) procedure was used in order to detect independent variables that could be successfully included in the model equation.

The litter size was analyzed using a GLM in which the total number of foetuses in the litter was the dependent variable. Females age class, considering only more than 1 year old females, was used as a fixed factor and females BMI and the percentage of males in the litter were covariates. We tested the difference between age classes using pairwise comparisons with adjustment for multiple comparisons.

The foetuses conditions (foetuses BMI) was assessed using the linear-mixed model (LMM) in which the mother was considered as random effect. The dependent variable was the foetuses BMI, the hunting seasons and litter size were fixed factors and the females BMI were covariates. LMM pairwise comparisons with adjustment for multiple comparisons were performed to test differences between fixed factors of the model.

Finally we checked birth periods using a General Linear Model (GLM), considering days of delay from December 1st as the dependent variable and hunting season, females age class and litter size as fixed factors. The females BMI was insert as a covariate variable.

All statistical analyses were performed using the SPSS 13.0 program. In all tests significance was set at $p < 0.05$.

RESULTS

We collected and aged, in all three hunting seasons, a total of 1239 lower jows of shot wild boar females (265 in 2006-2007, 459 in 2007-2008 and 515 in 2008-2009) (Table 1).

Hunting seasons	Females			
	Piglets	Subadults	Adults	Total
2006-2007	98	105	62	265
2007-2008	178	128	153	459
2008-2009	189	165	161	515
Total	465	398	376	1239

***Table 1**: Shot wild boar females analyzed sample size.*

We verified the high level of correlation between all female lower jaws lengths (Table 2). To calculate the females BMI, we therefore choose the LS measure because we had the higher sample size for it.

		LS	LAS	LCS
LS	Pearson Correlation	1	**,912**	**,852**
	Sig. (2-tailed)		,000	,000
	N	326	158	60
LAS	Pearson Correlation	**,912**	1	**,920**
	Sig. (2-tailed)	,000		,000
	N	158	158	60
LCS	Pearson Correlation	**,852**	**,920**	1
	Sig. (2-tailed)	,000	,000	
	N	60	60	60

***Table 2**: Lower jaws measurements correlations. Bold font indicate significant correlation.*

In all three hunting season, 975 uterus were analyzed, 236 of which were pregnant, 121 with visible foetuses, the remaining were at the beginning of pregnancy (just with corpora lutea).

The youngest pregnant female was found in 2007-2008 hunting season and it was 7-9 months-old, furthermore we noticed that any females with a body weight over 35 kg was pregnant (Figure 6).

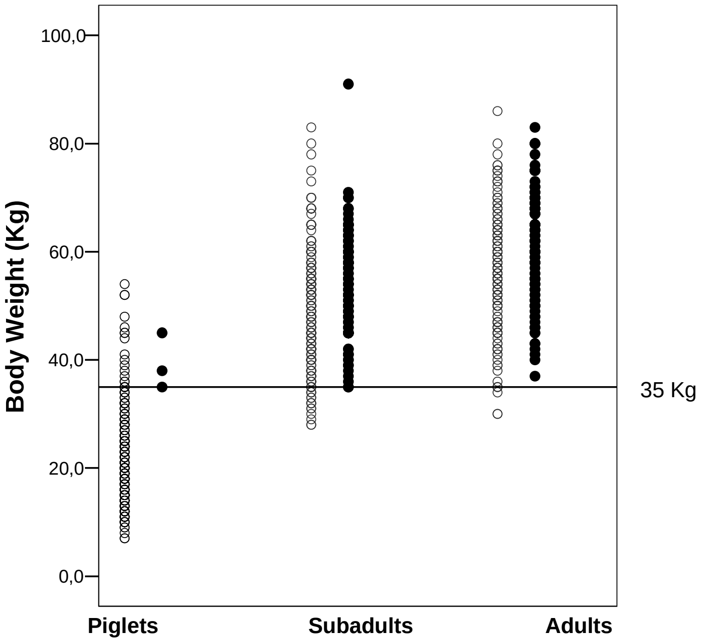

Figure 6*: Female body weights in relation to age classes and pregnancy status.*
Empty points = not pregnant females; Full points = pregnant females.

We found only 3 cases of piglet pregnant females with a mean body weight of 39.33 Kg versus a mean body weight of not piglet pregnant females of 21.35 Kg (N = 300). Subadult pregnant females (N = 115; mean body weight = 54.47 Kg) were heavier than not pregnant (N = 228; mean body weight = 49.09 Kg) (independent sample t-test: t = -4.664, df = 341, P < 0.001). The same result occurred in adult females, pregnant ones (N = 118) shown a mean body weight of 61.41 Kg, while the mean body weight of not pregnant females (N = 211) was 56.15 Kg (independent sample t-test: t = -4.655, df = 327, P < 0.001) (Table 3).

		Mean	SE	Lower Bound	Upper bound
Piglets	Not pregnant	21,35	0,55	20,28	22,42
	Pregnant	39,33	5,47	28,61	50,06
Subadults	Not pregnant	49,09	0,63	47,86	50,32
	Pregnant	54,47	0,88	52,74	56,20
Adults	Not pregnant	56,15	0,65	54,87	57,43
	Pregnant	61,41	0,87	59,70	63,12

Table 3*: Value of body weight estimated marginal means in relation to females age class and pregnancy status.*

According to the forward stepwise procedure of logistic regression females age class was excluded from the model. Chestnuts production during the previous year ($\beta = 0.493$, SE = 0.228, p = 0.031) and GI in the previous spring ($\beta = -0.023$, SE = 0.004, $P < 0.001$) seemed to affect pregnancy status. The increase of chestnuts production increase the chances for a female to be pregnant the year after. The GI in spring was the other variable that influenced the pregnancy status, given that its occurrence increased when GI decrease. From the total number of females shot we analyzed the percentage of pregnant females (Figure 7), even if the proportion of breeding females was under-estimated as we did not have access to the reproduction of females during the non-hunting season.

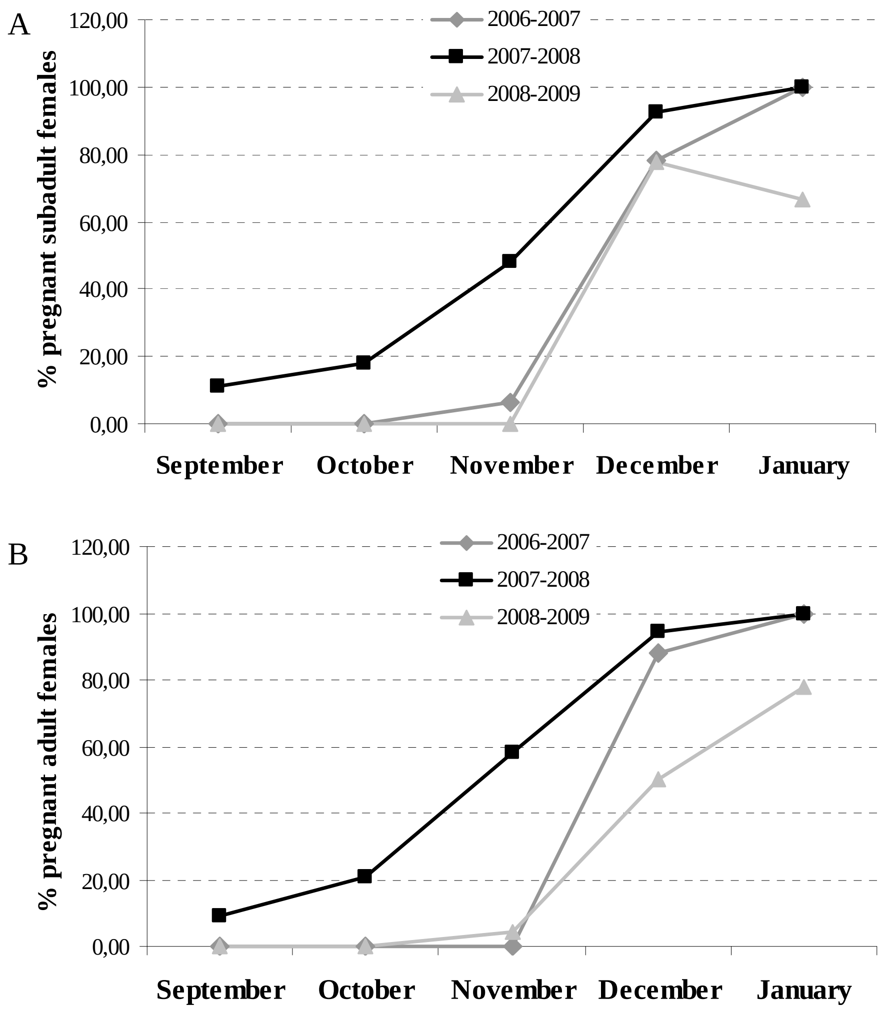

***Figure 7**: Percentage of subadult (A) and adult (B) pregnant females in three hunting seasons*

Hunting season	N	Min	Max	Mean	S.E.
2006-2007	20	1	7	4,10	0,347
2007-2008	76	2	9	4,96	0,128
2008-2009	25	2	7	4,60	0,258
Total	121	1	9	4,74	0,115

***Table 4**: Mean litter size in different hunting seasons.*

We obtained complete data from 121 litters. Litter size varied between 1 and 9 foetuses with a mean (± SE) of 4.74 ± 0.115 (Table 4).

The model derived from the GLM analysis showed a significant effect of female age classes (F = 4.372, df = 1, p = 0.040). Subadult females shown smaller litter sizes (mean ± SE: 4.615 ± 0.171) compared to the one of adult females (mean ± SE: 5.136 ± 0.179). From the analysis of litter size we calculate also the sex ratio of foetuses. In 2006-2007 the foetal sex ratio was 1 : 1.5 (males : females), in 2007-2008 was 1 : 0.98 and in 2008-2009 was 1 : 0.96.

Significant differences in foetuses BMI were detected according to hunting season ($F_{2,420}$ = 22.458, P < 0.001). This results underlined that the 2007-2008 hunting season foetuses were in better body conditions (mean ± SE: 2006-2007 0.369 ± 0.059; 2007-2008 0.571 ± 0.030; 2008-2009 0.355 ± 0.035) and the 2007-2008 hunting season was significantly different from the other two (2007-2008 vs 2006-2007: p = 0.001; 2007-2008 vs 2008-2009: P < 0.001; 2006-2007 vs 2008-2009: p = 0.826). Furthermore an influence on foetuses condition was given also by mother BMI ($F_{1,420}$ = 11.464, p = 0.001) and by litter size ($F_{6,420}$ = 6.034, P < 0.001). Females BMI had a direct effect on foetuses condition (parameter estimate = 0.137 ± 0.040). Moreover looking at the marginal means related to the influence of litter size on foetuses BMI, we observed that higher was the litter size better was the foetuses physical conditions.

The distribution of birth were analyzed starting from foetuses age. In the second hunting season (2007-2008) we observed a birth anticipation and a larger birth period, while in the other seasons there was a delay in births and a higher peak of births. In general the peak of births was located from February to April (Figure 8).

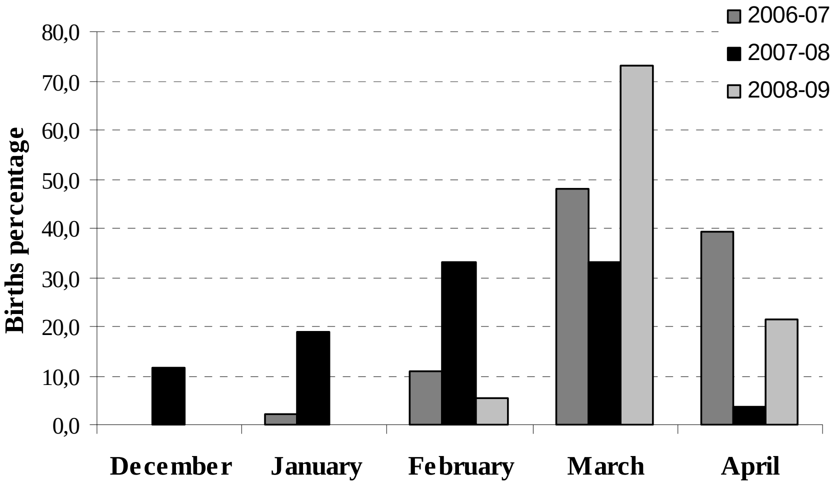

Figure 8: Births distribution.

Analyzing the delay of births from the first possible birth (December 1st) we underlined a significant difference between years (F = 10.610, df = 2, P < 0.001). Also the effect of interaction between females age class and hunting season seemed to influence the gestation and births period at the limit of significance (F = 2.701, df = 2, p = 0.074). In particular in the first and last hunting seasons subadult females always start the gestation with a delay in comparison with adult females. Instead in 2007-2008 we observed a general anticipation of gestation and consequently of births. Furthermore subadult females greatly anticipated gestation not only respect the other two seasons but also compared with adult females and consequently also births resulted anticipated. We observed that in 2007-2008 there were pregnant females in September while in the other two years there was a delay of pregnancy. Furthermore in the last hunting season (2008-2009) the percentage of pregnant females was low compared to other years, in which both subadults and adults reached 100% of pregnant females.

DISCUSSION

In this work we underlined the importance of female body weight on pregnancy status. Wild boar only reproduced when a threshold body mass has been reach like reported also for other ungulates (Coté and Festa-Bianchet, 2001; Gaillard et al., 1992). In our study area this threshold was 35 Kg (dressed weight), in contrast with previous studies conducted in France, in which the body weight threshold was lower: 20-25 Kg (Gaillard et al., 1993; Servanty et al., 2009). However was not observed the general rule that the threshold body mass to breed for the first time should be almost the 80% of the asymptotic adult mass, the value generally observed in ungulates (Gaillard et al., 2000b). Reached the body weight step also youngest females could breed, arriving to an high proportions of breeding females. The high proportion of pregnant females and the lower threshold body mass in relation to other species could be due to the high hunting pressure to whom wild boar were subjected in this study area. Comparing our result with other similar research we observed that, also if in our study area the hunting impact on population is higher (9.6 hunted boars/100 ha), the body weight threshold was higher than an other European cases. In France were observed 5.21 hunted boars/100ha and a threshold dressed weight of 20-25 Kg (Servanty et al., 2007); in Spain the hunting pressure was 0.063 hunted wild boar/100ha and 6.7% juvenile females were pregnant with the mean observed body mass of juvenile females was about 30 Kg (Herrero et al., 2008). Moreover the environment in the study area was quite homogeneous and rich, from a food availability point of view. Therefore the environment was able to support the great increase of population.

Such high proportions of pregnant females each year suggested that females should have the possibilities to meet the high energetic costs of a reproductive event. Therefore firstly they should arrive at the rut period in good conditions and this seems to depend on chestnuts availability of the food season before rut period (the previous autumn).

With reference to the litter size the mean we found in our analysis, 4.74 piglets per female, was similar to other studies conducted in Mediterranean basin (Massei et al., 1996; Saez-Royuela and Telleria, 1987), even if higher mean litter sizes were reported in studies in bibliography (Ahmad et al., 1995; Servanty et al., 2007). This divergence was in according with Bergmanns rule: the more northern populations tend to have an increased size of the litter (Abaigair et al., 1994; Saez-Royuela and Telleria, 1987). The litter size, as the percentage of pregnant females, could also be a result of heavy hunting activity within the area. The litter size increased appreciably in older females. Even if subadult females, that could be primiparous, made a contribution to the population growth, the most productive females, in term of litter size, were adult ones.

Whether litter size increase the births period tend to be postponed with latitude. In fact we observed the peak of birth between February and April, according with other studies performed in Southern Europe (Fernàndez-Llario and Carranza, 2000; Saez-Royuela and Telleria, 1987), where most births take place in March. But this result contrasted other European populations where the births period was mainly during April, May and June (Dardaillon, 1988), probably due to the higher latitudes at which these populations occurred.

An important feature of the litter was the physical conditions of foetuses (measured by foetuses BMI), that seemed to be directly related to females body conditions. Moreover whether a female was in good conditions it had enough energy to have a large litter with foetuses in good conditions.

Other explications were fundamental to completely describe our results, to do this we introduced some ecological features (temperatures, precipitations, GI, chestnuts production, population density). Favourable temperature conditions mainly reduced juvenile mortality, enhanced food availability is likely to boost reproductive success through younger age at first reproduction, larger litter size and earlier onset of oestrus within a season. It was known and clear the relationship between abundant food and the number of pregnant females, so we could assert that increasing the food abundance increased also the proportion of pregnant females.

Several studies have shown that good food conditions resulted in an earlier onset of oestrus, increased fertility and larger litter sizes and influences the age of first reproduction. The percentage of breeding females was mostly negative influenced by drought conditions (Fernàndez-Llario and Carranza, 2000). Different studies have indicated that older females are the earliest breeding boars, as they reach the necessary physical requirements sooner than other younger females (Fernàndez-Llario and Mateos-Quesada, 1998).

In this research we observed, in ecologically better conditions, an higher number of pregnant females, an pregnancy anticipation, earlier and larger births period, bigger litter sizes and better foetuses physical conditions, and subadult females bred earlier than adult females. The second sample year, in which we noticed these results, was characterized by high temperatures in spring, low rainfall in spring and a high GI in spring, an high production of chestnut a low population density the previous year.

Our results showed that the most important feature was the achievement of body weight threshold, independently from females age. Fixed this, seasonal characteristics were less important because females were able to adjust the timing of oestrus, consequently gestation and births period. We should consider that the life expectancy was quite low (70% of shot females were younger than 2 years old). Because of that we should attach importance to juvenile contribute to the population growth. Therefore the low body mass threshold, the low generation time and the great ability to adjust the breeding period could be a response to the high hunting pressure in the study area.

REFERENCES

Abaigair T, del Barrio G, Vericad JR. 1994. Habitat preference of wild boar (*Sus scrofa* L.) in a Mediterranean environment. Indirect evaluation by signs. Mammalia 58:201-210.

Ahmad E, Brooks JE, Hussain I, Khan MH. 1995. Reproduction in Eurasian Wild Boar in central Punjab, Pakistan. Acta Theriologica 40(2):163-173.

Boitani L, Mattei L. 1992. Aging Wild Boar (*Sus scrofa*) by tooth eruption. “Ongulés/Ungulates 91”. Paris-Toulouse: F. Spitz, G. Janeau, G. Gonzalez & S. Aulagnier (eds), S.F.E.P.M. - I.R.G.M. p 419-421.

Briedermann L. 1971. Zur Reproduktion des Schwarzwildes in der Deutschen Demokratischen Republik. Tag Ber Dt Akad Berlin 113:169-186.

Clutton-Brock TH. 1991. The evolution of parental care. Princeton: Princeton University Press.

Clutton-Brock TH, Albon SD. 1989. Red deer in the Highlands. Oxford: Blackwell Scientific Publications.

Clutton-Brock TH, Iason GR. 1986. Sex ratio variation in mammals. Q Rev Biol 61:339-374.

Coté SD, Festa-Bianchet M. 2001. Reproductive success in female mountain goats: the influence of age and social rank. Animal Behaviour 62:173-181.

Dajoz R. 1973. Précis d'écologie. Gauthier Villars.

Dardaillon M. 1988. Wild boar social groupings and their seasonal changes in the Camargue, southern France. Z Saugetierkunde 53:22-30.

Dzieciolowski RM. 1991. Ecological niches of five big ungulate in a forest tract. Folia Florestalia Polonica Series A-Forestry 33:56-70.

Fernàndez-Llario P, Carranza J. 2000. Reproductive performance of the wild boar in a Mediterranean ecosystem under drought condition. Ethology Ecology & Evolution 12:335-343.

Fernàndez-Llario P, Carranza J, Mateos-Quesada P. 1999. Sex allocation in a polygynous mammal with large litters: the wild boar. Animal Behaviour 58:1079-1084.

Fernàndez-Llario P, Mateos-Quesada P. 1998. Body size and reproductive parameters in the wild boar *Sus scrofa*. Acta Theriologica 43(4):439-444.

Fernàndez-Llario P, Mateos-Quesada P. 2005. Influence of rainfall on the breeding biology of Wild boar (*Sus scrofa*) in a Mediterranean ecosystem. Folia Zoologica 54(3):240-248.

Gaillard J-M, Boutin J-M, Delorme D, Van Laere G, Duncan P, Lebreton J-D. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. Oecologia 112:502-513.

Gaillard J-M, Pontier D, Brandt M, Jullien J-M, Allainé D. 1992. Sex differentiation in postnatal growth rate: a test in a wild boar population. Oecologia 90:161-171.

Gaillard JM, Brandt S, Jullien JM. 1993. Body weight effect on reproduction of young wild boar (*Sus scrofa*) females: a comparative analysis. Folia Zoologica 42:204–212.

Gaillard JM, Festa-Bianchet M, Delorme D, Jorgenson JT. 2000a. Body mass and individual fitness in female ungulates: bigger is not always better. Proc R Soc Lond 267:471-477.

Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo C. 2000b. Temporal variation in fitness components and population dynamics of large herbivores. Annu Rev Ecol Syst 31:367-393.

Garel M, Loison A, Gaillard J-M, Cugnasse J-M, Maillard D. 2004. The effects of a severe drought on mouflon lamb survival. Proc R Soc Lond 271:S471–S473.

Genov PV, Massei G, Barbalova Z, Kostova V. Aging Wild boar (*Sus scrofa* L.) by teeth; 1991. p 399-402.

Green WCH, Griswold JG, Rothstein A. 1989. Post-weaning associations among bison mothers and daughters. Animal Behaviour 38:847-858.

Hardy ICW. 1996. Possible factors inflluencing vertebrate sex ratios: an introductory overview. Applied Animal Behaviour Sd 51:217-241.

Herrero J, Garcıa-Serrano A, Garcıa-Gonzalez R. 2008. Reproductive and demographic parameters in two Iberian wild boar *Sus scrofa* populations. Acta Theriologica 53:355-364.

Hewison AJM, Gaillard JM. 1996. Birth-sex ratios and local resource competition in roe deer, Capreolus capreolus. Behavioral Ecology 7(4):461-464.

Huggett ASG, Widdas WF. 1951. The relation between mammalian foetal weight and conception age. J Physiol Lond 114:306-317.

Hwang YT, Larivière S, F. M. 2005. Evaluating body condition of striped skunks using noninvasive morphometric indices and bioelectrical impedance analysis. Wildlife Society Bulletin 33(1):195-203.

Jakob EM, Marshall SD, Utez GW. 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61-67.

Koecher TD, Thomas WK, Meyer A, Edwards SV, Paabo S, Villablanca FX, Wilson AC. 1989. Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers. Proc Nati Acad Sci USA 86:6196-6200.

Langvatn R, Albon SD, Burkey T, Clutton-Brock TH. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653-670.

Langvatn R, Mysterud A, Stenseth NC, Yoccoz NG. 2004. Timing and synchrony of ovulation in red deer constrained by short northern summers. American Naturalist 163:763–772.

Massei G, Genov PV, Staines BW. 1996. Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. Acta Theriologica 41:307-320.

Massei G, Toso S. 1993. Biologia e gestione del cinghiale. Istituto Nazionale per la Fauna Selvatica ed. 69 p.

Mauget R. 1972. Observations sur la reproduction du sanglier (*Sus scrofa* L.) a l'état sauvage. Ann Biol anim Bioch Biophys 12(2):195-202.

Mauget R. 1981. Seasonality of reproduction in the wild boar. Control of pig reproduction. Butterworths, London.

May RM, Rubesnstein DI. 1985. Reproductive strategies. Reproductive fitness 1-23 (CR Austin & RV Short, Eds). Cambridge: Cambridge Univ. Press.

Moya-Laraño J, Macías-Ordóñez R, Blanckenhorn WU, Fernández-Montraveta C. 2008. Analysing body condition: mass, volume or density? Journal of Animal Ecology 77:1099-1108.

Ostfeld RS, Keesing F. 2000. The function of biodiversity in the ecology of vector-borne zoonotic diseases. Canadian Journal of Zoology 78:2061-2078.

Pedone P, Mattioli L, Mattioli S, Siemoni S, Lovari C, Mazzarone V. Body growth and fertility in wild boars of Tuscany, central Italy; 1991; Godollo. p 604-609.

Pettorelli N, Gaillard GM, Duncan P, Ouellet J-P, Van Laere G. 2001. Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. Oecologia 128(3):400-405.

Saez-Royuela CJ, Telleria JL. 1987. Reproductive trends of the wild boar (*Sus scrofa*) in Spain. Folia Zoologica 36(1):21-25.

Servanty S, Gaillard J-M, Allainé D, Brandt S, Baubet E, Johnson AK. 2007. Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. Behavioral Ecology 18:427–432.

Servanty S, Gaillard JM, Toigo C, Brandt S, Baubet E. 2009. Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. Journal of Animal Ecology in press.

SECOND PART

Influence of biological and ecological features in shaping wild boar spatial behaviour

Chapter 2

Spatial behaviour and habitat selection in a wild boar population in a mountain area

SPATIAL BEHAVIOUR AND HABITAT SELECTION IN A WILD BOAR POPULATION IN A MOUNTAIN AREA

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ABSTRACT

Home range size and habitat selection of a wild boar *Sus scrofa* population were analyzed in Tuscan Apennine, Italy. The study was carried out from 2002 to 2008 using radio-telemetry. Seasonal home range size were not different but we found differences in spatial behaviour among years in relation to population density, although they resulted in contradiction to the "density-dependent hypothesis" that predicts an inverse relation between home range sizes and population density. According to "food-exploitation hypothesis" we have shown smaller home range when food availability was high. Wild boar females reacted to a variation in temperature conditions increasing their home range size during hot weather, reducing the activity range significantly when the ground was covered by snow (winter and spring). Wild boar males seemed not be influenced by these environmental factors. With regard to habitat selection our results didn't show any clear pattern of habitat preferences, probably as a consequences of the fine grain structure of the study area.

INTRODUCTION

During last decades in Italy wild boar (*Sus scrofa* L.) populations have rapidly increased, mainly because of environmental changes and human manipulations (Gazzola et al., in press). Wild boar has been considered a highly adaptable ungulate that occurs in a variety of habitats throughout their range (Lever, 1985). This species can reach high densities and this has been attributed to their omnivorous diet and plastic breeding biology (Fernàndez-Llario and Carranza, 2000; Saez-Royuela and Telleria, 1987). This flexibility may help wild boars to react to environmental conditions, adapting their seasonal home range sizes and moving to appropriate locations.

The factors influencing the wild boar home range have been studied in a wide variety of habitats. The most frequently considered factors were: seasonality, individual characteristics, such as sex and age of the wild boars, population density, environmental characteristics, including resources availability (food, water, shelter) or human disturbances.

Most authors showed larger home ranges during winter, assuming food shortage and space use influenced by hunting (Baubet et al., 1998; Boitani et al., 1994; Calenge et al., 2002; Howe et al., 1981; Maillard and Fournier, 1995). Other studies shown that summer home ranges of wild boar tended to be larger than in other seasons (Keuling et al., 2007). Whereas no seasonal changes seemed to occur in other cases (Russo et al., 1997). A further characteristic promoting uneven results in space use analyses is that wild boar is characterized by a high individual flexibility (Baubet et al., 1998; Fonseca et al., 2004; Keuling et al., 2008b).

Previous studies on wild boar and feral pigs are contradictory: some have reported males having larger home range than females (Baber and Coblentz, 1986; Saunders and Kay, 1991); others found no sex-related differences in the home range sizes of the wild boar(Boitani et al., 1994; Singer et al., 1981). Very few previous works have considered age as a factor affecting space use, but did not find differences (Boitani et al., 1994; Cousse et al., 1994; Keuling et al., 2007).

In many mammals, the “density-dependent hypothesis” predicts that home range size is inversely related to population density (Wood and Brenneman, 1980). Therefore, an inverse relationship between home range size and population density is expected where territorial behavior occurs (Huxley, 1934). If female boars are not territorial, a direct relationship between population density and home range size is logical, as seen for other nonterritorial ungulates (Kjellander et al., 2004).

Climatic factors have a strong effect on the wild boar movements, through their effect on food availability and breeding timing (Fernàndez-Llario, 1996) and this could cause non-uniforme individual distribution, those influencing directly food availability, as deep snow and drought (Acevedo et al., 2006; D'Andrea et al., 1995; Dardaillon, 1986). High temperature can be a further constraint because wild boar lack sweat glands or other efficient physiological cooling mechanism; thus are very sensitive to high temperatures and require shade and free water during hot temperature (Dexter, 1998; Dexter, 2003). The presence of water and mud is therefore important for the wild boar biology. Mud wallowing in fact can form a layer on the skin, contributing to the reduction of ectoparasites, the thermoregulation and the disinfection of wounds (Dardaillon, 1986; Fernàndez-Llario, 1996). Moreover moisture seems to be very important as it makes ground easier to root (Truvé and Lemel, 2003; Welander, 2000) and wild boars are as consequence more active under moist conditions (Truvé and Lemel, 2003).

Differential use of vegetation communities by ungulates is thought to be determined by their basic needs for food and water, shelter from weather, predators, rest and social interactions with conspecifics (Duncan, 1983). Monogastric ungulates showed less efficiency on fiber digestion than polygastric ungulates (Dulphy et al., 1994) but on the other hand monogastric ungulates showed higher plasticity in their feeding behaviour. Indeed the wild boar, as a generalist omnivore, can feed on a wide variety of foods for which the availability in space and time is not constant. Food availability can play a decisive role in promoting wild boar spatial behaviour and food availability changing may lead to variation in space and habitat use (Keuling et al., 2008a). In Mediterranean and temperate environment, the mast production constitutes the wild boar's staple food (Fournier-Chambrillon et al., 1995; Jedrzejewska and Jedrzejewski, 1998). Wild boar makes extensive use of acorns when available and a mast failure forces wild boar to diversify its diet according to the other food resources, forcing individuals to look for different foraging sites. As consequence the distribution and productivity of mast trees may have a strong influence on wild boar movement patterns, as predicted by the "food-exploitation hypothesis" (Larter and Gates, 1994). Apart from plants and seeds, the boar's diet includes insects, earthworms, small rodents and carrion. This adaptable diet contributes to the wide geographic distribution and the seasonality of habitat choice.

The home range of wild boar includes always feeding places and the areas with good thermal and hiding conditions. Several authors stated the preference for deciduous forests (Fonseca, 1997; Fonseca, 2007; Meriggi and Sacchi, 1991), that can guarantee food availability during most part of the year while coniferous forests are quite poor on food availability but offer proper bedding able to mitigate unfavourable temperatures. Many authors stated that wild boar is able to live in open habitats requiring forest or bush land for shelter in winter and using fields in summer (Fonseca, 2007; Fruzinski and Labudzki, 2002; Geisser and Reyer, 2004; Sodeikat and Pohlmeyer, 2001). Resting places and breeding nests are always located in areas of dense vegetation where they feel secure and are protected from bad weather (Dardaillon, 1986). Meriggi and Sacchi (1991) showed that most preferred habitat types were those that could assure food or shelter (deciduous long-trunked trees and old coppices).

The aim of our study was to investigate spatial behaviour evaluated in relation to age and sex classes, climatic and environmental characteristics.

We tested if spatial behaviour was influenced by age: adults wild boar can show smaller home range than subadults in relation to the knowledge of the environment or they can be of comparable size if older individuals in social groups are able to drive yougers.

We predict a different spatial behaviour in different seasons, because of the changing habitat, climate conditions and resources availability. According to the "density-dependent hypothesis", it would be expected that the home range size would decline when the population density was high. We further analyzed if mast does influence spatial behaviour. In particular we predict a mayor concentration of animals in areas with the higher food availability, in accordance with "food-exploitation hypothesis". Finally we predict that snow cover can limit the range of wild boars hampering their ability of movements.

METHODS

Study area - The study was performed in Tuscan Apennine (Arezzo province, Italy) in about 3600 ha area, a part of which is located in a protected area (Oasi Alpe di Catenaia, OAC). The altitude range varied from 300 m to 1514 m a.s.l. The climate was continental, characterized by hot and dry summers, cold and rainy winters, with high humidity rate. The snow period fell from October to April above 1000 m a.s.l., ground snow cover could persist for almost 90 days.

We defined 5 habitats: deciduous forests (dominated by *Quercus spp.* and *Fagus sylvatica*), coniferous forests (*Pinus nigra*, *Abies alba*, *Pseudotsuga menziesii*), bushes (*Erica spp*, *Rubus spp.*, *Rosa spp.*, *Prunus spinosa*, *Spartium junceum*, *Cytisus scoparius*, *Crataegus spp.*), chestnuts forests (*Castanea sativa*) and meadows. The wood cover exceed 80% of the study area, with more than 70% of deciduous woods (2,5% composed by chestnuts forests) and almost 10% coniferous woods. 6% of the study area was occupied by shrubs that offered a refuge area for wild boars (Figure 1). The study area showed a medium level of habitat diversity (Shannon's Biodiversity Index H' = 1.91).

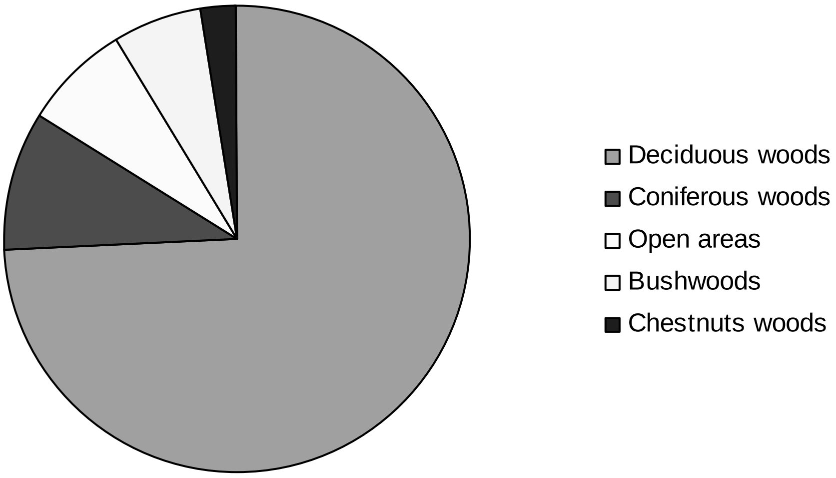

***Figure 1**: Habitat composition of the study area*

The area all around the OAC was intended for wild boar hunting. The hunting season started in September and went on till January. Hunting of wild boar occurred by drive hunts with a large number of dogs and 25-50 hunters.

In the study area the only other ungulate present apart from wild boar was roe deer (*Capreolus capreolus*). Predators were the red fox (*Vulpes vulpes*) that could prey on wild boar piglets and the wolf (*Canis lupus*). In Arezzo Province wolves were present at high densities with a mean pack size of 4.0 ± 0.6 (Apollonio and Mattioli, 2007; Capitani et al., 2004). In particular in OAC wolves were present with a resident pack and wild boar is the main prey during all the years (Gazzola et al., in press).

The National Institute of Forestry (Arezzo) reported annual deciduous woods production evaluated as seeds density (MG/ha) of chestnut (*Castanea sativa*), Turkey oak (*Quercus cerris*), beech (*Fagus sylvatica*). Temperature and snow cover data were collected by 4 stations located in and around the study area.

Methods - Wild boar were captured using both vertical drop nets and traps baited with maize. Captured animals were handled and only adult wild boars were treated with sedative Zoletil® (Fournier et al., 1995). Individuals were fitted with Televilt radio collars (Televilt, Sweden, 150-151 MHz wavebands), they were weighed, measured and aged, by teeth eruption and wear and then released. We used Wildlife Materials TRX-1000S receivers and a three-element hand-held Yagi antenna, connected with a coassial cable of 1,5m.

We captured a total of 68 wild boars, adult (>2 years old) and subadult (1-2 years old) (27 males and 41 females), between 2002 and 2008 (Table 1).

A

	Males		Females		
	Subadults	Adults	Subadults	Adults	TOT.
Spring	7	4	9	16	36
Summer	13	9	21	21	64
Autumn	4	6	11	21	42
Winter	1	6	5	12	24
TOT.	25	25	46	70	166

B

Males		Females		
Subadults	Adults	Subadults	Adults	TOT.
27	9	31	34	101

Table 1*: A: sample size subdivided in age and sex classes and seasons B: sample size subdivided into sex and age classes in all the study period*

Through radio tracking it has been possible to locate all individuals by triangulation using bearings obtained from three different points (White and Garrott, 1990) by the "loudest signal" method. Than we marked out bearings on a 1:10.000 scale map (Kenward, 1987) of the study area keeping into account that the error box should be smaller than 1 ha. The telemetry data were uniformly distributed over the 24 hours (discontinuous telemetry) (Swihart and Slade, 1985) with 8-12 locations per each boar per month, considering at least

12 hours between consecutive locations, to exclude data’s autocorrelation (Van Winkle, 1975).

The wild boars population density was estimated every year in spring by drive census conducted in both inside and outside the protected area (min = 7,542 boars/100ha; max = 32,801 boars/100ha).

Data analysis –Seasonal home range sizes were evaluated with Ranges VI software using the Kernel method (Worton, 1989) considering 90% of available locations for each animal (Borger et al., 2006). Statistical analysis were performed using SPSS 13.0 software (SPSS Inc., Chicago, Illinois). Home range data were analyzed to verify the normality of the distribution using Kolmogorov-Smirnov test therefore were transformed with natural logarithm to give a normal distribution and tested again. To analyze home range size we used the linear-mixed model (LMM), that give importance to random effects, as individual identity. This allowed us to control repeated measurements of the same individual. In linear-mixed model all variables were consider as fixed factors. We tested the influence on home ranges size of sex, age class (subadult: 1-2 years old; adult: >2 years old), season (spring: March-May; summer: June-August; autumn: September-November; winter: December-February) and population density. We merged years with a similar wild boar density in order to constitute 3 categories equally composed (low density years LDY < 7,542, medium density years MDY > 14,537 and < 16,490, high density years HDY > 23,162) (Table 2).

Year	Wild boar density	Density category
2002	15,32	medium
2003	32,8	high
2004	7,54	low
2005	14,54	medium
2006	16,49	medium
2007	23,16	high

Table 2*: Wild boar population density in the study area*

We tested than the difference between levels of population density using LMM pairwise comparisons with adjustment for multiple comparisons.

We calculate the best curve estimation to assess possible influences on home range size due to food availability (inverse regression), temperatures (quadratic regression) and snow cover (inverse regression).

Data collected in different years were analyzed all together to increase the sample size. In this way we analyzed data on habitat selection using ArcView 3.2 (*ESRI*). We employed compositional analysis to evaluate habitat selection, comparing used habitats with available ones at two different levels (Aebischer et al., 1993). At the first level we calculated the proportion of habitat in the home range with the one in the study area; the second level compared habitat proportion within the home range with the proportion of fixes in each habitat. To apply compositional analysis we used a Excel macro (Smith, 2003), that permitted also the randomization procedure recommended by Aebischer et al. (1993). At the second level, as suggested by Aebischer et al. (1993), we excluded the category less used. We tested for differences in habitat selection between seasons analysing Wilk's log-ratio matrices using a MANOVA test. In all statistical tests significance was established at $P \leq 0,05$.

RESULTS

Mean home range size (± S.E.) for females were 304.09 ha ± 86.72 in spring, 98.44 ha ± 14.34 in summer, 109.35 ha ± 20.44 in autumn and 90.44 ha ± 30.61 in winter. Males' mean home range sizes were 331.82 ha ± 107.84 in spring, 88.17 ha ± 14.93 in summer, 227.06 ha ± 73.65 in autumn and 847.81 ha ± 613.68 in winter (Table 3).

	Males		Females	
	Subadults	Adults	Subadults	Adults
Spring	10,23	171.81	19,13	7,86
Summer	124.60	3,23	108.70	166.66
Autumn	340.93	163.94	9,98	5,89
Winter	519,11	7,96	11,22	121.86

***Table 3**: Seasonal average home range size (ha) of a wild boar population*

We didn't find any difference on home range size in seasons (LME: $F_{3,156} = 1.411$, $P = 0.242$) and between different sex (LME: $F_{1,156} = 0.090$, $P = 0.764$) and age classes (LME: $F_{1,156} = 0.011$, $P = 0.918$). It seemed that an influence on space use was given by wild boar density (LME: $F_{2,156} = 7.787$, $P = 0.001$), higher was the density higher were home range sizes. A significant difference was found also concerning the influence of density on different age classes (LME: $F_{2,156} = 4.218$, $P = 0.016$). Wild boars home ranges in high population density periods are significantly different from home ranges in medium and low density periods (LME pairwise adjusted comparisons: high vs medium density: $P < 0.001$; high vs low density: $P = 0.003$). During period with low and medium density level home range size of subadults was smaller compared to home range during years with high density. Adults wild boars increased their home range with increasing population density. This resulted significant moving from a low to medium density, while there was no significant difference between medium and high population density.

A strong correlation was found between the mast trees productivity and home range sizes in autumn for females. Higher was the fruits availability, smaller were the home range sizes of the females (inverse: $R^2 = 0.476$, $P < 0{,}001$) (Figure 2).

The same influence of food availability on spatial behaviour was found also in males (inverse: $R^2 = 0.415$, $P = 0{,}044$) (Figure 3).

A link was found for females between daily maximum temperature in summer and home range size in the same season (quadratic: $R^2 = 0.173$, $P = 0{,}025$) (Fig. 4).

In males home range sizes were not significantly correlated with temperatures (quadratic: $R^2 = 0.001$, $P = 0{,}868$) (Figure 5).

During winter and spring higher was the ground snow cover, smaller were the home range sizes for females (inverse: $R^2 = 0.144$, $P = 0{,}013$) (Figure 6).

The statistical significance was not found in males (inverse: $R^2 = 0.008$, $P = 0{,}726$) (Figure 7).

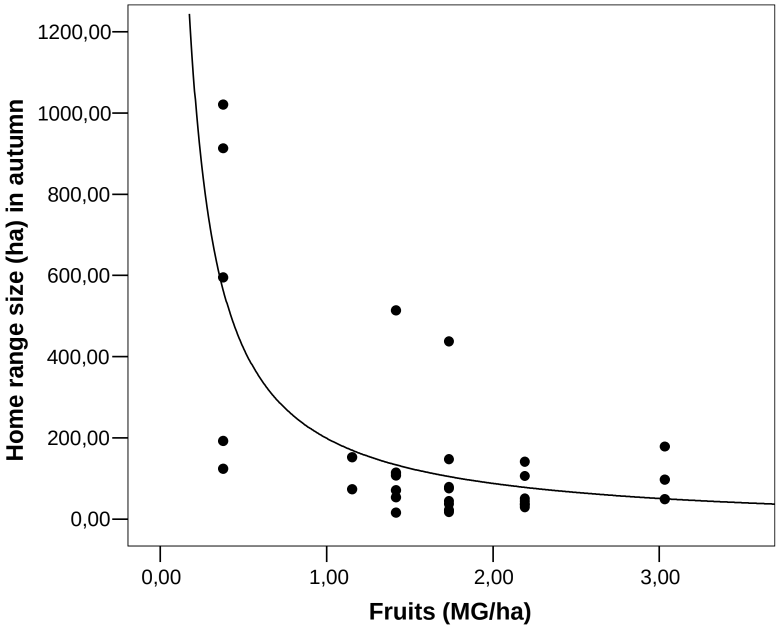

***Figure 2**: Correlation between fruits production and home range size in wild boar females in autumn*

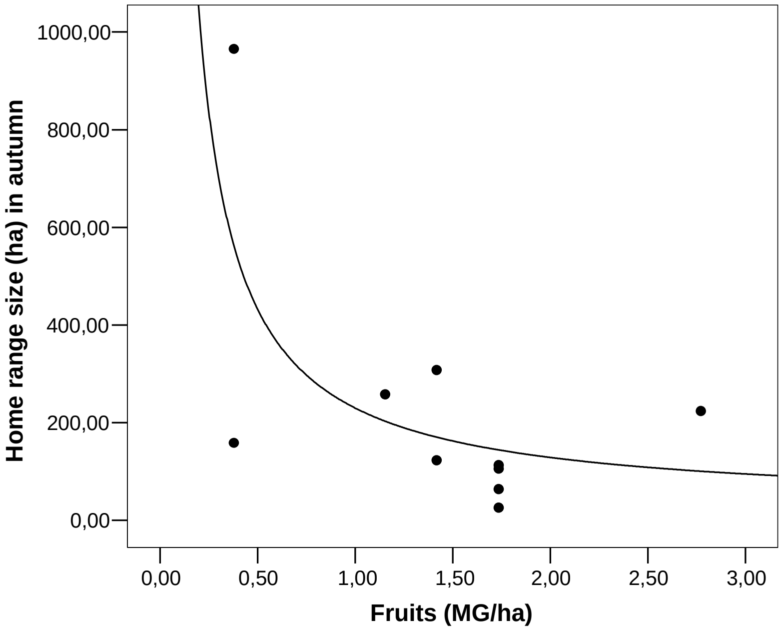

***Figure 3**: Correlation between fruits production and home range size in wild boar males in autumn*

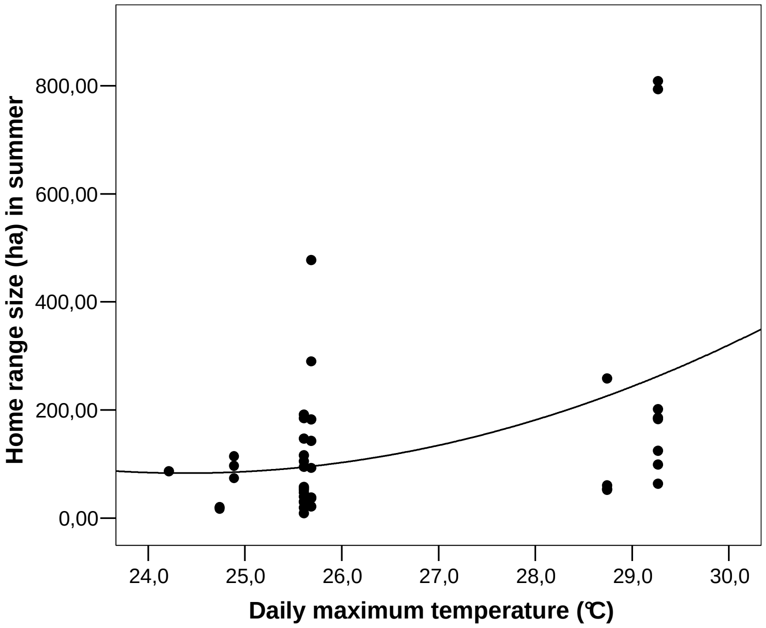

***Figure 4**: Correlation between daily maximum temperatures and home range size in wild boar females in summer*

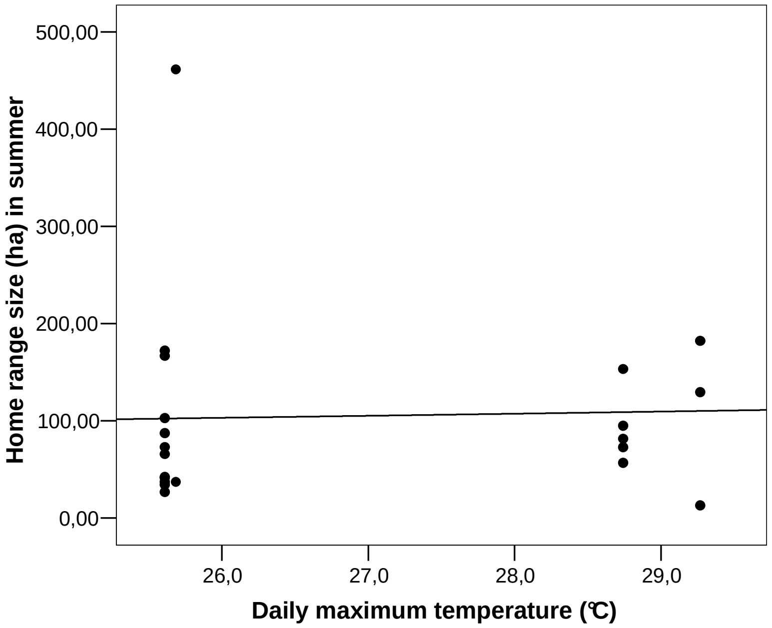

***Figure 5**: Correlation between daily maximum temperatures and home range size in wild boar males in summer*

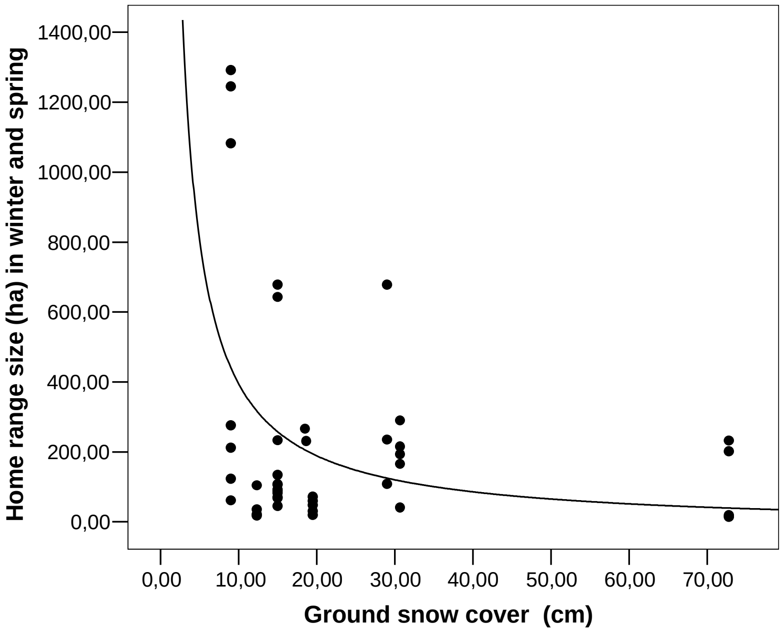

***Figure 6**: Correlation between snow ground cover and home range size in wild boar females in winter and spring*

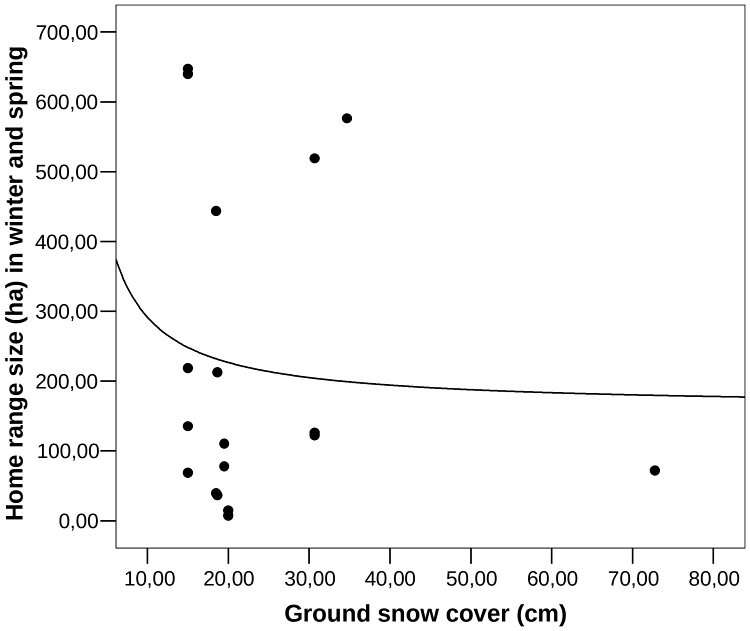

Figure 7*: Correlation between snow ground cover and home range size in wild boar males in winter and spring*

Compositional analysis showed at the first level for males a significant difference from random use in all seasons (Spring: λ = 0.25, P = 0.001; summer: λ = 0.31, P = 0.001; autumn: λ = 0.29, P = 0.001; winter: λ = 0.10, P = 0.002). At the second level of analysis compositional analysis revealed a significant departure from random use only in spring and summer (Spring: λ = 0.58, P = 0.032; summer: λ = 0.71, P = 0.020; autumn: λ = 0.71, P = 0.075; winter: λ = 0.55, P = 0.444).

In all seasons, at the first level (Figure 8), males positively selected deciduous forests (P < 0.05) (Spring: 71.62 ± 4.77 %; summer: 69.39 ± 4.44 %; autumn: 68.24 ± 3.63 %; winter: 66.94 ± 7.94 %) followed by bushes (Spring: 7.09 ± 2.23 %; summer: 13.61 ± 3.61 %; autumn: 12.19 ± 3.19 %; winter: 8.48 ± 2.02 %) and coniferous forests (Spring: 10.80 ± 2.76 %; summer: 11.02 ± 2.28 %; autumn: 11.94 ± 2.17 %; winter: 17.91 ± 4.23 %). Open areas were used marginally therefore they were excluded from the second level of the analysis.

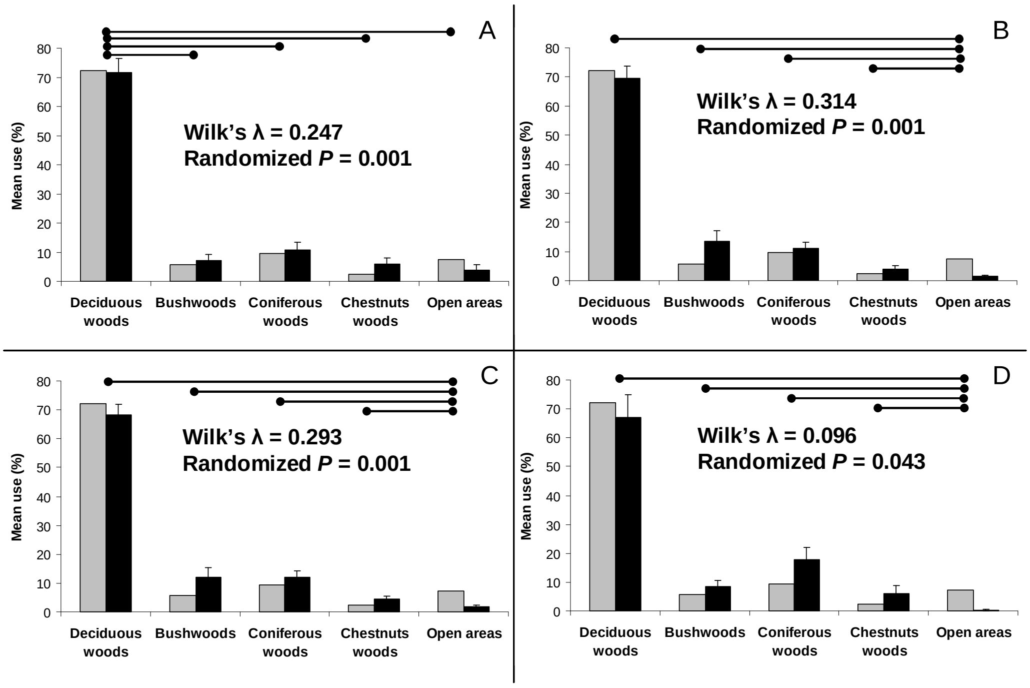

Figure 8: *Habitat selection by wild boar males in spring (A), summer (B), autumn (C) and winter (D), at the first level of compositional analysis. Grey columns represent available habitats, black columns show habitats used, and significant departure from random use is indicated by lambda and randomized P values. Lines indicate significant differences (P < 0.05 by compositional analysis) between connected habitat classes.*

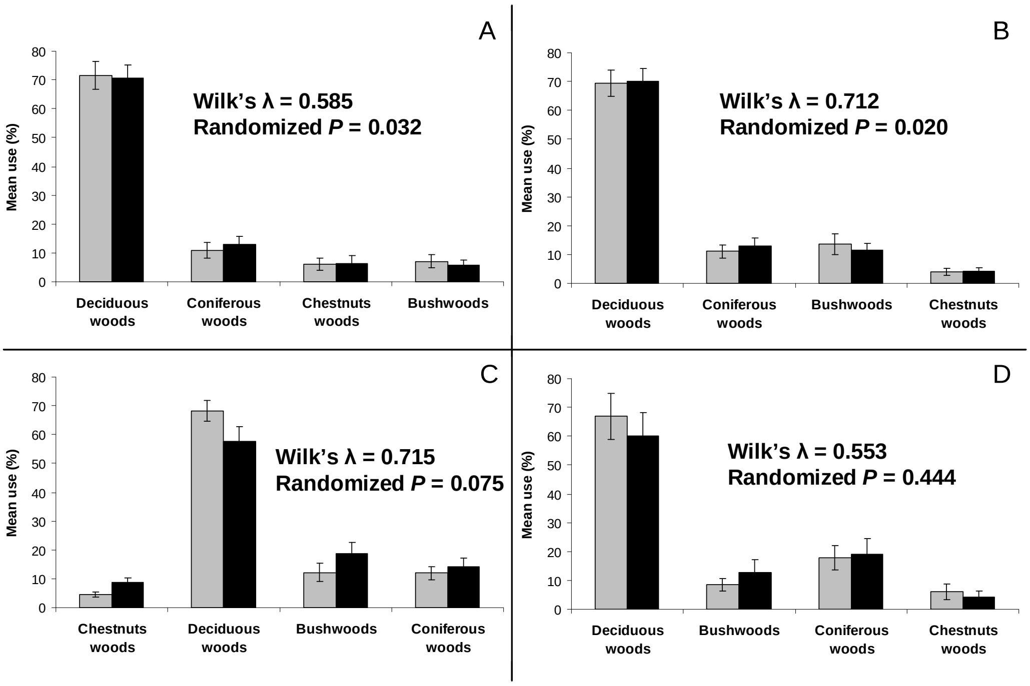

Figure 9: *Habitat selection by wild boar males in spring (A), summer (B), autumn (C) and winter (D), at the second level of compositional analysis. Grey columns represent available habitats, black columns show habitats used, and significant departure from random use is indicated by lambda and randomized P values. Lines indicate significant differences (P < 0.05 by compositional analysis) between connected habitat classes.*

The second level (Figure 9), of compositional analysis in every season didn’t show a preference on habitat choice.

Females compositional analysis showed at first level a significant difference from random use in all seasons (Spring: λ = 0.13, P = 0.001; summer: λ = 0.16, P = 0.001; autumn: λ = 0.14, P = 0.001; winter: λ = 0.0005, P = 0.001). At the second level of analysis, compositional analysis revealed a significant departure from random use in all seasons but in winter (Spring: λ = 0.74, P = 0.004; summer: λ = 0.81, P = 0.015; autumn: λ = 0.70, P = 0.001; winter: λ = 0.76, P = 0.068).

At the first level (Figure 10), deciduous forests were positively selected by females in all seasons except in winter in which coniferous forests were preferred (P < 0.05). In spring the rank order was: deciduous forests (63.31 ± 3.41 %), coniferous forests (17.87 ± 2.18 %), chestnuts forests (6.51 ± 1.18 %), bushwoods (9.37 ± 1.33 %) and open areas (1.52 ± 0.53 %). In summer and autumn the rank order was: deciduous forests (Summer: 63.35 ± 3.24 %, autumn: 59.80 ± 3.13 %), bushwoods (Summer: 10.43 ± 1.31 %, autumn: 12.91 ± 1.63 %), coniferous forests (Summer: 16.89 ± 2.38 %, autumn: 19.68 ± 1.90 %), chestnuts forests (Summer: 6.22 ± 1.01 %, autumn: 5.41 ± 0.94 %) and open areas (Summer: 1.90 ± 0.70 %, autumn: 1.51 ± 0.60 %). In winter the rank order was: coniferous forests (19.14 ± 1.93 %), deciduous forests (58.50 ± 4.42 %), chestnuts forests (10.60 ± 1.83 %), bushwoods (11.03 ± 1.99 %) and open areas were not used. In all seasons open areas were used marginally therefore they were excluded from the second level of the analysis.

At the second level of compositional analysis (Figure 11), deciduous forests were always selected. In winter there wasn’t a significant difference from random use. In spring the rank order was: deciduous forests, chestnuts forests, bushwoods and coniferous forests. While in summer and autumn the rank order was deciduous forests, coniferous forests, bushwoods and chestnuts forests.

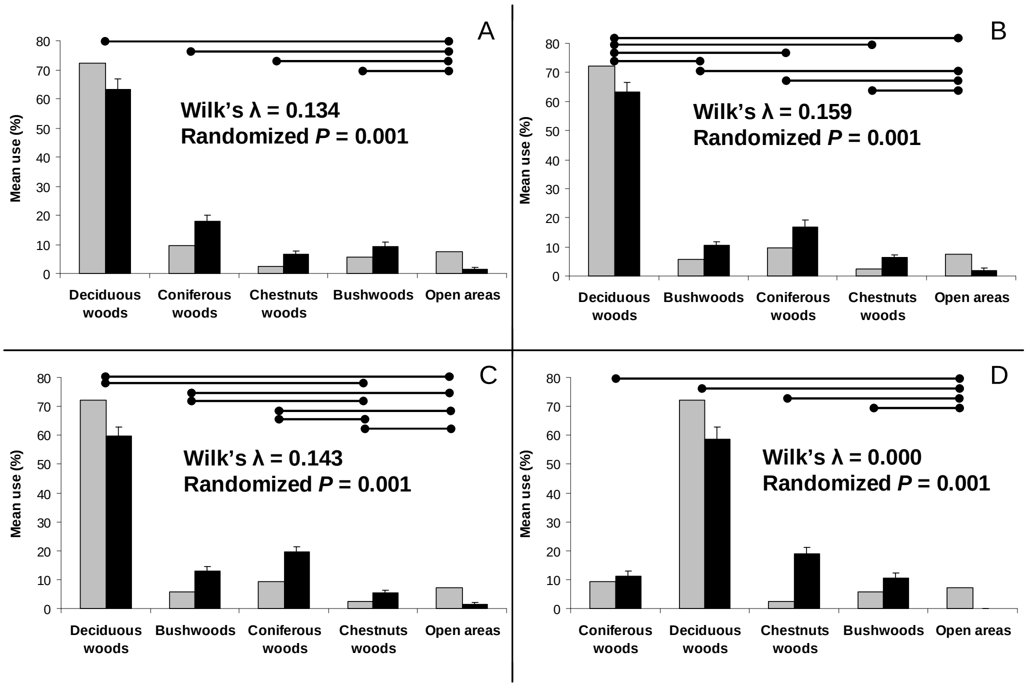

***Figure 10**: Habitat selection by wild boar females in spring (A), summer (B), autumn (C) and winter (D), at the first level of compositional analysis. Grey columns represent available habitats, black columns show habitats used, and significant departure from random use is indicated by lambda and randomized P values. Lines indicate significant differences (P < 0.05 by compositional analysis) between connected habitat classes.*

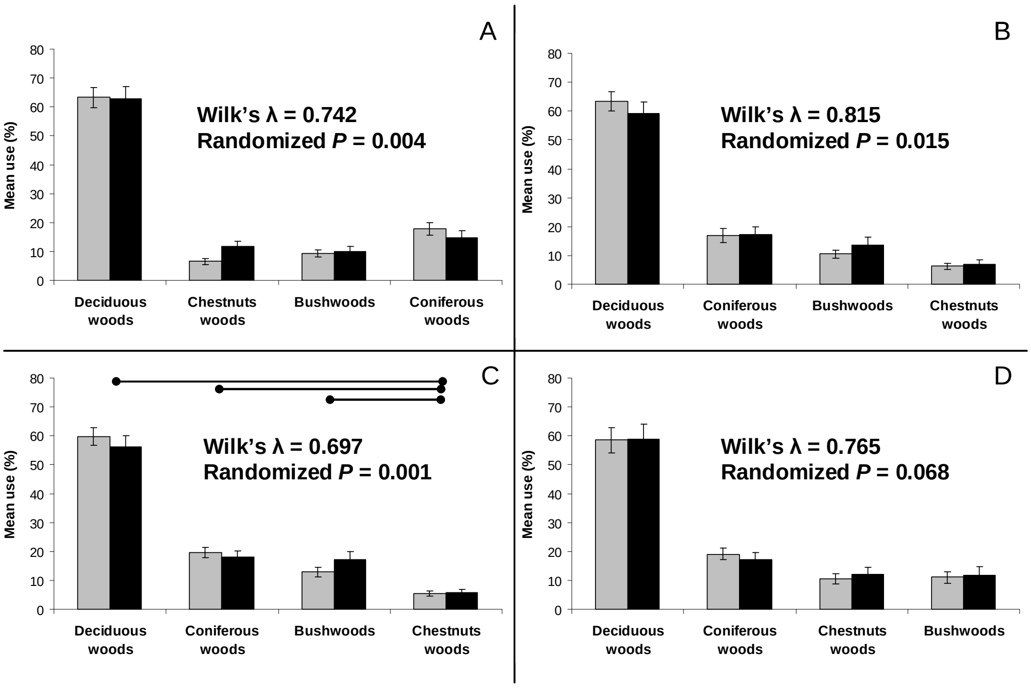

***Figure 11**: Habitat selection by wild boar females in spring (A), summer (B), autumn (C) and winter (D), at the second level of compositional analysis. Grey columns represent available habitats, black columns show habitats used, and significant departure from random use is indicated by lambda and randomized P values. Lines indicate significant differences (P < 0.05 by compositional analysis) between connected habitat classes.*

MANOVA didn’t show a strong different habitat selections between males and females (MANOVA λ = 0.932, F = 2.404, P = 0,053) and the difference is noticed in the use of all habitat typologies (deciduous woods: F = 9.482, P = 0.003; coniferous woods: F = 6.250, P = 0,014; bushwoods: F = 5.494, P = 0,021; chestnut woods: F = 4.939, P = 0,028). At the second level higher significant difference was underline between sexes (MANOVA λ = 0.904, F = 3.063, P = 0,032), but at this level the only difference was shown in the use of bushwoods (F = 3.912, P = 0,050). The age class didn’t influence habitat selection neither at the first level (MANOVA λ = 0.026, F = 0.838, P = 0,503) nor at the second (MANOVA λ = 0.983, F = 0.515, P = 0,673). Also the seasons didn’t influence habitat selection at both level of analysis (MANOVA first level: λ = 0.923, F = 0.892, P = 0,555; second level λ = 0.890, F = 1.150, P = 0,329).

DISCUSSION

The present study showed how wild boar home ranges appeared flexible, because several factors partially contributed to their size: age, sex, population density, abundance of resources, habitat conditions. The data presented above showed no differences in the size of seasonal home ranges. Our study area showed a medium biodiversity level, this means that different habitats were linked and closed between them, and wild boars could, consequently, find different resources without the necessity to modify significantly their home range size. Similar findings were described in previous works that analyzed seasonal and monthly home range size of females wild boar (Keuling et al., 2007; Massei et al., 1997a). On the other hand the reduced summer home range sizes of all wild boar groups were shown in various literature data (Baubet et al., 1998; Keuling et al., 2007; Maillard and Fournier, 1995; Singer et al., 1981). Moreover some research shown a decrease of home range size in winter (Boitani et al., 1994; Calenge et al., 2002; Maillard and Fournier, 1995; Sodeikat and Pohlmeyer, 2001) probably due to food shortage, hunting pressure and bad weather.

In this study no evidence was also found for intersexual differences in home range size. Wild boar shown in this area a slight sexual dimorphism that may drive to similar ecological requirements. Also in this case previous studies shown contradictory results, some reported males having larger home ranges than females (Baber and Coblentz, 1986; Saunders and Kay, 1991). While others studies found no sex-related differences in the space use of the wild boar (Boitani et al., 1994; Howe et al., 1981) confirming our result.

The results of this study contradict the "density-dependent hypothesis" that predicts an inverse relation between home range sizes and population density. We have obtained a result different from other studies (Massei et al., 1997a) conducted in a Mediterranean area located along the sea coast at a low altitude and different for what concerning vegetation, food availability and climate conditions. This study was performed in a rich habitat that could assure food availability during all the year long consisting in bulbs, fruits, seeds, earthworms and insects. Moreover the prevalent dense structure of woods could guarantee both feeding, safe resting place and thermoregulation limiting movements and the consequent energy expenditure. Furthermore differently from Mediterranean environment summer was not the limiting season. Food and climate conditions are known to be important factors for the population dynamics of many ungulate species. Optimal food and temperature conditions are very likely to boost reproductive success, decrease juvenile mortality simultaneously and, thereby, increase population density within a short time period. The importance of mast in the diet of wild boar is well known (Schley and Roper, 2003). Seasonal movements by wild boar have been reported as a response to food shortage, therefore food availability reflected in a different spatial behaviour. Wild boar prefer food of high energetic content which may be of natural origin (acorn mast) or anthropogenic (crop fields) (Genov, 1981; Schley et al., 2008; Schley and Roper, 2003) that become particularly valuable in years with low forage availability (Fournier-Chambrillon et al., 1995). According to "food-exploitation hypothesis" we have shown smaller home range when food availability was high. The same result was obtained by other studies (Boitani et al., 1994; Howe et al., 1981) but Massei et al. (1997a) reported smaller home ranges during poor nutritional conditions. Again the Mediterranean environment where this last study was conducted could help to explain the differences assumed from our results and those of Boitani et al. (1994) and Singer et al. (1981) that were conducted in more hilly and fresh environment. It’s interesting to merge these two last results, concerning the influence of density and food on home ranges size. During the period of high population density the availability of food was scarce so the resource competition was high and wild boar should go round searching for their need. When the population density was low and the food availability was high the resources competition was low and wild boar could settle in the place when they found enough food.

Females reacted to a variation in temperature conditions changing their home range size. In summer with the temperature increasing females shown larger home ranges, while males were not influenced by these variations. For wild boar females temperature conditions is essential for the survival of the newborn piglets. In our study area the peack of births was located between March and May, just before summer. In summer, adult females are still nursing piglets and need a higher energy intake than males (Mauget et al., 1984). Moreover summer is a difficult season for wild boars, because of high temperatures, drought conditions and difficulties on find food. Hence, increasing of temperatures are likely to reduce the piglets survival. To avoid hard conditions females aimed at searching more for suitable place for piglets growth, near to main resources (food, water and refuge areas). Females with piglets leave or enlarge their home range from spring (postnatal range) to summer. Moreover changing in food availability influences summer home range. Massei et al. (1997b) demonstrated the increased wild boar mortality in a Mediterranean area during the hot season, when more adult females and adult males died. The rapid decrease in mortality after the first precipitation suggested that food shortage due to the hard soil was possibly the main cause of mortality. Wild boars are sensitive to high temperatures and in this circumstances they require access to shade and water preventing them from foraging far from these resources and in turn influencing the home range size.

Furthermore, we have shown that wild boars females reduced the activity range significantly when the ground was covered by snow (winter and spring), while males seemed to not be affected by this. If the snow cover was deep enough wild boars concentrated in the few areas where they can have access to food. Snow cover and frozen soil make it difficult for wild boar to root and access vegetation and invertebrate food. In fact it was shown by Okarma et al. (1995) that in wild boar mortality from starvation was influenced mainly by snow cover.

Clutton-Brock (1989) hypothesized that, in mammals, resources distribution should determine females distribution, while females distribution should determine the males distribution in relation to competition for mates. This means that, in polygynous species, males have two constraints, females distribution and the distribution of other males competitors, while females have only one constraint, resources distribution. Moreover females should favour the survival and growth of their young, selecting habitats which provide good feeding but also protection from predators, particularly during neonatal period. Males should favour growth and the accumulation of fat reserves for the rut, seeking out the richest feedings areas. These theories could explain our results that shown similar results in a general level of survey. Both sexes shown a high flexible spatial behaviour, but in particular we have shown different answers from sexes to different environmental stimulus. Males were linked mostly on food availability only, while females were influenced not only by food availability but also by environmental and climate conditions.

With regard to habitat selection our results didn’t show any clear pattern of habitat preferences, probably owing to the high homogeneity of the study area (more than 70 % of deciduous forests), confirming also the highly adaptable spatial behaviour of wild boar. We haven’t underline differences between sexes and age classes.

The habitat selection showed in the general level of analysis a preference for deciduous forests that offered the mayor availability of food. Food items include tree and shrub seeds as well as under ground parts of herbs and grasses. Moreover the soft soil of deciduous forests offers the boars an enormous biomass of insects and earthworms (Baubet et al., 2003). In detail chestnuts forests were used, by females and males, more than availability in all seasons at the two levels of analysis of environmental selection. Data from previous studies are in accordance to the preference of the deciduous forests that we found (Abaigair et al., 1994; Fonseca, 2004; Herrero, 2003).

Home range of wild boars is expected to contain both foraging areas and appropriate bedding sites as coniferous forests, which are much more effective than deciduous forests in tempering unfavorable atmospheric conditions (Geiger, 1965). This could explain the large use of coniferous forest by females and males wild boar in our research. Furthermore bushwoods, used as refuge areas, at a larger scale were always used more than available in our study area. A fine scale showed a preference for this habitat during autumn and winter, when was higher the disturbance. Preference for more dense habitats may impart potential benefits to individuals that are independent of the role of these habitats in thermoregulation. Abundant vegetation seems to be a greet importance as a defence mechanism against human and predators.

REFERENCES

Abaigair T, del Barrio G, Vericad JR. 1994. Habitat preference of wild boar (*Sus scrofa* L.) in a Mediterranean environment. Indirect evaluation by signs. Mammalia 58:201-210.

Acevedo P, Escudero MA, Munoz R, Gortazar C. 2006. Factors affecting wild boar abundance across an environmental gradient in Spain. Acta Theriologica 51(3):327-336.

Aebischer NJ, Robertson PA, Kenward RE. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74(5):131-1325.

Apollonio M, Mattioli L. 2007. Il lupo in Provincia di Arezzo. Studi sulla biologia della fauna. Le Balze.

Baber DW, Coblentz BE. 1986. Diet, nutrition and conception in feral hog on Santa Catalina Island. The Journal of Wildlife Management 51:306-317.

Baubet E, Brandt S, Touzeau C. 1998. Effet de la chasse sur les stratégies d'occupation de l'espace des sangliers (*Sus Scrofa*). Analyses préliminaires. Gibier Faune Sauvage, Game Wildl 15:655-658.

Baubet E, Ropert-Coudert Y, Brandt S. 2003. Seasonal and annual variations in earthworm consuption by wild boar (*Sus scrofa scrofa* L.). Wildlife Research 30:179-186.

Boitani L, Mattei L, Nonis D, Corsi F. 1994. Spatial and activity patterns of Wild Boars in Tuscany, Italy. Journal of Mammalogy 75(3):600-612.

Borger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393-1405.

Calenge C, Maillard D, Vassant J, Brandt S. 2002. Summer and hunting season home ranges of wild boar (*Sus scrofa*) in two habitats in France. Game and Wildlife Science 19:281–301.

Capitani C, Bertelli I, Varuzza P, Scandura M, Apollonio P. 2004. A comparative analysis of wolf (*Canis lupus*) diet in three different Italian ecosystem. Mammalian Biology 69(1):1-10.

Clutton-Brock TH. 1989. Mammalian mating systems. Proceeding of Royal Society London 236:339-372.

Cousse S, Spitz F, Hewison M, Janeau G. 1994. Use of space by juveniles in relation to their postnatal range, mother, and siblings: an example in the wild boar, *Sus scrofa* L. Canadian Journal of Zoology 72:1691-1694.

D'Andrea L, Durio P, Perrone A, Pirone S. 1995. Preliminary data of the Wild Boar (*Sus scrofa*) space use in mountain environment. Ibex Journal of Mountain Ecology 3:117-121.

Dardaillon M. Some aspects of the orientation in space of *Sus scrofa* as revealed by data on home range, habitat use and movements. In: Beugnon G., editor; 1986. p 63-70.

Dexter N. 1998. The influence of pasture distribution and temperature on habitat selection by feral pigs in a semi-arid environment. Wildlife Research 25:247-559.

Dexter N. 2003. The influence of pasture distribution, and temperature on adult body weight of feral pigs in a semi-arid environment. Wildlife Research 30:75-79.

Dulphy JP, Jouany JP, Martin-Rosset W, Theriez M. 1994. Aptitudes comparées de différentes espèces d’herbivores domestiques a ingérer et digérer des fourrages distribués à I’auge. Annales Zootechniques 43:11-32.

Duncan JL. 1983. Determinants of the use oh habitat by horses in a Mediterranean wetland. Journal of Animal Ecology 52:93-109.

Fernàndez-Llario P. 1996. Ecología del jabalí en Doñana: parámetros reproductivos e impacto ambiental: University of Extremadura.

Fernàndez-Llario P, Carranza J. 2000. Reproductive performance of the wild boar in a Mediterranean ecosystem under drought condition. Ethology Ecology & Evolution 12:335-343.

Fonseca C. 1997. Influence of landscape and environmental factors upon harvest rate and habitat selection of wild boar in central Portugal. Journal of Wildlife Research 2(3,4):296-302.

Fonseca C. 2007. Winter habitat selection by wild boar *Sus scrofa* in southeastern Poland. European Journal of Wildlife Research.

Fonseca C, Santos P, Monzón A, Bento P, Alves da Silva A, Alves J, Silverio A, Soares AMVM, Petrucci-Fonseca E. 2004. Reproduction in the wild boar (*Sus scrofa* Linnaeus, 1758) populations of Portugal. Galemys 16 (n° especial):53-65.

Fonseca CMMS. 2004. Population dynamics and management of wild boar (*Sus scrofa* L.) in Central Portugal and Southeastern Poland. Aveiro: University of Aveiro.

Fournier-Chambrillon C, Maillard D, Fournier P. 1995. Diet of the wild boar (*Sus scrofa* L.) inhabiting the Montpellier garrigue. Ibex Journal of Mountain Ecology 3:174-179.

Fournier P, Fournier-Chambrillon C, Maillard D, Klein F. 1995. Zoletil© immobilization of Wild Boar (*Sus scrofa* L.). Ibex Journal of Mountain Ecology 3:134-136.

Fruzinski B, Labudzki L. 2002. Management of wild boar in Poland. Zeitschrift Fur Jagdwissenshaft 48 (Supplement):201-207.

Gazzola A, Bongi P, Capitani C, Mattioli L, Donaggio E, Bassi E, Apollonio M. in press. Functional response to wild ungulate availability in wolf diet: the influence of hunting, prey preference and structure of ungulate community. Oikos.

Geiger R. 1965. The climate near the ground. Press HU, editor. Cambridge, Massachusetts.

Geisser H, Reyer H-U. 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. Journal of Wildlife Management 68:939–946.

Genov P. 1981. Significance of natural biocenosis and agrocenoses as the source of food for wild boar (*Sus scrofa* L.). Ekologia Polska 29(1):117-136.

Herrero J. Adaptación funcional del jabalí *Sus scrofa* L. a un ecosistema forestal y a un sistema agrario intensivo en Aragón.; 2003. p Zaragoza.

Howe T, Singer FJ, Ackerman BB. 1981. Forage relationship of European wild boar invading Northern hardwood forest. The Journal of Wildlife Management 45:748-754.

Huxley JS. 1934. A natural experiment on the territorial instinct. British Birds 27:270-277.

Jedrzejewska B, Jedrzejewski W. 1998. Predation in vertebrate communities: the Białowieza Primeval Forest as a case study. Ecological Studies 135.

Kenward R. 1987. Wildlife radio Tagging. London: Academic Press. 222 p.

Keuling O, Stier N, Roth M. 2007. Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. European Journal of Wildlife Research.

Keuling O, Stier N, Roth M. 2008a. Commuting, shifting or remaining? Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. Mammalian Biology.

Keuling O, Stier N, Roth M. 2008b. How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.? European Journal of Wildlife Research 54:729-737.

Kjellander P, Hewison AJM, Liberg O, Angibault JM, Bideau E, Cargnelutti B. 2004. Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus* L.): a comparison of two long-term studies. Oecologia 139(3):478-485.

Larter NC, Gates CC. 1994. Home-range of wood bison: effects of age, sex, and forage availability. Journal of Mammalogy 75:142-149.

Lever C. 1985. Naturalised Mammals of the World. London: Longman.

Maillard D, Fournier P. 1995. Effects of shooting with hounds on size of restings range of Wild Boar (*Sus scrofa*) groups in Mediterranean Habitat. Ibex Journal of Mountain Ecology 3:102-107.

Massei G, Genov P, Staines BW, Gorman ML. 1997a. Factors influencing home range and activity of wild boar (*Sus scrofa*) in a Mediterranean coastal area. Journal of Zoology 242:411-423.

Massei G, Genov P, Staines BW, Gorman ML. 1997b. Mortality of wild boar, *Sus scrofa*, in a Mediterranean area in relation to sex and age. Journal of Zoology, London 242:394-400.

Mauget R, Campan R, Spitz F, Dardaillon M, Janeau G, Pepin D. Synthèse des connaissances actuelles sur la biologie du sanglier, perspectives de recherche.; 1984. p 15-50.

Meriggi A, Sacchi O. Habitat selection by Wild Boars in Northern Apennines (N-Italy); 1991. p 435-438.

Okarma H, Jedrzejewski B, Jedrzejewska W, Krasinski Z, Milkowski L. 1995. The role of predation, snow cover, acorn crop, and man-related factors on ungulate mortality in Bialowieza Primeval Forest, Poland. Acta Theriologica 40(2):197-217.

Russo L, Massei G, Genov PV. 1997. Daily home range and activity of wild boar in a Mediterranean area free from hunting. Ethology, Ecology & Evolution 9:287-294.

Saez-Royuela CJ, Telleria JL. 1987. Reproductive trends of the wild boar (*Sus scrofa*) in Spain. Folia Zoologica 36(1):21-25.

Saunders G, Kay B. 1991. Movements of Feral Pigs (*Sus scrofa*) at Sunny Corner, New South Wales. Wildlife Research 18:49-61.

Schley L, Dufrene M, Krier A, Frantz AC. 2008. Patterns of crop damage by wild boar (*Sus scrofa*) in Luxemburg over a 10-year period. European Journal of Wildlife Research.

Schley L, Roper T. 2003. Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. Mammals Review 33(1):43-56.

Singer FJ, Otto DK, Tipton AR, Hable CP. 1981. Home ranges, movements, and habitat use of European Wild Boar in Tennessee. Journal of Wildlife Management 45(2):343-353.

Smith PG. 2003. Compos Analysis, version 5.1 standard [software]. Abergavenny, UK: Smith Ecology Ltd.

Sodeikat G, Pohlmeyer K. 2001. Temporary home range modifications of wild boar family groups (*Sus scrofa* L.) caused by drive hunts in Lower Saxony (Germany). European Journal of Wildlife Research 48:161-166.

Swihart RK, Slade NA. 1985. Testing for independence of observation in animal movements. Ecology 66(4):1176-1184.

Truvé J, Lemel J. 2003. Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. Wildlife Biology 9 (suppl. 1):51-57.

Van Winkle W. 1975. Comparison of several probabilistic Home range models. The Journal of Wildlife Management 33:118-123.

Welander J. 2000. Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. Journal of Zoology, London 252:263-271.

White GC, Garrott RA. 1990. Analysis of wildlife radio-tracking data. San Diego. London: Academic Press.

Wood GW, Brenneman RE. 1980. Feral hog movement and habitat use in South Carolina. Journal of Wildlife Management 44:420-427.

Worton BJ. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70(1):164-168.

Chapter 3

Influence on environmental water on wild boar spatial behaviour

INFLUENCE ON ENVIRONMENTAL WATER ON WILD BOAR SPATIAL BEHAVIOUR

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ABSTRACT

The availability of water sources is believed to influence many ecological aspects of ungulates. In this study we analysed the influence of water in the environment on spatial behaviour of a wild boar (*Sus scrofa*) population in a mountainous area. Wild boar locations were collected between 2002 and 2009, with an intensive year-long study in 2007 and 2008. Results were based on three different levels: a larger time scale, considering drought and rainy periods of each year; a finer time scale, referred to monthly period; and a detailed analysis, with daily behaviour. In the intensive study period we collected, in detail, every two weeks, the presence of water in ditches in the study area.

In the large scale analysis we didn't notice influences of individual characteristics, such as sex and age, on the home range size and between the drought and rainy period. We were able to shown changes in the home range size considering length/area (LA) index and Gaussen Index. We did not documented, by compositional analysis, changes in habitat between drought and rainy seasons. In the finer scale, monthly home range study shown a different behaviour of piglets. Moreover we underlined the influence of LA and GI on the monthly home range size. The most detailed scale shown the decrease of distance from ditches with the decrease of water in ditches. These results reflected the importance of water presence in the environment also in an area with limited drought excesses during hot season.

INTRODUCTION

Water is essential for animals to maintain body condition and carry out important metabolic body functions. Wildlife obtains water from free water (streams, lakes, puddles, ditches), water contained in vegetation, and metabolic water (water produced as a by-product of the oxidation of organic compounds containing hydrogen). Water sources can be a critical habitat component especially during summer (Boyce et al., 2003; Whiting et al., 2009). Previous studies have demonstrated that seasonality of rainfall, water availability, spatial and temporal surface of water distribution influences daily and seasonal movements of water-dependent species, particularly during dry season. In ungulates it was demonstrated a tendency to dispersal during wet seasons and to concentrate of animals during dry seasons (Boyce et al., 2003; Fryxell and Sinclair, 1988; Redfern et al., 2003; Western, 1975). Location of water is considered to be a major factor influencing ungulates distribution and selection of foraging areas on seasonal range (Roath and Krueger, 1982). If water distribution is scarce, ungulates may have large home range sizes, or be concentrated near water sources (Webb et al., 2007). More in general water sources may exert a greater influence on ungulates distribution patterns.

Suids are among the most adaptable and widespread animals in the world. With or without human activities they have achieved a global distribution where they occupy a wide range of habitats and climates (Powell, 2004). The wild boar (*Sus scrofa*) is the most common among wild pigs, found on all continents except Antarctica (Powell, 2004; Spitz, 1999).

The great increase of the wild boar population during the last century all over European has been explained to different causes: socio-economic changes (abandonment of rural areas, shift to industry and tertiary activites) which improved the environmental conditions changes in dominant crops, reintroductions, lack of predators, supplementary food (Saez-Royuela and Telleria, 1986). The wild boar should be considered a typically r-selected species with high ecological plasticity and a very high reproductive potential relative to its body size (Geisser and Reyer, 2005). Wild boar may start to breed during the first year of life (Gethöffer et al., 2007) and may give birth throughout the whole year (Calenge et al., 2002; Fruzinski and Labudzki, 2002). In the Apennine environment primiparity age might occur before the first year of life, whereas mean litter size was 4.74 ± 0.115 (Cappai et al., submitted, see Chapter 1). The importance of water and humidity for suids, is also linked to their needs of thermoregulation. In fact wild boar lack sweat glands or other efficient physiological cooling mechanism; thus are very sensitive to high temperatures and require shade and free water during hot weather (Dexter, 2003). Previous studies shown how the water, expressed by rainfall, can condition wild boar survival, especially during dry seasons (Caley, 1993; Massei et al., 1997b; Woodall, 1983). Caley (1993) showed that, in a savannah habitat, the dry season coincided with a noticeable reduction in body weight, particularly in sows with piglets. The higher water demands during gestation and lactation reflects on reproductive performance. Fernandez-Llario and Carranza (2000) shown that the reproductive parameter most heavily influenced by drought conditions is the percentage of breeding females. Also Massei et al. (1996) for another Mediterranean area states that about 90% of females were lactating in a rainy year compared with only 18% in a drought year. On the other hand it is known that, in central European areas, the reproductive performance of wild boar is affected by heavy snowfall and low temperatures in populations located in areas were the harshest season is winter (Berthon et al., 1993; Heptner et al., 1989; Manners and McCrea, 1963; Markov, 1997). Despite wild boar ecological plasticity, water, forage, shade and high snow depth are the limiting factors that can determine geographical distribution and survival of this specie (Fernàndez-Llario and Carranza, 2000; Massei et al., 1997b; Melis et al., 2006).

The importance of water is tied to the need of thermoregulation by either mud bath (wallowing) or resting in cool, shaded earth (Diong, 1982). Over 37.77°C, domestic pigs may die if deprived of water to spray on their skin or the opportunity to wallow (Curtis et al., 2001). Wild boar frequently visit wetlands, either to feed on the roots of aquatic plants or to acquire a protective mud layer on their skin. Furthermore up to 24% of wild boar diet may consist of roots and bulbs of aquatic vegetation, especially from the late autumn to early summer with maximum in winter (Dardaillon, 1987). When environmental conditions are poor wild boar have to roam searching for water in dry seasons (Baber and Coblentz, 1986; Massei et al., 1997a), when the water assimilate by food is poor.

During hot dry days wild boar seek the cool moist forests with an abundance of wallowing sites (Howe et al., 1981). Moisture is very important as the ground is easier to root and scents can be perceived better (Truvé and Lemel, 2003; Welander, 2000): as a consequence wild boars are more active under moist conditions (Truvé and Lemel, 2003).

As water is essential to wild boar survival, their home range must contain water bodies (Leaper et al., 1999). Barrett (1978) found seasonal shifts in home range as a result of changes in temperature and availability of food and water. Feral pigs were irregularly sedentary, in the sense that they remain in an area with suitable cover only as long as there is food and water availability. Habitat use by pigs suggests a significant preference for protected creek lines in all seasons. Movements to a source of water are particularly important during the summer when vegetation cannot provide water requirements. Creek lines are covered by heavy vegetation which would provide favoured refuge and resting sites (Barrett, 1978).

Resting places are often located in areas with dense vegetation cover where wild boar lie in a ground depression sometimes lined with nesting material (Spitz, 1986). In particular nest sites are always located in close proximity to water (Dardaillon, 1986; Fernàndez-Llario, 1996). It has been seen that water shortage in the proximities of piglets has direct consequences on their own thermoregulation, with deaths occurring by dehydratation and in less extreme cases, on behaviour of the litter (Fraser et al., 1990). In the same way, Fernandez-Llario and Carranza (2000) showed that in the first days after birth piglets mortality rate is higher under dry conditions than in rainy seasons.

Little is known about the importance of water for wild boars dealing with precipitations and water in the environment (Thurfjell et al., 2009) and rarely dealing with spatial behaviour (Massei et al., 1997b). In this paper we examine the importance of water in the environment on a wild boar population. Our goals are: 1) to determine if water availability condition the wild boar spatial behaviour; 2) to evaluate if individuals characteristics, such as sex and age classes, have an influence on spatial behaviour in a drought condition.

METHODS

Study area - The study area was located in Tuscan Apennine (Arezzo province, Italy) in about 3600 ha area, around a protected area (Oasi Alpe di Catenaia, OAC). The altitude range varied from 300 m to 1514 m a.s.l. The climate was continental, characterized by hot and dry summers, cold and rainy winters, with high humidity rate. We obtain meteorological data (temperature and rainfall) from four weather stations located in the study area and all around. The amount of precipitation could vary from a minimum of 44.8 cm in a drought season to a maximum of 485.1 cm in a rainy season. The snow period fell from October to April above 1000 m a.s.l.

The wood cover exceed 80% of the whole study area, with more than 70% of deciduous woods (dominated by *Quercus spp.*, *Castanea sativa* and *Fagus sylvatica*), and almost 10% coniferous woods (*Pinus nigra*, *Abies alba*, *Pseudotsuga menziesii)*. 6% of the study area was occupied by shrubs (*Erica spp*, *Rubus spp.*, *Rosa spp.*, *Prunus spinosa*, *Spartium junceum*, *Cytisus scoparius*, *Crataegus spp.*) that offered a refuge area for wild boars.

Inside OAC (Figure 1) hunting was strictly forbidden while outside area was open to wild boar hunting.

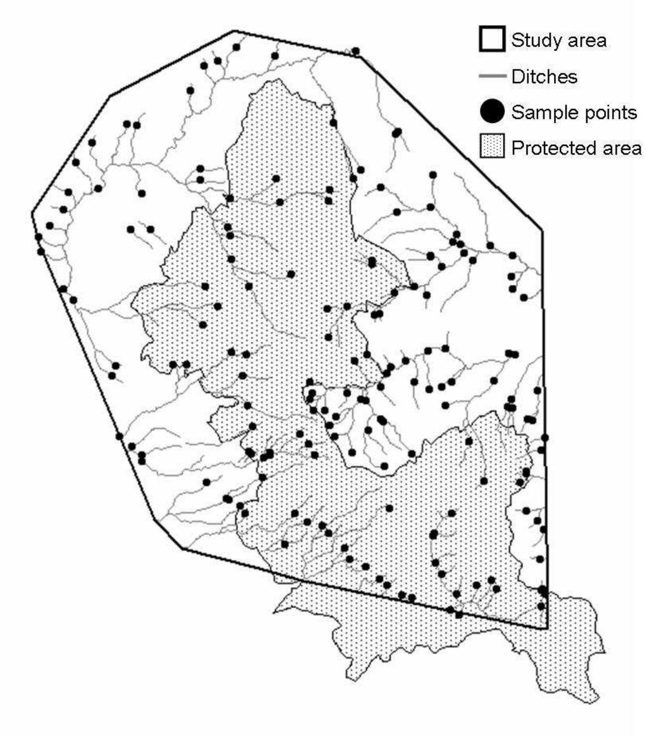

Figure 1*: Study area*

The hunting season started in September and went on till January. Hunting of wild boar occurred by drive hunts with a large number of dogs and 25-50 hunters. The hunting pressure in the study area was quantify as 9.6 hunted boars/ha.

In the study area the wild boars average density was estimated, by drive census conducted every year in spring, in 16,7 individuals per 100 ha. The only other ungulate present was roe deer (*Capreolus capreolus*). Predators were the red fox (*Vulpes vulpes*) that could prey on wild boar piglets and the wolf (*Canis lupus*). In Arezzo Province wolves were present at high densities with a mean pack size of 4.0 ± 0.6 (Apollonio and Mattioli, 2007; Capitani et al., 2004). In particular inside OAC wolves were present with a resident pack (Gazzola et al., submitted).

Methods – Wild boar were captured using both vertical drop nets and traps baited with maize. Captured animals were handled and only adult wild boars were treated with sedative Zoletil® (Fournier et al., 1995). Before releasing individuals were fitted with Televilt radio collars

(Televilt, Sweden, 150-151 MHz wavebands), weighed, measured and aged, by teeth eruption and wear according to Briedermann (1990). In this way it has been possible to distinguish 3 age classes: piglets (less than 1 year old), subadults (1-2 years old) and adults (more than 2 years old). We used Wildlife Materials TRX-1000S receivers and a three-element hand-held Yagi antenna, connected with a coassial cable of 1,5m. We located boar by triangulation using bearings from three different points (White and Garrott, 1990) by the "loudest signal" method. We marked out bearings on a 1:10.000 scale map (Kenward, 1987) with grid of 100 meters.

From 2002 to 2009 we radio-located 94 wild boar subadults and adults (33 males and 61 females). All individuals were locate through radio tracking by triangulation from three different points (White and Garrott, 1990). We applied discontinuous telemetry distributing uniformly the telemetry data over the 24 hours (Swihart and Slade, 1985) with 8-12 locations per each boar per month, considering at least 12 hours between consecutive locations, to exclude data's autocorrelation (Van Winkle, 1975).

For an intensive study we located 1 sample point for each ditch shorter than 1 km and we increased the sampling points proportionally for ditches longer than 1 km. As result we obtain a total of 134 sample points in the whole study area (Fig. 1). Regularly every 15 days for 12 months the same author measured, using a graduated stick, in each station the quantity of water (cm) in the ditch. Each time the water sampling required two days of work. In the intensive study we radio-located a sample of 38 wild boar, divided in different age and sex classes (20 males and 18 females). One wild boar location for all the sample and water presence were recorded in the same day In this way we had exactly the location of wild boars, knowing the water quantity in ditches in that moment.

Weather data (temperatures and precipitations) were collected by Corpo Forestale dello Stato from 1968 by 4 weather stations located in and around the study area.

Data analysis – Seasons considered were: spring (March - May), summer (June - August), autumn (September - November), winter (December - February). Analyzing meteorological data from 1968 to 2008 we identified the drought and the rainy periods, considering the three-months periods off all years with the lowest and the highest quantity of rain. The drought season corresponded exactly to summer (June, July, August) while the rainy season was located in October, November and December. Home range sizes (in the drought and rainy periods and at in a monthly scale) were evaluated with Ranges VI software using the Kernel method (Worton, 1989) considering 90% of available locations for each boar (Borger et al., 2006). The drought and rainy home range were composed by at least 10 locations each animals per period, while monthly home range were composed by at least 6 locations each animals per month. Home ranges, distances from ditches and water quantity in ditch were analyzed to verify the normality distribution using Kolmogorov-Smirnov test therefore were transformed with natural logarithm to give a normal distribution and tested again.

We calculated the Gaussen Index (GI) as the amount of precipitation minus twice the mean temperature (Dajoz, 1973). The GI is a measure of the water available for vegetation (Dajoz, 1973), and has been previously related to ungulate performance (Gaillard et al., 1997; Garel et al., 2004).

We calculated the ratio between the length of ditches in the home range and home range area (LA) as an index of water available in the home ranges.

To analyze the effects on home range size we used the linear-mixed model (LMM), with individuals as random factor in order to avoid problems of repeated measurements of the same animal.

We excluded piglets in the model used to analyze the drought and rainy periods because of newborns quick development that could lead in a three months period to a strong variance. We considered home range size as a dependent variable. Independent variables, considered as fixed factors, were sex, age classes and periods (drought or rainy). LA and GI index were considered as covariate variables.

Monthly home range analysis considered only data of intensive year and we included also piglet data. The dependent variable was the monthly home range size and independent variables, considered as fixed factors, were sex, age classes and seasons. LA and GI index were considered as covariate variables. We tested the difference between age classes and seasons by means of LMM pairwise comparisons with adjustment for multiple comparisons.

Finally we performed a model considering as dependent variable the distance between wild boar locations and ditches. The independent variables, considered as fixed factors, were sex, age classes and seasons. The water quantity in ditches was a covariate.

We analyzed data on habitat selection using ArcView GIS 3.2 (*ESRI*). We used compositional analysis to evaluate habitat selection in the drought and rainy periods, comparing used habitats with available ones at two different levels (Aebischer et al., 1993). To apply compositional analysis we used a Excel macro (Smith, 2003), that allowed to perform the randomization procedure recommended by Aebischer et al. (1993). At the second level, as suggested by Aebischer et al. (1993), we excluded the category less used. We tested for differences in habitat selection between seasons, sexes and age classes analysing Wilk's log-ratio matrices using a MANOVA test.

Statistical analysis were done using SPSS 13.0 software (SPSS Inc., Chicago, Illinois). In all statistical tests significance was established at $P \leq 0,05$.

RESULTS

A total of 293 home range was calculated in drought and rainy period from 2002 and 2009. Mean home range size (± S.E.) for subadult males were 109.37 ha ± 23.69 in the drought period and 323.48 ha ± 139.50 in the rainy period. Adult males home range size were 65.51 ha ± 12.93 in the drought period and 207.07 ha ± 83.55 in the rainy period. Mean home range size for subadult females were 130.92 ha ± 30.99 in the drought period and 248.40 ha ±

100.31 in the rainy period. Adult females home range size were 113.32 ha ± 21.17 in the drought period and 298.71 ha ± 130.76 in the rainy period.

We didn't underline any difference on home range size in the two periods between age classes (LME: $F_{1,128} = 2.354$, $P = 0.127$), sexes (LME: $F_{1,128} = 2.147$, $P = 0.145$) and different periods (LME: $F_{1,128} = 0.726$, $P = 0.396$). We found an influence on home range size due to the LA (LME: $F_{1,128} = 36.010$, $P < 0.001$) and to the GI (LME: $F_{1,128} = 5.314$, $P = 0.023$) (Table 1). In the case of LA the parameter estimate was -0.034 ± 0.006 indicating a negative effect on the home range size. The GI had a positive effect (parameter estimate = 0.002 ± 0.001), so increasing the GI wild boars reacted increasing their home range sizes.

Independent variables	Fixed effects	d.f.	F	Sig.
Home range size in drought and rainy periods (Denominator df = 128)	Sex	1	2,147	0,145
	Age class	1	2,354	0,127
	Period	1	0,726	0,396
	LA	1	36,010	**0,000**
	GI	1	5,314	**0,023**
Monthly home range size (Denominator df = 107)	Sex	1	0,034	0,854
	Age class	2	9,402	**0,000**
	Season	3	2,609	**0,055**
	LA	1	7,544	**0,007**
	GI	1	17,051	**0,000**
Distance between locations and ditches (Denominator df = 115)	Sex	1	0,128	0,721
	Age class	1	0,982	0,324
	Season	3	0,953	0,418
	Water in ditches	1	5,089	**0,026**

Table 1*: Linear mixed model analysis of wild boar in all time scale.*

Level of analysis	Period	Females			Males		
		Wilk's λ	Rand P	Ranked habitat typologies	Wilk's λ	Rand P	Ranked habitat typologies
First	Drought	0.21	0.001	DW>>>BW>CW>>>MW>>>OA	0.32	0.001	DW>BW>CW>>>MW>OA
	Rainy	0.07	0.001	CW>BW>DW>>>MW>>>OA	0.23	0.001	DW>CW>BW>>>MW>OA
Second	Drought	0.43	0.001	DW>CW>BW>MW	0.45	0.013	DW>BW>CW>MW
	Rainy	0.51	0.001	DW>CW>BW>MW	0.37	0.029	DW>CW>BW>MW

***Table 2**: Habitat selection of wild boar as determined by compositional analysis. DW: deciduous forests; CW: coniferous forests; BW: bushwoods; MW: mixed woods; OA: open areas.*

In the two periods (drought and rainy) we applied compositional analysis: open areas were always used marginally therefore they were excluded from the second level of the analysis. Compositional analysis showed for females a significant difference from random use in all periods in both level of analysis (Table 2).

At the first level, females positively selected ($P < 0.05$) deciduous forests in the drought period. While in the rainy period females firstly ranked coniferous forests (Figure 2).

Open areas were always avoided. At the second level both periods showed the same rank order, ranking firstly deciduous woods than coniferous woods and bushwoods (Figure 3).

Males compositional analysis showed a significant difference from random use in both periods in all analysis level (Table 2). At the first level, males firstly ranked in both periods deciduous forests (Figure 2). Mixed woods and open areas were always avoided by males. Deciduous forest were also selected by males at the second level in both periods (Figure 3).

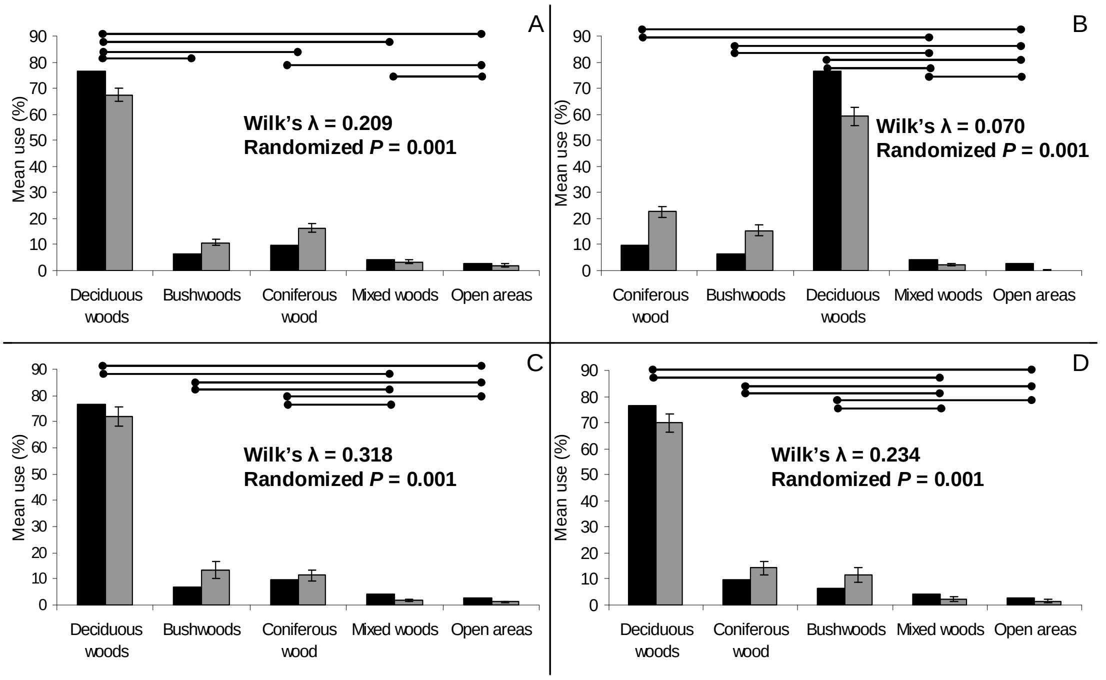

Figure 2*: Habitat selection by wild boar females in drought period (A) and rainy period (B) and by males in drought period (C) and rainy period (D), at the first level of compositional analysis. Grey columns represent available habitats, black columns show habitats used, and significant departure from random use is indicated by lambda and randomized P values. Lines indicate significant differences (P < 0.05 by compositional analysis) between connected habitat classes.*

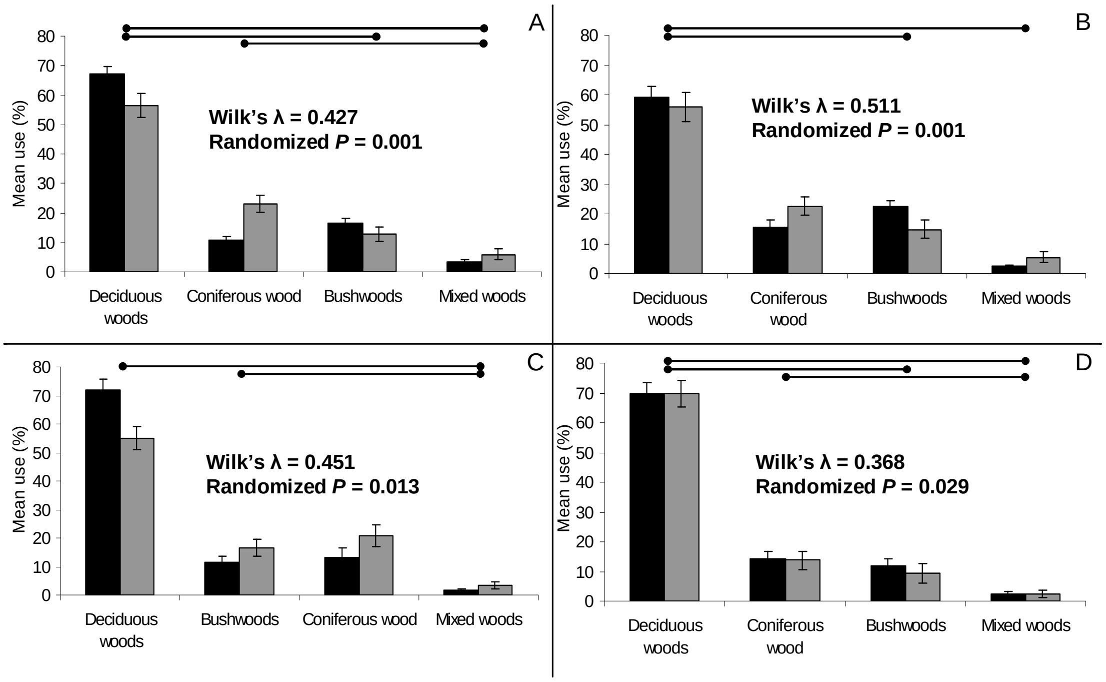

Figure 3*: Habitat selection by wild boar females in drought period (A) and rainy period (B) and by males in drought period (C) and rainy period (D), at the second level of compositional analysis. Grey columns represent available habitats, black columns show habitats used, and significant departure from random use is indicated by lambda and randomized P values. Lines indicate significant differences (P < 0.05 by compositional analysis) between connected habitat classes.*

MANOVA didn't show a different habitat selections between sexes (MANOVA λ = 0.951, F = 1.996, P = 0,098). No differences were underlined considering the two periods (MANOVA λ = 0.957, F = 1.731, P = 0,146). The age class influenced habitat selection at the first level (MANOVA λ = 0.941, F = 2.430, P = 0,050) and the difference was noticed in the use some habitat typologies (coniferous woods: F = 4.544, P = 0,035; bushwoods: F = 8.727, P = 0,004; mixed woods: F = 4.372, P = 0,038). At the second level MANOVA didn't show a different habitat selections between sexes, age classes and periods.

Considering the intensive study, 151 individual monthly home ranges were calculated. No significant differences on home range sizes were found between sexes (LME: $F_{1,107} = 0.034$, $P = 0.854$). Monthly home range size were influenced by age classes (LME: $F_{2,107} = 9.402$, $P < 0.001$) (Table 1). Piglets shown a different behaviour from subadults and adults (LME pairwise adjusted comparisons: piglets vs subadults: P = 0.001; piglets vs adults: P < 0.001), piglets generally had smaller home ranges than other wild boars (Figure 4). Subadults and adults had a similar spatial behaviour at a monthly scale (LME pairwise adjusted comparisons: subadults vs adults: P = 0.188).

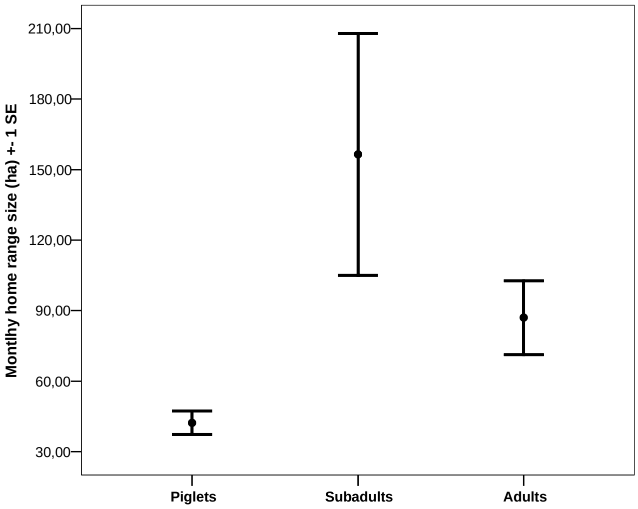

***Figure 4**: Monthly home range size (ha).*

Wild boars shown a quite significant different behaviour among seasons (LME: $F_{3,107} = 2.609$, $P = 0.055$). No differences were found between spring and winter (LME pairwise adjusted comparisons: spring vs winter: $P = 0.984$) and between summer and autumn (LME pairwise adjusted comparisons: summer vs autumn: $P = 0.967$). While in other cases were found significant differences (LME pairwise adjusted comparisons: spring vs summer: $P = 0.018$; spring vs autumn: $P = 0.015$; summer vs winter: $P = 0.015$; autumn vs winter: $P = 0.013$). So we could merge spring and winter vs summer and autumn. Significant differences were shown also considering the LA (LME: $F_{1,107} = 7.544$, $P = 0.007$) and the GI (LME: $F_{1,107} = 17.051$, $P < 0.001$). LA had a negative influence on monthly home range size (parameter estimate = -0.016 ± 0.006), while GI shown a positive effect on monthly home range size (parameter estimate = 0.025 ± 0.006).

Considering the fine scale data we analyzed distances between ditches and animals locations in the same day of water survey. Significant influence was found taking into account the quantity of water in ditches (LME: $F_{1,115} = 5.089$, $P = 0.026$) (Table 1). The available water had a positive influence on wild boar movements, if the water in ditches increased animals reacted moving away from ditches (parameter estimate = 0.975 ± 0.432). No differences were found between sexes (LME: $F_{1,115} = 0.128$, $P = 0.721$), seasons (LME: $F_{3,115} = 0.953$, $P = 0.418$) and age classes (LME: $F_{3,115} = 0.982$, $P = 0.324$).

DISCUSSION

This study was pointed to a relationship between ambient conditions, measured as water present in ditches and consequently in the environment. This study shown that wild boars react to variations on water availability, considering both water quantity in small creeks and rainfall. Wild boar reaction were generally sex and age unrelated, except for piglets.

At a larger time scale analysis we did not find individual differences, so any influence of age and sex classes. Subadult and adult wild boars shown similar ecological and spatial behaviour. In general this reflected on similar environmental requirements. Wild boars needs, related to water, were expressed by LA ratio and GI. These were two indices that expressed the amount of water courses in the area and also related it to temperatures. Both indices indicated that the higher was the availability of water in the environment, the wider were wild boar movements and searching for other resources. Limited differences were found in habitat choice in drought and rainy periods. This result may be explained by the main requirements, ecological and energetical, were probably more or less constant all over year. The study areas in which this work has been performed was an medium heterogeneous land, that could assure all the fundamental needs, such as feeding, resting and thermoregulation places. Furthermore the climate was continental characterized by hot and dry summer but not extreme as the Mediterranean climate in which summer were really drought seasons with high temperature and a low level of humidity. In this cases the mortality rate could drastically increase (Massei et al., 1997b) and summer season became a limiting time of the year. In our study area in the summer the duration of harsh condition is more restricted than in Mediterranean region.

Similar needs of subadults and adults, were found also in the intensive year-long study. This similarity between subadults and adults was reflected on similar monthly home range sizes. On the other hand piglets shown a different spatial behaviour in the monthly scale analysis. Piglets had more specific needs being more sensitive immediately at birth to temperature. Piglets might be affected by dry conditions due to their continuous water requirements during early development (Fraser et al., 1990), being highly sensible to dehydration as a consequence of low water consumption (Fraser et al., 1990). Therefore piglets were particularly susceptible to thermal characteristics of the environment and so the mortality risk was higher than subadults and adults. Fernández-Llario and Carranza (2000) showed that in the first days after birth piglet mortality rate is higher under dry conditions than in rainy seasons. Both for piglets and older wild boar the drought period has been considered the most critical period, consequently we noticed a different spatial behaviour at a seasonal level, spring and winter versus summer and autumn. Therefore the more rainy and cold seasons from the more drought and hot seasons. Also at this fine scale of analysis we found the same influence of LA and GI than at the large scale study. These two indices confirmed the effect of the amount of water available present in the environment. Wild boars tended to be concentrated near the water sources during drought periods, on the contrary in water abundance times wild boar expanded their range. Furthermore there could be two situations, higher quantity of ditches in the home range and a small home range or a low quantity of ditches in a bigger home range. In any case wild boar are able to adjust their home range sizes depending on their needs.

In the higher level of detail we have found the positive relation between the quantity of water in ditches and the distance of animals from ditches. This result underlined further on the importance of water for this species. When the water in ditches and consequently in the environment was low wild boar were bind to places in which there was water that was close to ditches, that could assure water and humidity. More water was in ditches more water was, in general, in the environment and wild boars could move more, searching for other needs. This results is in according to other studies that affirmed that, when water became scarce in June, white-tailed deer moved closer to permanent water, but dispersed when summer rains starter. Furthermore during dry seasons when surface water becomes scarce, deer may concentrate near remaining sources of water (Michael, 1965; Webb et al., 2007). Wild boars are poorly adapted to arid environments and must rely on free water to a greater extent than other species. Therefore, water appeared to exert a strong influence on wild boar daily activity patterns, movements, and home ranges.

REFERENCES

Aebischer NJ, Robertson PA, Kenward RE. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74(5):131-1325.

Apollonio M, Mattioli L. 2007. Il lupo in Provincia di Arezzo. Studi sulla biologia della fauna. Le Balze.

Baber DW, Coblentz BE. 1986. Diet, nutrition and conception in feral hog on Santa Catalina Island. The Journal of Wildlife Management 51:306-317.

Barrett RH. 1978. The feral hog on the Dye Creek Ranch, California. Hilgardia 46:283-355.

Berthon D, Herpin P, Duchamp C, Dauncey MJ, Le Dividich J. 1993. Modification of thermogenic capacity in neonatal pigs by changes in thyroid status during late gestation. Journal of Development Physiology 19:252-261.

Borger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393-1405.

Boyce MS, Turner MG, Fryxell J, Turchin P. 2003. Scale and heterogeneity in habitat selection by elk Yellowstone National Park. Ecoscience 10(4):421-431.

Briedermann L. 1990. Schwarzwild. Berlin, Germany: VEB Deutscher Landwirtschaftsverlag.

Calenge C, Maillard D, Vassant J, Brandt S. 2002. Summer and hunting season home ranges of wild boar (*Sus scrofa*) in two habitats in France. Game and Wildlife Science 19:281–301.

Caley P. 1993. Population dynamics of feral pigs (*Sus scrofa*) in a Tropical riverine habitat complex. Wildlife Research 20:625-636.

Capitani C, Bertelli I, Varuzza P, Scandura M, Apollonio P. 2004. A comparative analysis of wolf (*Canis lupus*) diet in three different Italian ecosystem. Mammalian Biology 69(1):1-10.

Cappai N, Bertolotto E, Donaggio E, Grignolio S, Apollonio M. submitted. Factors affecting fertility and reproduction in wild boar (*Sus scrofa*) in a mountainous environment.

Curtis SE, Edwards SA, Gonyou HW. 2001. Ethology and psychology. In: Pond WG, Mersmann HJ (eds) Biology of the domestic pig. Cornell University Press, New York, pp 41–78.

Dajoz R. 1973. Précis d'écologie. Gauthier Villars.

Dardaillon M. Some aspects of the orientation in space of *Sus scrofa* as revealed by data on home range, habitat use and movements. In: Beugnon G., editor; 1986. p 63-70.

Dardaillon M. 1987. Seasonal feeding habits of the wild boar in a Mediterranean wetland, the Camargue (southern France). Acta Theriologica 32:389-401.

Dexter N. 2003. The influence of pasture distribution, and temperature on adult body weight of feral pigs in a semi-arid environment. Wildlife Research 30:75-79.

Diong CH. 1982. Population biology and management of the feral pig (*Sus scrofa*) in Kipahulu Valley, Maui.: Ph.D. Thesis, University of Hawaii, Honolulu.

Fernàndez-Llario P. 1996. Ecología del jabalí en Doñana: parámetros reproductivos e impacto ambiental: University of Extremadura.

Fernàndez-Llario P, Carranza J. 2000. Reproductive performance of the wild boar in a Mediterranean ecosystem under drought condition. Ethology Ecology & Evolution 12:335-343.

Fournier P, Fournier-Chambrillon C, Maillard D, Klein F. 1995. Zoletil© immobilization of Wild Boar (*Sus scrofa* L.). Ibex Journal of Mountain Ecology 3:134-136.

Fraser D, Patience JF, Phillips PA, McCleese JM. 1990. Water for piglets and lactating sows: Quantity, quality and quandries. Pages 137–160 in Recent Advances in Animal Nutrition. W. Haresign and D. J. A. Cole, ed. Butterworths, London, UK.

Fruzinski B, Labudzki L. 2002. Management of wild boar in Poland. Zeitschrift Fur Jagdwissenshaft 48 (Supplement):201-207.

Fryxell J, Sinclair ARE. 1988. Seasonal migration by white-eared kob in relation to resources. African Journal of Ecology 26:17-31.

Gaillard J-M, Boutin J-M, Delorme D, Van Laere G, Duncan P, Lebreton J-D. 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. Oecologia 112:502-513.

Garel M, Loison A, Gaillard J-M, Cugnasse J-M, Maillard D. 2004. The effects of a severe drought on mouflon lamb survival. Proceedings of Royal Society London 271:S471–S473.

Gazzola A, Bongi P, Capitani C, Mattioli L, Viviani A, Alboni M, Apollonio M. submitted. Functional response of wolf diet to wild ungulate availability: the influence of structure of ungulate community, prey preference, and hunting. Journal of Applied Ecology.

Geisser H, Reyer H-U. 2005. The influence of food and temperature on population density of wild boar *Sus scrofa* in the Thurgau (Switzerland). Journal of Zoology, London 267:89-96.

Gethöffer F, Sodeikat G, Pohlmeyer K. 2007. Reproductive parameters of wild boar (*Sus scrofa*) in three different parts of Germany. European Journal of Wildlife Research 53:287-297.

Heptner VG, Nasimovich AA, Bannikov AG. 1989. Mammals of the Soviet Union. Vol. I, Ungulates. New Delhi: Amerind Publishing Co. Put. Ltd.

Howe T, Singer FJ, Ackerman BB. 1981. Forage relationship of European wild boar invading Northern hardwood forest. The Journal of Wildlife Management 45:748-754.

Kenward R. 1987. Wildlife radio Tagging. London: Academic Press. 222 p.

Leaper R, G. M, L. GM, R. A. 1999. The feasibility of reintroducing Wild Boar (*Sus scrofa*) to Scotland. Mammal Review 29(4):239-259.

Manners MJ, McCrea M. 1963. Changes in the chemical composition of sow-reared piglets during the first month of life. British Journal of Nutrition 17:495-513.

Markov NI. 1997. Population dynamics of wild boar, *Sus scrofa*, in Sverdlovsk oblast and its relation to climatic factors. Russian Journal of Ecology 28:269-274.

Massei G, Genov P, Staines BW, Gorman ML. 1997a. Factors influencing home range and activity of wild boar (*Sus scrofa*) in a Mediterranean coastal area. Journal of Zoology 242:411-423.

Massei G, Genov P, Staines BW, Gorman ML. 1997b. Mortality of wild boar, *Sus scrofa*, in a Mediterranean area in relation to sex and age. Journal of Zoology, London 242:394-400.

Massei G, Genov PV, Staines BW. 1996. Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. Acta Theriologica 41:307-320.

Melis C, Szafranska PA, Jedrzejewska B, Barton K. 2006. Biogeographical variation in the population density of wild boar (*Sus scrofa*) in Western Eurasia. Journal of Biogeography 33:803-811.

Michael ED. 1965. Movements of white-tailed deer on the Welder Wildlife Refuge. Journal of Wildlife Management 29(1):44-52.

Powell DM. 2004. Pigs (*Suidae*). In Kleiman, D.G., Geist, V. & McDade, M. (eds.), Grzimek´s animal life encyclopedia, second edition, volume 15, Mammals IV. - Gale, Farmington Hills: 275-290.

Redfern JV, Grant CC, Biggs HC, Getz WM. 2003. Surface water constraints on herbivore foraging in the Kruger National Park, South Africa. Ecology 84(8):2092–2107.

Roath LR, Krueger WC. 1982. Cattle grazing behavior on a forested rangeland. Journal of Range Management 35:332-335.

Saez-Royuela C, Telleria JL. 1986. The increased population of the Wild Boar (*Sus scrofa* L.) in Europe Mammal Review 16(2):97-101.

Smith PG. 2003. Compos Analysis, version 5.1 standard [software]. Abergavenny, UK: Smith Ecology Ltd.

Spitz F. 1986. Current state of knowledge of wild boar biology. Pig News and Information 7(2):171-175.

Spitz F. 1999. *Sus scrofa* Linnaeus, 1758. In Mitchell-Jones A.J., Amori G., Bogdanowicz W., Krystufek B., Reijnders P.J.H., Spitzenberger F., Stubbe M., Thissen J.B.M., Vohralik V. & Zima J. (eds.), The atlas of European mammals. - Poyser, London: 380-381. .

Swihart RK, Slade NA. 1985. Testing for independence of observation in animal movements. Ecology 66(4):1176-1184.

Thurfjell H, Ball JP, Åhlén P-A, Kornacher P, Dettki H, Sjöberg K. 2009. Habitat use and spatial patterns of wild boar *Sus scrofa* (L.): agricultural fields and edges. European Journal of Wildlife Research 55:517–523.

Truvé J, Lemel J. 2003. Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. Wildlife Biology 9 (suppl. 1):51-57.

Van Winkle W. 1975. Comparison of several probabilistic Home range models. The Journal of Wildlife Management 33:118-123.

Webb SL, Hewitt DG, Hellickson MW. 2007. Effects of permanent water on home ranges and movements of adult male white-tailed deer in southern Texas. The Texas Journal of Science.

Welander J. 2000. Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. Journal of Zoology, London 252:263-271.

Western D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. East Africa Wildlife Journal 13:265-286.

White GC, Garrott RA. 1990. Analysis of wildlife radio-tracking data. San Diego. London: Academic Press.

Whiting JC, Bowyer RT, Flinders JT. 2009. Annual use of water sources by reintroduced Rocky Mountain bighorn sheep *Ovis canadensis canadensis*: effects of season and drought. Acta Theriologica 54(2):127-136.

Woodall PF. 1983. Distribution and population dynamics of Dingoes (*Canis familiaris*) and feral pigs (*Sus scrofa*) in Queensland, 1945-1976. Journal of Applied Ecology 20:85-95.

Worton BJ. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70(1):164-168.

Chapter 4

Sex and age differences in anti-predator behaviour in a wild boar population

SEX AND AGE DIFFERENCES IN ANTI-PREDATOR BEHAVIOUR IN A WILD BOAR POPULATION

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ABSTRACT

We studied the influence of predation and human disturbance on wild boar spatial behaviour in a protected area, where two predators, i.e. wolves and foxes were found and both of them predated on wild boar population, especially on piglets. Furthermore in Autumn and Winter human disturbance increased thanks to hunting. In our study, conducted from 2002 to 2009, we did not underline influence on home range size of daylight and hunting activities. We therefore choose to evaluate anti-predator behaviour taking into account the proximity of wild boar locations to refuge areas identify in dense shrubs. This intensive study was performed between 2006 and 2008, using radio-locations of 82 wild boars. Subadult and adult females stayed closer to shrub patches than males. Females and males piglets did not differ on what concerning distances from shrubs and they were closer to this areas especially during the resting phase. In general, we observed that wild boars were nearer shrubs during the day, dawn and dusk, while during night, they were active, and moved around looking for food. Females preferred areas closer to shrub lands during Spring, that correspond to the birth period, while males come closer to shrubs in Autumn and Winter.

INTRODUCTION

Habitat value include besides food resources, protection from disturbance (Strohmeyer et al., 1999), predation (Alldredge et al., 1991; Linnell et al., 1999) and thermal protection through the use of cover or favourable aspect (Merrill, 1991; Mysterud and Ostbye, 1999). Wild ungulates react in different ways to predation or human disturbance or adverse weather.

Hunted wild ungulates can display increased movement (Kilpatrick and Lima, 1999; Root et al., 1988), an enlarged resting range (Jeppesen, 1987) or changes in habitat selection (Kufeld et al., 1988). In some cases, animals remain within the established home range but shift their centre of activity (Kilpatrick and Lima, 1999). In several cases, changes in spatial behaviour are transitory: hunted animals move to a refuge area outside of their home range during the hunting season, but in some cases they move back within a few days (Jeppesen, 1987), while in other cases they move back at the end of the hunting season (Millspaugh et al., 2000). Cover includes, by definition, anything which veils or conceals, shelters or protects and can be both vegetation and topography. As climatic factors are long know to affect use of cover by ungulates, cover can be used as thermal cover, rain-interception and snow-interception cover. Numerous studies have documented how cervids selectively use cover to relieve heat and cold stress. Especially for ungulate fawns it is show that they bed down in bushes. It is well documented that ungulates use cover for its protective properties. There is some features of cover that may benefit by providing prey animals with refuges to decrease vulnerability to predators. Furthermore, plant cover could also be useful to visually obstruct detection of predators or conspecifics. Collectively, this evidence suggests that tree canopies and shrubs function as refuges for prey animals that decrease their vulnerability to predators. The seemingly contradictory results regarding the effect of plant cover on animal vigilance may, to some extent, be related to differences in the relative costs and benefits associated to overhead and lateral obstruction to visibility. Thus, animals might benefit from use of overhead cover to hide from predators at no major cost regarding their ability to detect conspecifics or food sources (Mysterud and Ostbye, 1999).

Furthermore it is observed the different behaviour between males and females regarding on anti-predator strategies. Males and females show contrasted life-history tactics, males should maximize their body mass that in turn will affect their chance to gain access to females and ultimately their fitness, while females to gain the same result have to maximize offspring survival. Predation risk may be relevant as it may elicit anti-predator strategies, modifying the home range size and habitat selection of females with kids, or changing the group dimension (Barten et al., 2001; Ciuti et al., 2006; Grignolio et al., 2007).

Ungulates are viewed as being highly susceptible to predation during the first weeks or months of life. In most populations of large herbivores, juvenile survival is relatively low and variable compared to adult survival (Gaillard et al. 1998b; Eberhardt 2002), so that variation in juvenile survival is potentially an important contribution to changes in population dynamics (Gaillard et al. 2000; Coulson et al. 2005). Juveniles adopt different tactics to minimize the risk of predation. The hiding tactic lead to choosing bed site both to hide from predators and to protect from adverse influences of microclimate. The selection of a bed site by a fawn takes place within the limits of the maternal home range. The general location of the bed site is thus largely determined by the mother. Early-life survival is very sensitive to climatic conditions (Gilbert and Raedeke 2004; Jones et al. 2005); hypothermia has been shown to be one of the most important causes of fawn mortality in the absence of predators (Andersen and Linnell 1998; Olson et al. 2005). In particular, the period shortly after birth is critical due to limited energy reserves and the small body size of fawns. The protection provided by bed sites against climatologic influences therefore is expected to be important.

Few studies have monitored the effects of hunting activities on wild boar spatial behaviour (Baubet et al., 1998; Gaillard et al., 1987). Hunted boar may enlarge their resting range, increase their length of movement or move to un-hunted areas outside their resting ranges

(Calenge et al., 2002; Sodeikat and Pohlmeyer, 2003), though contrasting results have shown that boar remain within established resting ranges (Keuling et al., 2008). Differently from hunting that is confined to a well defined season, natural predation by wolves and foxes, is exerted all year long and piglets in their first year of life seems to be more susceptible to it.

In this study we analyse the use of refuge areas in wild boar by age, sex, daily light and season. In particular, as wild boar are subject to human disturbance and wolf predation in our study site, we tested also for differences in home range between night and day and between hunting and non hunting season. To do that we analyzed the use of high vegetation cover sites, as resting sites.

METHODS

Study area - The study was performed in Tuscan Apennine (Arezzo Province, Italy) in about 2700 ha located in a protected area (Oasi Alpe di Catenaia, OAC) surrounded by hunting districts. The altitude range varied from 400 m to more than 1400 m a.s.l. The continental climate was characterized by hot and dry summers, cold and rainy winters, with high humidity rate. The snow period fell from October to April above 1000 m a.s.l.. The wood cover exceed 80% of the study area and 6% of the study area was occupied by shrubs that offered a refuge area for wild boars. The area all around the OAC was intended for wild boar hunting with hounds. The hunting season started in September and went on till January. Hunting of wild boar occurred by drive hunts with a large number of dogs and 25-50 hunters.

In the study area the only other ungulate present apart from wild boar was roe deer (*Capreolus capreolus*). Predators were the wolf (*Canis lupus*) and the red fox (*Vulpes vulpes*). In Arezzo Province wolves were present at high densities with a mean pack size of 4.0 ± 0.6 (Apollonio and Mattioli, 2007; Capitani et al., 2004). In particular in OAC wolves were present with a resident pack and wild boar is the main prey species (Gazzola et al., in press).

Methods – Wild boar were captured using both vertical drop nets and traps baited with maize. Captured animals were handled and only adult wild boars were treated with sedative Zoletil® (Fournier et al., 1995). Before releasing individuals were fitted with Televilt radio collars (Televilt, Sweden, 150-151 MHz wavebands), they were weighed, measured and aged, by teeth eruption and wear according to Briedermann (1990). In this way it has been possible to divide animals in 3 age classes: piglets (less than 1 year aged), subadults (1-2 years old) and adults (more than 2 years old). We used Wildlife Materials TRX-1000S receivers and a three-element hand-held Yagi antenna, connected with a coassial cable of 1,5m.

We collected wild boar locations from June 2002 to August 2009, in which the discontinuous telemetry was performed as a previous work conducted in the same study area (Bertolotto et al., submitted. See Chapter 2). To performed this study we considered telemetry data coming from 168 wild boars: piglets (less than 1 years old), subadults (1-2 years old) and adults (>2 years old) (Figure 1).

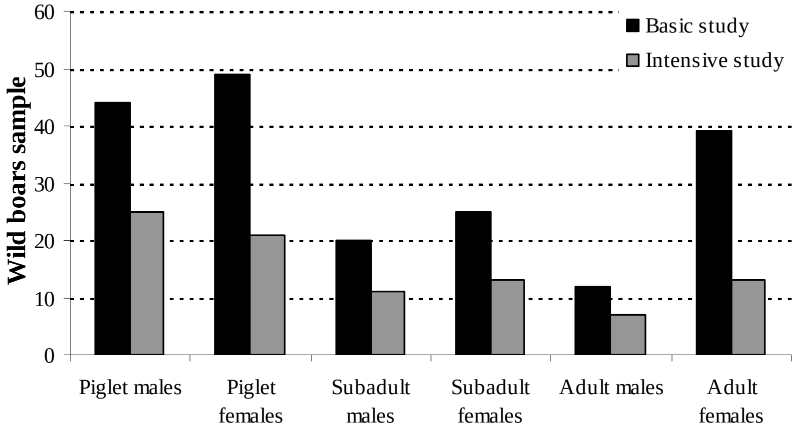

***Figure 1**: Sample size in both study periods.*

From April 2007 to July 2007 a digital map showing all dense shrub area was created (Figure 2) by mapping all the dense vegetation areas constituted by *Rubus spp*., *Erica spp*., *Crataegus spp*., *Prunus spinosa*, *Spartium junceum* and *Cystus scoparius*, that were present in the OAC. The mapped shrub areas reached 8 ha.

Figure 2*: Oasi Alpe di Catenaia (OAC) with mapped shrub lands (grey).*

In the intensive study, we intended to analyze the influence of shrub lands on wild boar spatial behaviour, we considered all locations collected from September 2006 to November 2008. In this period we used 3368 locations of 82 wild boars, subdivided in the two sexes and 3 age classes: piglets (less than 1 years old), subadults (1-2 years old) and adults (>2 years old) (Figure 1). We recorded for each location the light conditions using 4 different categories: night, dawn, day and dusk and the active/inactive condition of each wild boar.

Data analysis –Diurnal, nocturnal and dawn/dusk (we merged locations collected during dawn and dusk) home range sizes were evaluated with Ranges VI software using the Kernel method (Worton, 1989) considering 90% of available locations for each animal (Borger et al., 2006). We calculated home ranges considering two different periods during the year: hunting season (from September to January) and non hunting season (from February to August). Furthermore we merged locations collected during dawn and dusk. Dawn and dusk were considered the two moments of 24 hours in which animals should have a similar spatial behaviour between them. In this way for each animal we had in both periods 3 different home ranges: day, night and dawn/dusk. The analysis of home range size were performed using the linear-mixed model (LMM), that gave importance to random effects, as individual identity. This allowed us to control repeated measurements of the same individual. We tested the influence on home range size of variables, considered as fixed factors, like age, sex, part of the day (day, night, dawn/dusk) and hunting.

Using data collection from 2006 to 2008 we calculated the distance of each wild boar locations from the nearest mapped shrub land, using the GIS software ArcView 3.2 (*ESRI*). We used a linear-mixed model (LMM), using as random effects the individual identity. In this analysis fixed factors were sex, age class, activity, part of the day and seasons. Seasons were considered as follow: spring: March-May; summer: June-August; autumn: September-November; winter: December-February.

Home ranges and distance from shrubs were analyzed to verify the normality distribution using Kolmogorov-Smirnov test therefore were transformed with natural logarithm to give a normal distribution and tested again.

All statistical analysis were performed using SPSS 13.0 software (SPSS Inc., Chicago, Illinois).

RESULTS

According to LMM analysis wild boar spatial behaviour wasn't affect by part of the day ($F_{2,284}$ = 2.355, P = 0.097) or hunting activities ($F_{1,284}$ = 0.028, P = 0.867). Also crossed variables didn't show any significant differences (Table 1).

	Df (denominator df = 284)	F	Sig.
Light	2	2.355	0.097
Period	1	0.028	0.867
Sex * Light	2	1.365	0.257
Sex * Period	1	0.028	0.866
Age * Light	4	1.662	0.159
Age * Period	2	0.062	0.940
Light * Period	2	1.143	0.320

***Table 1**: Linear mixed model analysis of daily home range size*

We reported the effect of single and combined biological and ecological features on distances between wild boar locations and shrub lands. Individual characteristics that had effects on spatial movements were sex ($F_{1,3350}$ = 32.176, p < 0.001), age class ($F_{2,3350}$ = 22.998, P < 0.001) and activity ($F_{1,3350}$ = 4.995, P = 0.025) (Table 2).

	Df (denominator df = 3350)	F	Sig.
Sex	1	32,176	< **0.001**
Age	2	22,998	< **0.001**
Activity	1	4,995	**0.025**
Season	3	1,290	0.276
Light	2	3,277	**0.038**
Age*Sex	2	26,488	< **0.001**
Age*Activity	2	3,528	**0.029**
Sex*Season	3	2,783	**0.039**

***Table 2**: Linear mixed model analysis of distance from wild boar locations to shrub land.*

Males were generally farer (mean ± SE: 4.347 ± 0.094) from shrub lands than females (3.348 ± 0.087) (LME pairwise adjusted comparisons: $p < 0.001$). Considering age class, piglets showed the lower distance from shrub lands (3.727 ± 0.084) respect on subadults (4.336 ± 0.112) and adults (4.230 ± 0.099). The LME pairwise adjusted comparisons shown a significant difference between piglets and the other age classes (subadults and adults $p < 0.001$), while between subadults and adults there was not difference ($P = 0.337$). The combined effect between age class and sex showed that there was not differences on the distance from shrubs in piglets between males and females (males: 3.636 ± 0.098; females: 3.817 ± 0.107). This differences was shown in subadults (males: 4.618 ± 0.154; females: 4.053 ± 0.130) and adults (males: 4.787 ± 0.131; females: 3.674 ± 0.109), confirming that females were closer to dense vegetation (Figure 3).

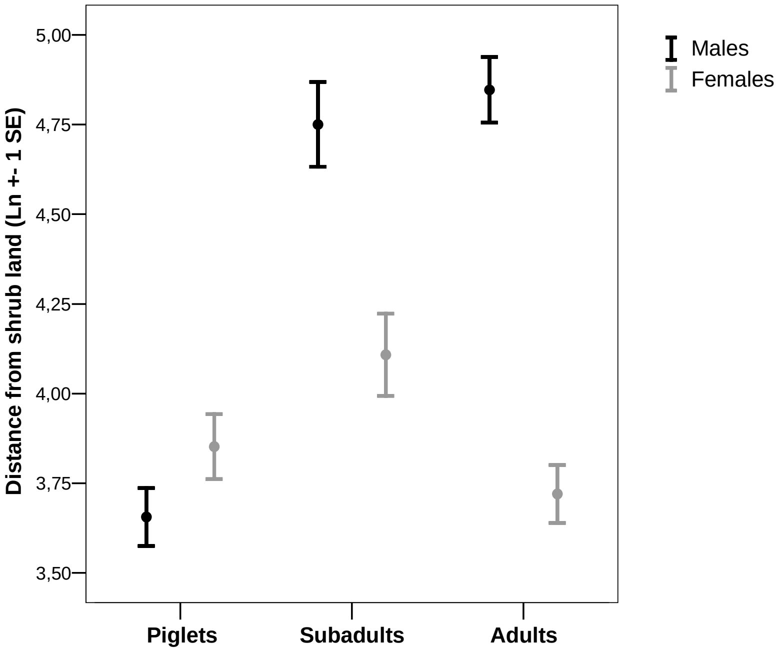

Figure 3*. Distance from shrub land (ln mean ± SE) in wild boar males and females with age class distinction.*

Generally inactive wild boars were closer to shrub lands (4.006 ± 0.091) in comparison with active individuals (4.189 ± 0.088) (LME pairwise adjusted comparisons: P = 0.025). This was clear in piglets only (inactive: 3.502 ± 0.107; active: 3.952 ± 0.097), while subadults (inactive: 4.291 ± 0.142; active: 4.380 ± 0.136) and adults (inactive: 4.225 ± 0.115; active: 4.236 ± 0.123) were not showing different proximity to cover in relation to their activity (Figure 4).

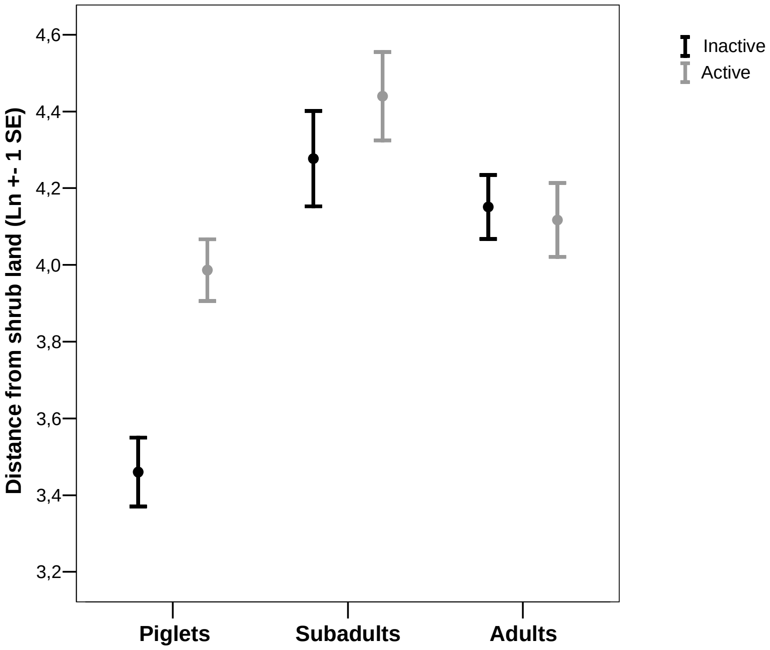

Figure 4*: Distance from shrub land (ln mean ±SE) in inactive or active wild boars with age class distinction*

In LMM we considered also the importance of seasons and day period (Table 2). On a seasonal scale there were no differences in the distance from shrub lands ($F_{3,3350}$ = 1.290, P = 0.276). There was a combined effect considering season and sex ($F_{3,3350}$ = 2.783, P = 0.039). In particular there was a great difference between males and females in spring (males: 4.488 ± 0.145; females: 3.651 ± 0.138) and in summer (males: 4.541 ± 0.116; females: 3.903 ± 0.120). Limited differences were observed between sexes in autumn (males: 4.263 ± 0.126; females:

3.925 ± 0.105) and no differences were noticed in winter (males: 4.096 ± 0.177; females: 3.914 ± 0.152) (Figure 5).

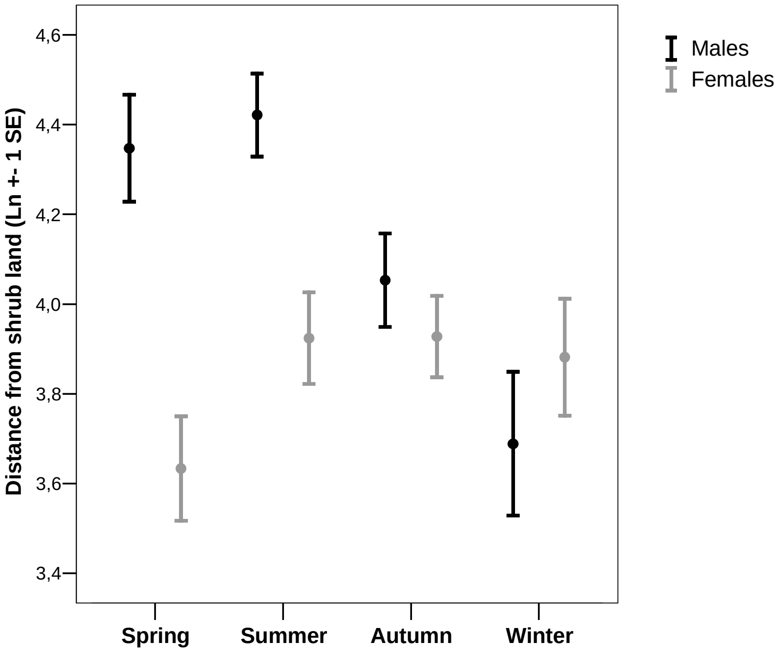

***Figure 5**: Distance from shrub land (ln, mean ± SE) in male and female wild boars with a seasonal distinction*

As assessed by the Linear Mixed Effect model analysis, the distance from high cover vegetation differed significantly according to part of the day ($F_{2,3350}$ = 3.277, P = 0.038).The shorter distance between shrub land and locations was found during the dawn/dusk period (3.996 ± 0.212), followed by day (4.042 ± 0.053) and during the night were recorded the highest distances (4.255 ± 0.071). Specifically differences were found between night and day periods (LME pairwise adjusted comparisons: P = 0.012). On the other hand no differences were found between night and dawn/dusk periods (LME pairwise adjusted comparisons: P = 0.239) and between day and dawn/dusk period (LME pairwise adjusted comparisons: P = 0.831) (Figure 6).

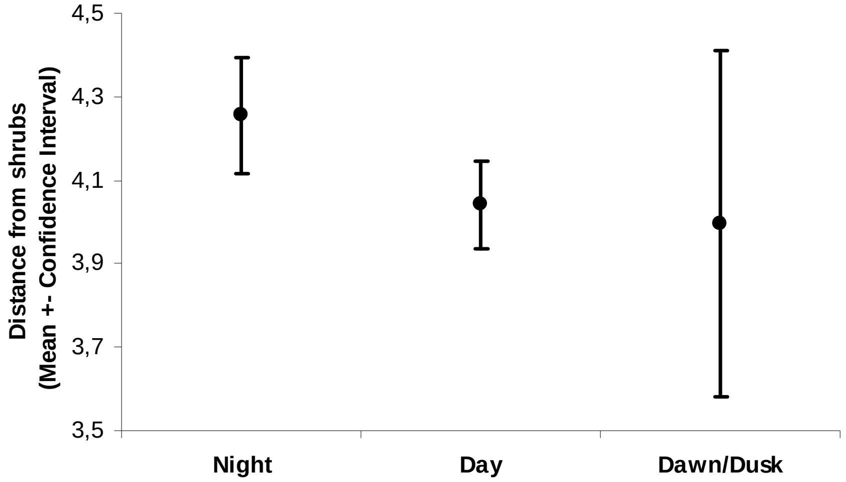

***Figure 6**: Distance from shrub land in wild boars with a part of the day distinction*

DISCUSSION

Some authors shown a modification on spatial behaviour due to hunting practises (Baubet et al., 1998; Calenge et al., 2002). In this study area we haven't found any modification neither at a seasonal scale (Bertolotto et al., submitted. See Chapter 2) nor taking into account the time of the day and hunting season combined. This homogeneity was probably due to the too wide temporal scale in which the analysis has been performed.

Moving deeply in this analyses we considered the use of dense vegetation cover, refuge areas which are mainly influenced by the shelter provided rather than by the abundance of food resources or by weather conditions.

We observed that females generally were closer to shrub lands than males. Females should maximize the protection of themselves and their offspring, selecting habitats with higher cover and lower predation risk even if these habitats may have a poorer forage quality. In particular, looking at the interaction between sex and season, females were closer to high cover vegetation during spring, i.e. the birth period (Cappai et al., submitted. See Chapter 1).

Piglet males and females didn’t show a different behaviour because they have similar needs, as are still in the same family group and being vulnerable tend to stay as close as possible to safer areas. Differences between sexes were found in subadults and adults: females were closer to shrub land in comparison with males. No differences were found between adult and subadult females and between adult and subadult males. Their needs were comparable, because females could be pregnant quite early in subadult age (Cappai et al., submitted. See Chapter 1). Furthermore subadults and adults should have an high knowledge of the area, in which they range, that allowed them to find the right compromise between security and richness of the area. Consequently differences between sexes in distance from shrub lands are pronounced in spring and summer were females, bear the responsibility of their litter. In autumn and winter also males came closer to bushes, at distances similar to female ones, especially in winter. This could be due to hunting effect. The disturb, starting from September, could cause wild boar males to search for safer areas, represented by high cover vegetation. When hunting season closes males moved more distant from refuge areas.

The choice of breeding females to protect their piglets reacted in the spatial behaviour of piglets, that generally stayed closer to shrubs respect on subadults and adults. The piglets mortality risk was higher than other wild boars, because of particular needs during the first weeks of life and because of higher risk of predation. To minimize these risks the mother choose safer places in which gave birth and in which piglet could stay there till they became bigger and more independent. Just before births, females start building an appropriate place for the piglets to be born. Females needed to find the right place for the nest, the most important feature of nest site should be the highest protection that was possible. The aim should be create with vegetation a complete cover, in this way the visibility of the litter became void (Brandt et al., 1997). Anti-predator behaviour constitutes a major constraint on ungulate behaviour, especially when small, vulnerable offspring are present (Berger, 1991; Festa-Bianchet, 1988). Because of this it is important to underline the considerable presence of red foxes and wolves in the study area. Especially red foxes could have an high impact on piglets survival, shaping their spatial behaviour. It was demonstrated in a study performed in the same area that the main preys of red foxes were wild boars piglets (individual weighting less than 10 Kg) and roe deer fawns (individuals less than 1 year old) (Donaggio et al., 2009, submitted). The wild boar constituted almost 60 % of wolf diet and wolves positively selected bigger wild boar piglets (between 10 and 35 Kg) (Donaggio et al., 2009, submitted). In response to high risk of predation for neonates, wild boar have evolved spatial strategies for avoiding predators, over-using high vegetation cover.

As shrub lands had a poor food availability and quality, these areas were used as refuge area during the resting period, while in the active, nocturnal periods wild boar should search for food. This allowed the boars to compromise in the optimal way the need to minimize the predation risk and disturbance and to find food needed. As piglets were the more suitable prey, when they were in resting phase, they were more deep inside the shrub land also far away from rich areas. Subadults and adults could choose the area, that better provide to refuge, food and water, in this way they could move less between resting and feeding areas. Wild boar is generally biphasic with a nocturnal active phase (Mauget et al., 1984). During the nocturnal active phase wild boar were more secure and can search for food, farer from shrub lands. While in daily and dawn and dusk hours, in which the human disturb was higher, wild boars preferred stay in refuge areas in shrubs. Furthermore the peak of activity and hunting of wild boar is at dawn and dusk (Theuerkauf et al., 2003).

This study was conducted in a protected area, surrounded by hunting territories. It was perceivable an hunting disturbance near the protected area border and animals could potentially increase the use of the protected areas to avoid being hunted during particular seasons. Not only hunted species, but also non-target species, as wolves and foxes, could benefit of the “reserve effect”. Therefore, during hunting activity, other than wild boar human disturbance all around the protected area, there could be also an effect of a density increasing of predators in the OAC during hunting season. These factors reflected on wild boar survival, and wild boar tend, especially during the harsh season, to use more the high vegetation cover.

Behaviours that may be adopted to evade predators, such as those patterns described here, are an important component of predator–prey population dynamics and have implications for conservation. Variation in how individuals respond to predation may shape variation in survival. Thus, anti-predator movement strategies may mediate effects of predation or human disturbance on population trajectories.

In this research we therefore underline the importance of a micro-scale habitat selection for this species. We could also hypothesize that, different needs according to sexes, induced individuals to a micro scale sexual segregation, in a species generally considered social and gregarious.

REFERENCES

Alldredge AW, Deblinger RD, Peterson J. 1991. Birth and Fawn Bed Site Selection by Pronghorns in a Sagebrush-Steppe Community. Journal of Wildlife Management 55(2):222-227.

Apollonio M, Mattioli L. 2007. Il lupo in Provincia di Arezzo. Studi sulla biologia della fauna. Le Balze.

Barten NL, Bowyer RT, Jenkins KJ. 2001. Habitat use by female caribou: tradeoffs associated with parturition. Journal of Wildlife Management 65:77-92.

Baubet E, Brandt S, Touzeau C. 1998. Effet de la chasse sur les stratégies d'occupation de l'espace des sangliers (*Sus Scrofa*). Analyses préliminaires. Gibier Faune Sauvage, Game Wildl 15:655-658.

Berger J. 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. Animal Behaviour 41:61-77.

Bertolotto E, Grignolio S, Pizza B, Donaggio E, Bongi P, Apollonio M. submitted. Spatial behaviour and habitat selection in a wild boar population in a mountain area.

Borger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology 75:1393-1405.

Brandt S, Voyard N, Vassant J. 1997. Le "chaudron" chez la laie: choix du site et des matériaux. Bulletin mensuel de l'Office national de la chasse 223:4-11.

Briedermann L. 1990. Schwarzwild. Berlin, Germany: VEB Deutscher Landwirtschaftsverlag.

Calenge C, Maillard D, Vassant J, Brandt S. 2002. Summer and hunting season home ranges of wild boar (*Sus scrofa*) in two habitats in France. Game and Wildlife Science 19:281–301.

Capitani C, Bertelli I, Varuzza P, Scandura M, Apollonio P. 2004. A comparative analysis of wolf (*Canis lupus*) diet in three different Italian ecosystem. Mammalian Biology 69(1):1-10.

Cappai N, Bertolotto E, Donaggio E, Grignolio S, Apollonio M. submitted. Factors affecting fertility and reproduction in wild boar (*Sus scrofa*) in a mountainous environment.

Ciuti S, Bongi P, Vassale S, Apollonio M. 2006. Influence of fawning on the spatial behaviour and habitat selection of female fallow deer (*Dama dama*) during late pregnancy and early lactation. Journal of Zoology, London 268:97-107.

Donaggio E, Cappai N, Bernardi M, Gazzola A, Apollonio M. 2009, submitted. The predation impact on a wild ungulate community by two sympatric predators: red fox and wolf.

Festa-Bianchet M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75(4):580-586.

Fournier P, Fournier-Chambrillon C, Maillard D, Klein F. 1995. Zoletil© immobilization of Wild Boar (*Sus scrofa* L.). Ibex Journal of Mountain Ecology 3:134-136.

Gaillard JM, Vassant J, Klein F. 1987. Quelques caractéristiques de la dynamique des popolations de Sangliers (*Sus scrofa scrofa* L.) en milieu chassé. Gibier Faune Sauvage 4(31-47).

Gazzola A, Bongi P, Capitani C, Mattioli L, Donaggio E, Bassi E, Apollonio M. in press. Functional response to wild ungulate availability in wolf diet: the influence of hunting, prey preference and structure of ungulate community. Oikos.

Grignolio S, Rossi I, Bassano B, Apollonio M. 2007. Predation risk as a factor affecting sexual segregation in alpine ibex. Journal of Mammalogy 88:1488–1497.

Jeppesen JL. 1987. Impact of human disturbance on home range size, movements and activity of red deer (*Cervus elaphus*) in a Danish environment. Danish Review of Game Biology 13(2):1-38.

Keuling O, Stier N, Roth M. 2008. How does hunting influence activity and spatial usage in wild boar Sus scrofa L.? European Journal of Wildlife Research 54:729-737.

Kilpatrick HJ, Lima KK. 1999. Effects of Archery Hunting on Movement and Activity of Female White-Tailed Deer in an Urban Landscape. Wildlife Society Bulletin 27(2):433-440.

Kufeld RC, Bowden DC, Shrupp DL. 1988. Influence of hunting on movements of female mule deer. Journal of Range Management 41:70-72.

Linnell JDC, Nijhuis P, Teurlings I, Andersen R. 1999. Selection of bed-sites by roe deer Capreolus capreolus fawns in a boreal forest landscape. Wildlife Biology 5:225-231.

Mauget R, Campan R, Spitz F, Dardaillon M, Janeau G, Pepin D. Synthèse des connaissances actuelles sur la biologie du sanglier, perspectives de recherche.; 1984. p 15-50.

Merrill EH. 1991. Thermal constraints on use of cover types and activity time of elk Applied Animal Behaviour Science 29:251-267.

Millspaugh JJ, Brundige GC, Gitzen RA, Raedeke KJ. 2000. Elk and Hunter Space-Use Sharing in South Dakota. Journal of Wildlife Management 64(4):994-1003.

Mysterud A, Ostbye E. 1999. Cover as a Habitat Element for Temperate Ungulates: Effects on Habitat Selection and Demography. Wildlife Society Bulletin 27(2):385-394.

Root BG, Fritzell EK, Giessman NF. 1988. Effects of Intensive Hunting on White-Tailed Deer Movement. Wildlife Society Bulletin 16(2):145-151.

Sodeikat G, Pohlmeyer K. 2003. Escape movements of family groups of wild boar Sus scrofa influenced by drive hunts in Lower Saxony, Germany. Wildlife Biology 9(1):257-263.

Strohmeyer DC, Peek JM, Bowlin TR. 1999. Wapiti Bed Sites in Idaho Sagebrush Steppe. Wildlife Society Bulletin 27(3):547-551.

Theuerkauf J, Jędrzejewski W, Schmid K, Okarma H, Ruczyński I, Śnieżko S, Gula R. 2003. Daily patterns and duration of wolf activity in the Białowieża Forest, Poland. Journal of Mammalogy 84:243-253.

Worton BJ. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70(1):164-168.

CONCLUSIONS

I described the reproductive parameters of a wild boar population **(Chapter 1)**. The hunting pressure in the study area is strong and could bring strong recoil on dynamic population, the wild boar reacts with an higher and plastic reproductive potential. In detail, in case of good biological and environmental conditions, i.e. where females reach the body weight threshold of 35 Kg, also piglet females (less than 1 year old) may contributed to the population growth. Furthermore in my study area the mean litter size was higher (4.74 ± 0.115) in comparison with other ungulate species even if similar to other wild boar populations. Mother characteristics, such as age and physical conditions, shaped the litter size, the birth period and the foetuses physical conditions. All these results confirm the r demographic strategy of the species and the high population growth potential.

Apart from the reproductive adaptability I observed that also the spatial behaviour appeared flexible and homogeneous between sexes and age classes **(Chapter 2)**. I point out how food availability is able to shape the spatial behaviour. In detail my findings confirm the “food-exploitation hypothesis”, with a decrease of home range size when food availability was high. Sexes showed a different reaction to climate features. While females varied their spatial behaviour according to temperature (increasing home range size during hot periods) and snow cover (decreasing movements with tick snow cover), males did not appeared influenced by these features. Spatial behaviour described in this study area was appreciably different from the one reported for a wild boar population in a Mediterranean environment (Massei et al., 1997). Climatic and environmental (mountain heterogeneous forests versus Mediterranean habitats with high abundance of maquis shrubs) conditions induce different spatial behavioural responses. It is confirmed also by habitat selection analysis the low habitat specificity of wild boar at a large analysis scale as well as its known behavioural plasticity.

It was known that wild boars require shade and free water during hot weather (Dexter, 2003). I described spatial behaviour in response to different water availability in the environment **(Chapter 3)**. Piglets were more affected by dry conditions, while subadults and adults showed similar needs. In general, wild boars react to climatic condition varying their spatial behaviour, adapting the ditches presence in the home range and staying closer to water in drought periods.

The wild boar population, object of this study, was submitted to predation by two populations of predators, red fox and wolf. I underlined the presence of an anti-predator behaviour, expressed with the distance between locations and shrub lands **(Chapter 4)**. I expected that younger age classes and females during weaning period showed a more accentuated anti-predator behaviour and our findings agree with this prediction. While males used bushes in Autumn and Winter when, outside the protected area, started hunting activities. Furthermore considering high impact of hunt, in districts surrounding protected area, likely human harassment induce also an increase of predators in the protected area and consequently changes in the spatial behaviour. Wild boar used safe areas meeting all individual requirements and, since males and females have different needs, I could conjecture that, at a fine spatial scale, the presence of a sexual segregation in the specie.

The findings in this thesis suggested that wild boar has limited requirements and high plasticity. The most important resources are food, climate conditions, water and refuge areas. Differently to the information available in literature, our findings point out that, at fine scale, sex, age different classes have different spatial behaviour. Natural conditions are likely to set the base of the species' features and have to be considered to set management aims. However it is important to monitor also the outcome of management applications, to evaluate their efficiency, in front of high variability and adaptability of this species.

REFERENCES

Dexter N. 2003. The influence of pasture distribution, and temperature on adult body weight of feral pigs in a semi-arid environment. Wildlife Research 30:75-79.

Massei G, Genov P, Staines BW, Gorman ML. 1997. Factors influencing home range and activity of wild boar (*Sus scrofa*) in a Mediterranean coastal area. Journal of Zoology 242:411-423.

ANNEX

Research Article

Influence of the Kid on Space Use and Habitat Selection of Female Alpine Ibex

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ABSTRACT Mammalian females change their behavior during the last stages of pregnancy and during the weaning as a response to new energetic requirements and antipredator behavior. From March 2001 to December 2004, we studied the effects of parturition and weaning on home-range sizes and habitat selection in 28 female Alpine ibex (*Capra ibex*) in a 1,700-ha free area in the Gran Paradiso National Park (Western Italian Alps). We calculated Kernel home range enclosing 95% of each female's locations according to seasonal and bimonthly timescales. Pregnancy did not seem to modify spatial behavior. Lactating females showed smaller home ranges than nonlactating ones after the birth period in June–July. Hot summers slowed kids' growth and prolonged maternal care, modifying mothers' behavior. In summer 2003, which was hotter and drier than usual, weaning females showed even smaller home ranges. Because of their use of antipredator tactics during the weaning season, lactating females showed a higher use of safer habitats, such as rocky slopes. Our results are consistent with the findings of previous cervid and bovid studies, and they suggest that ungulate mothers may move to suboptimal, but safer, habitats during weaning to reduce the predation risk for their offspring. (JOURNAL OF WILDLIFE MANAGEMENT 71(3):713–719; 2007)

DOI: 10.2193/2005-675

KEY WORDS Alpine ibex, *Capra ibex*, compositional analysis, habitat selection, Italy, parental care, spatial use.

According to life-history theory, animals are likely to show levels of parental investment such that the energy expenditure for current offspring is balanced against the effects on the parents' chances of survival and future reproduction (Roff 1992, Stearns 1992). Mammalian females change their behavior during the last stages of pregnancy and weaning as a response to new energetic requirements, mobility difficulties, their kids' feeding, and the increased necessity to avoid predators (Svare 1981). Pregnant females or those engaged in maternal care are likely to modify different aspects of their behavior: space use (Berger 1991, Green 1992*a*, Tufto et al. 1996, Boschi and Nievergelt 2003, Ciuti et al. 2006), aggregation with other pairs (de Vos et al. 1967, Clutton-Brock and Guinness 1975, Green 1992*b*, Schwede et al. 1993, Boschi and Nievergelt 2003), time budget (Guinness et al. 1978, Langbein et al. 1998, Ruckstuhl and Festa-Bianchet 1998, Ruckstuhl 1999, Toigo 1999), and antipredator behavior (Byers and Bailey 1983, Bergerud et al. 1984, San José and Braza 1992, Kohlmann et al. 1996, Barten et al. 2001). In regard to space use, researchers reported that the female is likely to enlarge her home range during weaning (*Capra pyrenaica*, Escos and Alados 1992; *Capreolus capreolus*, Tufto et al. 1996; *Rupicapra rupicapra*, Boschi and Nievergelt 2003) or to reduce it (*Odocoileus virginianus*, Schwede et al. 1993; *Dama dama*, Ciuti et al. 2006).

Neonate survival rate depends on the use of appropriate behaviors by mothers and the young to ensure that the latter are adequately fed, nurtured, and protected (Dwyer 2003). Ungulates have evolved different strategies of response to the high risk of predation for neonates. The hiding strategy, which is typical in closed habitats, implies that the mother conceals the newborn during the first weeks of life. Moreover, reducing the newborn's activity allows offspring to grow faster (Carl and Robbins 1988). The following strategy implies that the newborn follows its mother from the first day, and it is characterized by the use of open habitats, the larger size of the groups of animals, and the use of collective antipredator strategies (i.e., vigilance; Lent 1974, Barrett 1984). In many ungulates, social isolation at parturition is considered essential for proper formation (e.g., imprinting) of the mother–infant bond (Lent 1974) and serves as additional protection against predators (Ozoga et al. 1982).

Spatial behavior and habitat selection are essential for correct management of an ungulate population. It is important for wildlife managers to know how, and how long, pregnancy and lactation modify mothers' spatial behavior and habitat selection. Especially when developing conservation and management plans, wildlife managers should take into account differing behaviors, particularly the habitats used by mothers. Yet, female Alpine ibex (*Capra ibex*) spatial behavior, its habitat selection in particular, is poorly understood (Wiersema 1984, Villaret and Bon 1995, Villaret et al. 1997, Grignolio et al. 2004). Therefore, we investigated the changes in home-range sizes and habitat selection between lactating and nonlactating Alpine ibex females in the only autochthonous population.

In particular, we formed the following predictions:

1. a) If pregnant female home-range sizes were actually smaller than nonpregnant female home-range sizes, we

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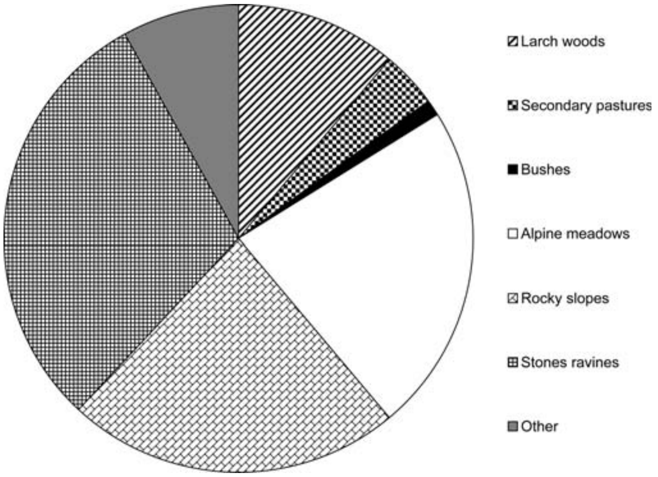

Figure 1. Habitat composition of the study area of Alpine ibex (2001–2004) in the Gran Paradiso National Park, Italy.

assumed that they modified their spatial behavior in the last part of pregnancy because of mobility problems. b) On the contrary, if pregnant female home-range sizes were similar to those of nonpregnant female home ranges, we assumed that spatial behavior of pregnant females was not modified because of mobility problems.

2. a) If during the weaning period lactating female home-range sizes were smaller than nonlactating female home ranges, we assumed that mothers reduced their home ranges because kids limited their movements. b) On the contrary, if lactating female home-range sizes were larger than nonlactating female home ranges, we assumed that females with kids enlarged their home ranges to use more foraging sites and to meet the bigger energetic requirements related to lactation.
3. a) If mothers selected more rocky slopes (refuge areas), we assumed that it was a consequence of a higher predation risk and that kid presence modified mother antipredator behavior. b) On the contrary, if mothers selected more Alpine meadows (foraging areas), we assumed that it was a consequence of bigger energetic requirements.

STUDY AREA

We conducted the study in the Gran Paradiso National Park (45°26′N, 7°08′E; Western Italian Alps), in Valsavarenche valley (1,700 ha; altitude range: 1,700–3,300 m above sea level). We used satellite photographs to divide the area into 7 habitat categories and to locate them onto a digital map (1:10,000). The categories were larch woods (mainly *Larix decidua*), bushes (*Rhododendron ferrugineum*, *Juniperus communis*), secondary pastures (*Poa* spp., *Festuca* spp.), Alpine meadows (*Carex* spp., *Festuca* spp.), steep slopes and rocks, stone ravines, and other (glaciers, rivers, and inhabited areas; Fig. 1). An automatic station recorded temperature data (24 records/d) and precipitation (property of the Aosta Valley Region; Figs. 2, 3).

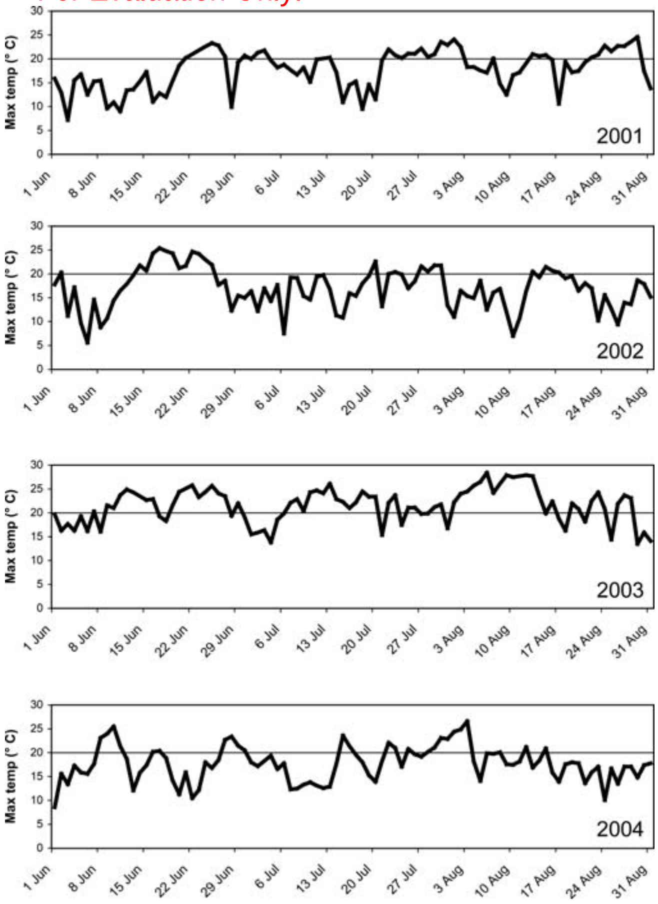

Figure 2. Maximum air temperature recorded during the summer in a 4-year study (2001–2004) on Alpine ibex in the Gran Paradiso National Park, Italy.

The area had been free from the most relevant predators, such as lynx (*Lynx lynx*) and wolf (*Canis lupus*), for about a century, whereas livestock had been absent for about 15 years. The study area female population ranged from 109 in 2001 to 129 in 2004, and the number of kids ranged from 13 in 2001 to 46 in 2004 (Fig. 4). The kid–female ratio was 0.12 in 2001, 0.29 in 2002, 0.22 in 2003, and 0.36 during 2004. At the end of each summer, the survival rate of kids of

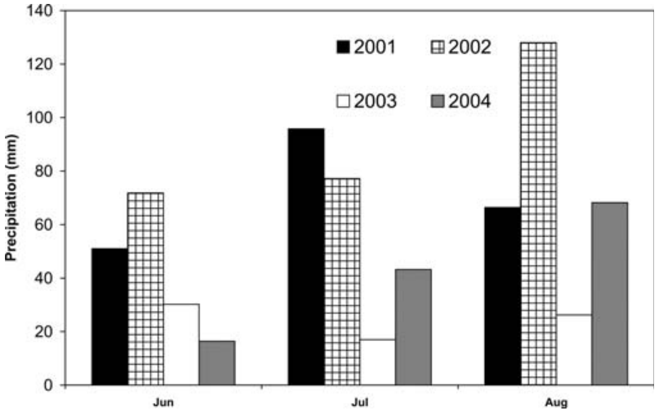

Figure 3. Monthly rain recorded during the summer in a 4-year study (2001–2004) on Alpine ibex in the Gran Paradiso National Park, Italy.

marked females was 1.00 in 2001, 2002, and 2004 and 0.66 in 2003.

METHODS

Data Collecting

During 5 consecutive springs (2000–2004), we captured 28 ibex females by telenarcosis (Bassano et al. 2004) and fitted them with radiocollars (150–151 MHz, Televilt, Lindesberg, Sweden). We tracked each individual by direct observation (71%) or by triangulation using radiotechniques ≥12 times per month (from Mar 2001 to Dec 2004). We uniformly distributed the observation times over the light hours and separated them by an interval of ≥4 hours to achieve independence of fixes (Swihart and Slade 1985). We calculated locations by triangulation, that is, employing bearings from 3 different reference points (White and Garrott 1990). From previous field analyses, we assessed a mean error distance of 62.5 m. We collected direct observations by binoculars (8–10×), telescopes (Leica 20–60×), and homing-in radiotracking (MacDonald et al. 1980, White and Garrott 1990). We plotted all locations onto a 1:10,000 digital map (Kenward 1987). The birth period occurs throughout June and early July. Given that Alpine ibex is a following species and that the mother–kid bond is strong during the kid's early months, we determined that the presence of a kid near a marked female provided enough evidence for regarding her as a lactating female.

We confirm that the procedures we used in this work conform to all relevant Italian wildlife and animal welfare legislation.

Data Analysis

We used the Ranges VI software package for the spatial analysis calculation. We analyzed spatial use and habitat selection according to 2 timescales: seasonal (spring: Mar–May; summer: Jun–Aug; autumn: Sep–Nov; winter: Dec–Feb) and bimonthly. For each period, we calculated the area including 95% of each individual's use distribution. We used the Kernel method (Worton 1989) to define the home range. Because home-range size data were normally distributed (Kolmogorov–Smirnov test), we used parametric statistic tests (Sokal and Rohlf 1995) to analyze the spatial use. To check the homoscedasticity, we tested the data using Levene's test. In all tests, we set significance at $P \leq 0.05$. We considered the spatial behavior of each ibex as independent from each other. We did not find any fixed association between ≥2 recognizable individuals.

We obtained data on habitat selection by processing each individual location on the habitat-use map by means of ArcView 3.2. We used compositional analysis that takes the individual rather than the location as a sample unit (Aebischer et al. 1993). We examined habitat selection only during the summer and autumn 2004. As recommended by Aebischer et al. (1993), we repeated this analysis at 2 different levels. First, we compared the proportion of habitats in the study area (habitat availability) with the proportion of the habitat within the individual home range (contour line of the Kernel 95% estimation; habitat used).

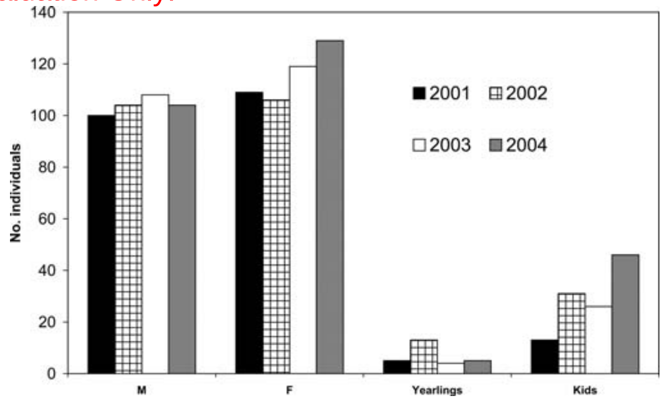

Figure 4. Number of Alpine ibex recorded during 4 consecutive censuses (2001–2004) in the study area in the Gran Paradiso National Park, Italy.

Second, we assessed the habitat selection by comparing the proportion of the habitat within each individual home range (contour line of the Kernel 95% estimation; habitat availability) with the proportions of fixes in each habitat within the same home range (habitat used). The same authors suggested that the least-selected habitat cover should not be taken into consideration in the second-level analysis to minimize the bias of the technique. Finally, we tested for differences between lactating and nonlactating females by adding this parameter as an independent variable in the Wilk's log–ratio matrices and analyzing these matrices with a multivariate analysis of variance (MANOVA) test (Aebischer et al. 1993). To carry out a compositional analysis, we used an Excel (Microsoft, Redmond, WA) macro (Smith 2003), which allowed for the randomization procedure recommended by Aebischer et al. (1993).

RESULTS

Spatial Behavior

Females with and without kids had similar home-range sizes in spring (Student's *t*-test independent sample, 2003: $t=0.17$, df = 8, $P = 0.87$), whereas mothers showed smaller home ranges when compared with females without kids in summer. During summer, mean home-range sizes (±SE) for barren females were reported to be 196.87 ± 28.74 ha in 2002, 221.74 ± 18.78 ha in 2003, and 237.09 ± 29.48 ha in 2004. On the contrary, home-range size of females with kids were 71.30 ± 6.23 ha in 2002, 108.38 ± 32.95 ha in 2003, and 160.50 ± 18.56 ha in 2004 (Fig. 5A; Student's *t*-test independent sample, 2002: $t=3.36$, df=6, $P=0.017$; 2003: $t=2.53$, df=16, $P=0.022$; 2004: $t=2.74$, df=14, $P=0.016$). Lactating females had smaller autumn home-range sizes only in 2003, that is, 134.95 ± 19.65 ha versus 268.74 ± 32.10 ha (Student's *t*-test independent sample, 2002: $t=1.05$, df=7, $P=0.33$; 2003: $t=3.55$, df=13.8, $P=0.003$; 2004: $t=0.036$, df=15, $P=0.972$), whereas spatial use of the 2 groups of females was never different in winter (Student's *t*-test independent sample, 2002: $t=0.64$, df=8, $P=0.54$; 2003: $t=1.21$, df=16, $P=0.24$). For each female, we compared the seasonal home-range values for the years when it was with kid with the values for the years when it was without kid. The only evident

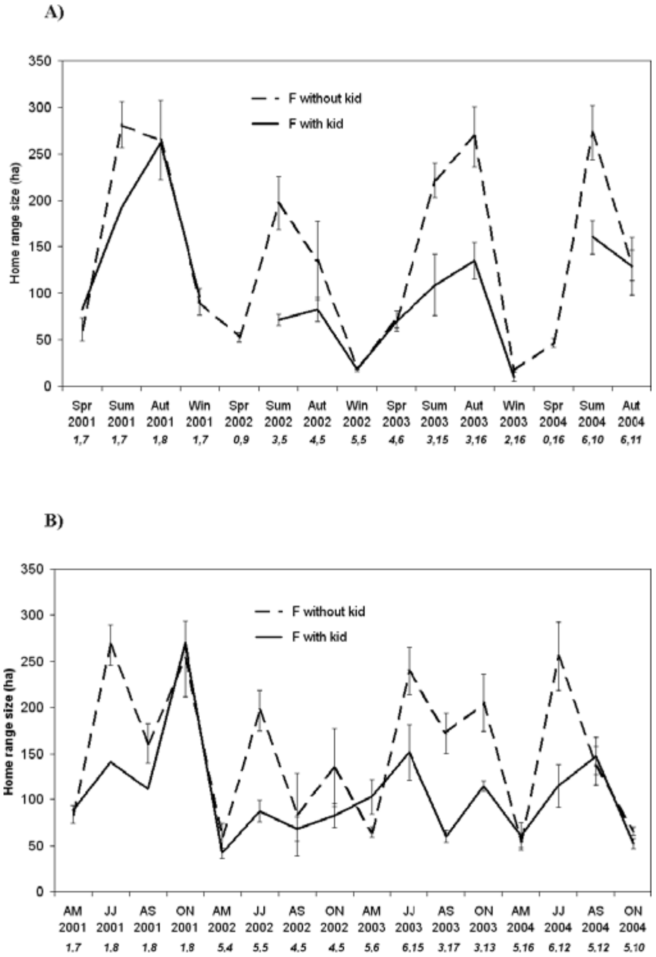

Figure 5. (A) Seasonal and (B) bimonthly (2001–2004) home-range size ($\bar{x}$ ± SE) of female Alpine ibex with and without kid in the Gran Paradiso National Park, Italy. Numbers under seasons represents, respectively, the number of lactating and nonlactating females. (Spr = Spring, Sum = Summer, Aut = Autumn, Win = Winter, AM = Apr–May, JJ = Jun–Jul, AS = Aug–Sep, ON = Oct–Nov).

difference was for summer home ranges (Student's *t*-test paired sample, $t = 4.73$, df = 7, $P = 0.002$).

We used bimonthly data for April and May to check possible differences between pregnant and nonpregnant females (Fig. 5B). We considered the individuals with kid when observed in the following summer to have been pregnant in these months, but we found no difference between the 2 groups of females (Student's *t*-test independent sample, 2002: $t = 1.16$, df = 6, $P = 0.29$; 2003: $t = -1.96$, df = 4.68, $P = 0.11$; 2004: $t = -0.46$, df = 14, $P = 0.66$). During the birth period in June–July, mothers showed smaller home ranges when compared with females without kids (Student's *t*-test independent sample, 2002: $t = 4.64$, df = 7, $P = 0.002$; 2003: $t = 2.01$, df = 18, $P = 0.045$; 2004: $t = 2.55$, df = 16, $P = 0.021$). We found no significant difference in the subsequent bimonthly home ranges, August–September (Student's *t*-test independent sample, 2002: $t = 1.05$, df = 7, $P = 0.33$; 2004: $t = -0.30$, df = 15, $P = 0.77$) and October–November (Student's *t*-test independent sample, 2002: $t = 1.05$, df = 7, $P = 0.33$; 2004: $t = 1.87$, df = 13, $P = 0.09$), except in 2003 (Aug–Sep: nonlactating F 172.39 ± 21.87 ha vs. lactating 59.93 ± 6.32 ha; Student's *t*-test independent sample: $t = 4.94$, df = 17.79, $P < 0.001$; Oct–Nov: 243.90 ± 32.53 ha vs. 114.54 ± 5.94 ha; Student's *t*-test independent sample: $t = 3.91$, df = 12.73, $P = 0.002$). To check whether mothers lived closer together during summer, we measured the distance between the activity center of each mother and that of the other lactating and nonlactating females. We found a significant difference when we considered the mean distance between mothers (697.3 ± 43.82 m) and the mean distance between mothers and the other females (922.86 ± 22.89 m; Student's *t*-test paired sample: $t = -4.65$, df = 5, $P = 0.006$).

Habitat Selection

During summer, lactating and nonlactating females exhibited habitat selection at the first level of analysis. Indeed, compositional analysis showed a significant departure from random use (lactating F: $\lambda = 0.031$, $P = 0.036$; nonlactating F: $\lambda = 0.11$, $P = 0.002$; Fig. 6A, C). Nonlactating females mostly used Alpine meadows ($\bar{x}$ 45.7 ± 3.53% SE), and their use was significantly more intense than all the others ($P < 0.05$). On the other hand, rocky slope was the most-used habitat by lactating females (44.3 ± 2.18%) followed by Alpine meadows (42.24 ± 3.27%) and stone ravines (12.35 ± 3.27%). Pastures and larch wood were used marginally, and we excluded them from the following step of analysis. The compositional analysis of habitat use within summer home ranges did not show a random use of habitat by mothers ($\lambda = 0.83$, $P = 0.93$; Fig. 6B). On the contrary, we detected significant habitat selection for females without kid ($\lambda = 0.031$, $P = 0.004$; Fig. 6D), and Alpine meadows were still the highest-ranking habitat, followed by rocks (33.15 ± 1.48%) and stone ravines (18.90 ± 3.22%). We found significantly different habitat use between lactating and nonlactating females in summer, both on a broad (MANOVA $\lambda = 0.329$, $F = 5.602$, $P = 0.01$) and on a fine scale (MANOVA $\lambda = 0.045$, $F = 31.52$, $P = 0.01$).

At the first level of study, compositional analysis revealed a significant departure from random use in autumn for all females, with ($\lambda = 0.027$, $P = 0.025$; Fig. 7A) or without kid ($\lambda = 0.016$, $P = 0.001$; Fig. 7C). Compositional analysis ranked ibex habitat in the same order: Alpine meadows, then rocky slopes, stone ravines, larch woods, and pastures. At the second level of analysis, compositional analysis also revealed a significant departure from random use in autumn but only for females without kid ($\lambda = 0.035$, $P = 0.006$; Fig. 7D). This was not the case for the mothers, which, instead, showed random habitat use ($\lambda = 0.52$, $P = 0.34$; Fig. 7B). In the first step of compositional analysis, MANOVA did not show different habitat selections between females with and without kid (MANOVA $\lambda = 0.582$, $F = 0.239$, $P = 0.87$); the same applied to the second level, although significance was almost reached (MANOVA $\lambda = 0.062$, $F = 15.18$, $P = 0.06$).

DISCUSSION

This study clearly showed that weaning Alpine ibex females reduced their home ranges and modified their habitat selection during the first months of their kids' life, but this was not true during the last part of pregnancy. In fact, in April

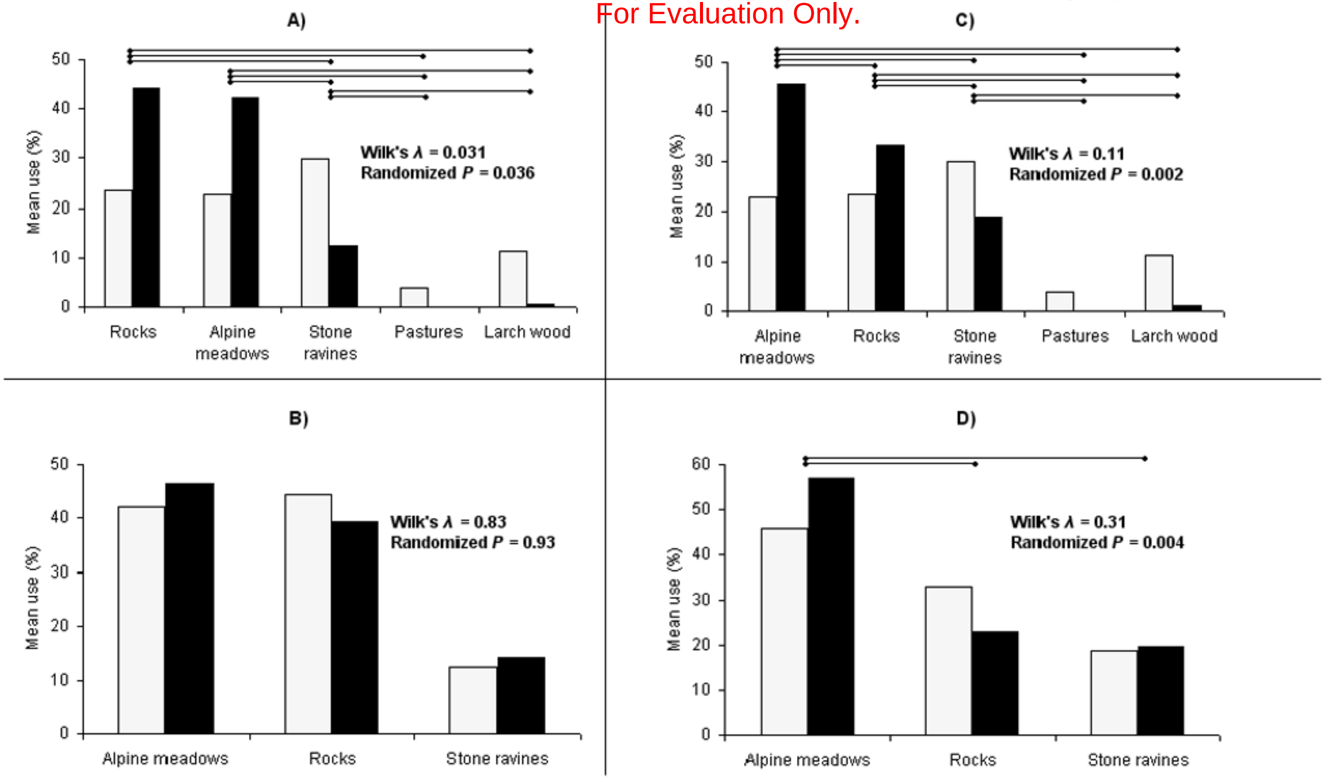

Figure 6. Summer (2001–2004) habitat selection by Alpine ibex female in the Gran Paradiso National Park, Italy. (A and B) Graphs show the selection by lactating females at the first and second level of compositional analysis, respectively. (C and D) Graphs show the selection by nonlactating females. White columns represent available habitats, black columns show habitats used, and significant departure from random use is indicated by lambda and randomized *P* values. In each graph (A–D), habitat classes to the left are selected over those to the right. Lines indicate significant differences ($P < 0.05$ by compositional analysis) between connected habitat classes.

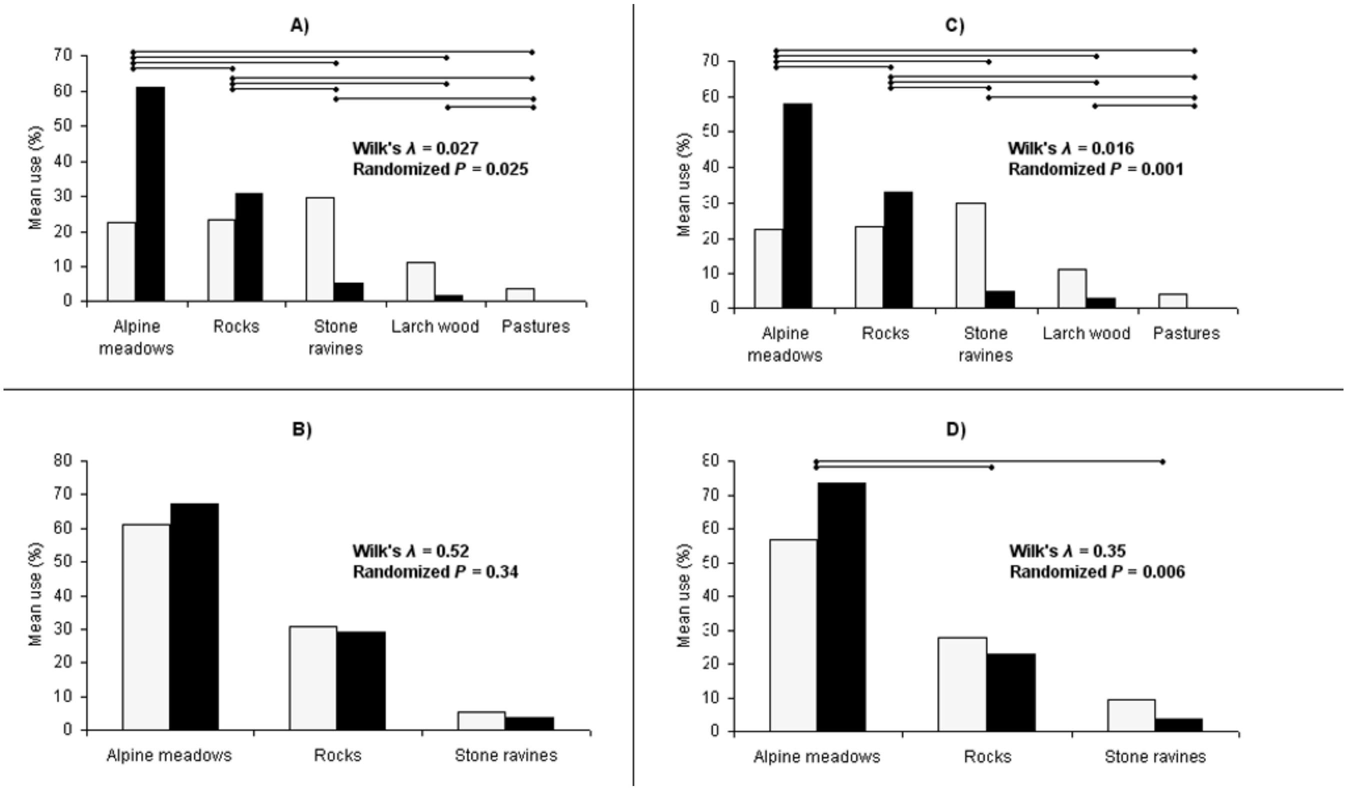

Figure 7. Autumn (2001–2004) habitat selection by (A and B) lactating and (C and D) nonlactating female of Alpine ibex in the Gran Paradiso National Park, Italy. White columns represent available habitats, black columns show habitats used, and significant departure from random use is indicated by lambda and randomized *P* values. In each graph (A–D), habitat classes to the left are selected over those to the right. Lines indicate significant differences ($P < 0.05$ by compositional analysis) between connected habitat classes.

and May no difference was evident between home-range sizes of pregnant and nonpregnant females (prediction 1b).

Because the Alpine ibex is a following species, we hypothesized that mothers would reduce their home range after the birth because of the kids' lesser mobility (prediction 2a). During the 4 years we analyzed, weaning females used areas about half the size of those used by nonlactating females. It is thus clear that the presence of kid influenced mothers' spatial behavior only during the first growing stage. Indeed, looking at bimonthly home ranges, a difference between the 2 female groups was evident in June–July but was not evident later (Aug–Sep or Oct–Nov), with the exception of 2003. The summer of 2003 in Europe was characterized by high temperatures and scarce precipitation for a long period (Figs. 2, 3). In the study area, the pastures dried up in the second half of July, well before the time of the year when it usually happens. Meteorological circumstances presumably influenced the mothers' conditions, particularly their milk quality, bringing about a delay in the kids' growth (Festa-Bianchet 1988, Clutton-Brock et al. 1989, Festa-Bianchet and Jorgenson 1998). This delay prolonged maternal care and modified the mothers' behavior. In autumn 2003 (as well as in Aug–Sep and Oct–Nov) home-range sizes of females with kids were significantly smaller than those of barren females. Moreover, during the same summer, 4 marked female kids (i.e., 34% of the sample of that yr) died, a higher mortality than during all other years. It might be argued that climatic variables influenced young and adult survival and, consequently, influenced population dynamic. According to our prediction 3a, we expected that during summer, mothers should select refuge areas (rocky slopes) more intensively to keep their offspring safe. Weaning females preferred rocky areas first and then Alpine meadows, whereas females without kids selected Alpine meadows first, followed then by rocks, thus showing an inverse selection. In accordance with other studies on several ungulate species (Barten et al. 2001, Ciuti et al. 2006) in autumn, when kids were bigger and more independent, mothers showed a similar habitat selection to that of other females. Female ibexes engaged in maternal care showed a clear antipredator behavior in their habitat selection. Loudon (1985) showed that pregnancy and weaning increase the energetic requirements of female ungulates (approx. 40% during late gestation and 150% during lactation). The growth of energetic costs during lactation is due to several factors, such as milk production, changes in metabolic rate, and activity level (Thompson and Nicoll 1986, Oftedal and Gittleman 1989). Our findings suggest another source of energetic costs: antipredator behavior forces mothers to use a safer, but suboptimal, habitat (rocky slopes), characterized by a scarce quantity of forage. Presumably, mothers must compensate for this disadvantage by increasing their food intake, by foraging every day for longer, and by taking more bites (*Cervus elaphus*, Clutton-Brock et al. 1982; *Ovis dalli stonei*, Seip and Bunnel 1985; *Vicugna vicugna*, Bosch and Svendsen 1987; *Acinonyx jubatus*, Laurenson 1995; *Ovis canadensis*, Ruckstuhl and Festa-Bianchet 1998). Indeed, Neuhaus and Ruckshtul (2002) reported that in the days immediately after birth, female Alpine ibexes modify their time budget to increase their feeding.

Byers (1997) defined the presence of an antipredator behavior in the absence of predators as the ghost of predators past. These behaviors have coevolved in ungulates and their predators for thousands of years, and an absence of the predators for a few centuries is not sufficient to remove them. Considering that the study area has been free from predators for about a century, Alpine ibex females seem to exhibit the ghost of predators past behavior. Weaning females preferred safer habitats and lived closer together. There is clear evidence that predators may influence lower trophic levels by both killing prey and altering prey behavior. Ibex behavior could differ in the presence of wolves and could influence trophic cascades in different ways (i.e., reducing pressure on Alpine meadows); yet no one has analyzed the influence of this ungulate on the meadows. Ripple et al. (2001) showed that in the larger Yellowstone ecosystem and in the absence of predation, elk (*Cervus elaphus*) exercised a strong browsing pressure on aspen that caused aspen biomass to decline strongly. Aspen benefited from the reintroduction of wolves because elk were forced to modify their distribution as well as their foraging strategy, thus reducing browsing pressure on that tree species.

MANAGEMENT IMPLICATIONS

Managers should account for the presence of safe habitats when carrying out ibex reintroduction projects and management plans because we have demonstrated the relevance of safe habitats to lactating females. Managers should consider the influence of kid on mothers' spatial behavior and habitat selection in summer as an important aspect for management activities. Management plans should also account for hot summers, which may extend the kid influence on spatial behavior and habitat selection until autumn.

ACKNOWLEDGMENTS

We are grateful to Gran Paradiso National Park for the economic and logistic support. We thank the wardens of the Gran Paradiso National Park for their help in the field and, particularly, for their contribution in capturing the ibexes. S. Grignolio extends special thanks to S. Ciuti for his ideas, advice, and continuous support throughout this project. We thank 2 anonymous reviewers for reviewing an earlier version of this manuscript. Finally, we are grateful to F. Parrini, S. Pighetti, M. Landini, T. Monti, A. Vacchi, and G. Caneparo for their help during data collection. We are grateful to A. Binelli for linguistic revision of the manuscript.

LITERATURE CITED

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1310–1325.

Barrett, M. W. 1984. Movements, habitat use and predation on pronghorn fawns in Alberta. Journal of Wildlife Management 48:452–550.

Barten, N. L., R. T. Bowyer, and K. J. Jenkins. 2001. Habitat use by female caribou: tradeoffs associated with parturition. Journal of Wildlife Management 65:77–92.

Bassano, B., D. Gauthier, L. Jocollé, and V. Peracino. 2004. Cattura di ungulati di montagna con tele-sedazione—capture d'Ongulés de montagne par téléanesthésie. Parco Nazionale Gran Paradiso, Torino, Italy, and Parc National de la Vanoise, Chambery Cedex, France. [In Italian and French.]

Berger, J. 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. Animal Behaviour 41:61–77.

Bergerud, A. T., H. E. Butler, and D. R. Miller. 1984. Antipredator tactics of calving caribou: dispersion in mountains. Canadian Journal of Zoology 62:1566–1575.

Bosch, P. C., and G. E. Svendsen. 1987. Behaviour of male and female vicuna (*Vicugna vicugna* Molina 1782) as it relates to reproductive effort. Journal of Mammalogy 68:425–429.

Boschi, C., and B. Nievergelt. 2003. The spatial patterns of Alpine chamois (*Rupicapra rupicapra rupicapra*) and their influence on population dynamics in the Swiss National Park. Mammalian Biology 68:16–30.

Byers, J. A. 1997. American pronghorn. Social adaptations and the ghosts of predators past. University of Chicago Press, Illinois, USA.

Byers, J. A., and K. Z. Bailey. 1983. Do pronghorn mothers reveal the locations of their hidden fawns? Behavioral Ecology and Sociobiology 13: 147–156.

Carl, G. R., and C. T. Robbins. 1988. The energetic cost of predator avoidance in neonatal ungulates: hiding versus following. Canadian Journal of Zoology 66:239–246.

Ciuti, S., P. Bongi, S. Vassale, and M. Apollonio. 2006. Influence of fawning on the spatial behaviour and habitat selection of female fallow deer (*Dama dama*) during late pregnancy and early lactation. Journal of Zoology, London 268:97–107.

Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1989. Fitness costs of gestation and lactation in wild mammals. Nature 337:260–262.

Clutton-Brock, T. H., and F. E. Guinness. 1975. Behaviour of red deer (*Cervus elaphus* L.) at calving time. Behaviour 55:287–300.

Clutton-Brock, T. H., G. R. Iason, S. D. Albon, and F. E. Guinness. 1982. Effects of lactation on feeding behaviour and habitat use in wild Red deer hinds. Journal of Zoology, London 198:227–236.

de Vos, A., P. Brokx, and V. Geist. 1967. A review of social behaviour of the North American Cervids during the reproductive period. The American Naturalist 77:390–417.

Dwyer, C. M. 2003. Behavioural development in the neonatal lamb: effect of maternal and birth-related factors. Theriogenology 59:1027–1050.

Escos, J., and C. L. Alados. 1992. The home range of the Spanish ibex in spring and fall. Mammalia 56:57–63.

Festa-Bianchet, M. 1988. Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate and sex. Animal Behaviour 36: 1445–1454.

Festa-Bianchet, M., and J. T. Jorgenson. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behavioral Ecology 9:144–150.

Green, W. C. H. 1992*a*. The development of independence in bison: pre-weaning spatial relations between mothers and calves. Animal Behaviour 43:759–773.

Green, W. C. H. 1992*b*. Social influences on contact maintenance interactions of bison mothers and calves: group size and nearest-neighbour distance. Animal Behaviour 43:775–785.

Grignolio, S., I. Rossi, F. Parrini, B. Bassano, and M. Apollonio. 2004. Seasonal variations of spatial behaviour in female Alpine ibex (*Capra ibex ibex*) in relation to climatic conditions and age. Ethology Ecology & Evolution 16:255–264.

Guinness, F. E., R. M. Gibson, and T. H. Clutton-Brock. 1978. Calving times of Red deer (*Cervus elaphus*) on Rhum. Journal of Zoology, London 185:105–114.

Kenward, R. 1987. Wildlife radio tagging: equipment, field techniques and data analysis. London Academic Press, London, United Kingdom.

Kohlmann, S. G., D. M. Muller, and P. U. Alkon. 1996. Antipredator constraints on lactating Nubian ibexes. Journal of Mammalogy 77:1122–1131.

Langbein, J., J. Streich, and K. M. Scheibe. 1998. Characteristic activity patterns of female mouflons (*Ovis orientalis musimon*) in the lambing period. Applied Animal Behaviour Science 58:281–292.

Laurenson, M. K. 1995. Behavioural costs and constraints of lactation in free-living cheetahs. Animal Behaviour 50:815–826.

Lent, P. C. 1974. Mother-infant relations in ungulates. Pages 15–55 *in* V. Geist and F. Walther, editors. The behaviour of ungulates and its relation to management. IUCN, Morges, Switzerland.

Loudon, A. S. I. 1985. Lactation and neonatal survival of animals. Symposium of Zoology Society of London 54:183–207.

MacDonald, D. W., F. G. Ball, and N. G. Hough. 1980. The evaluation of home range size and configuration using radio tracking data. Pages 405–424 *in* D. W. MacDonald, editor. A handbook on biotelemetry and radiotracking. Pergamon, Oxford, United Kingdom.

Neuhaus, P., and K. E. Ruckstuhl. 2002. Foraging behaviour in Alpine ibex (*Capra ibex*): consequences of reproductive status, body size, age and sex. Ethology Ecology & Evolution 14:373–381.

Oftedal, O. T., and J. L. Gittleman. 1989. Energy output during reproduction in carnivores. Pages 355–378 *in* J. L. Gittleman, editor. Carnivore behavior, ecology and evolution. Corner University Press, New York, New York, USA.

Ozoga, J. J., L. J. Verme, and C. S. Bienz. 1982. Parturition behavior and territoriality in white-tailed deer: impacts on neonatal mortality. Journal of Wildlife Management 46:1–11.

Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation 102:227–234.

Roff, D. A. 1992. The evolution of life histories. Chapman & Hall, London, United Kingdom.

Ruckstuhl, K. E. 1999. Aspect of mother-kid behavior in Alpine chamois, *Rupicapra rupicapra rupicapra*. Zeitschrift fur Säugetierkunde 64:76–84.

Ruckstuhl, K. E., and M. Festa-Bianchet. 1998. Do reproductive status and lamb gender affect the foraging behavior of Bighorn Ewes. Ethology 104: 941–954.

San José, C., and F. Braza. 1992. Antipredator aspects of fallow deer behaviour during calving season at Donana National Park (Spain). Ethology Ecology & Evolution 4:139–149.

Schwede, G., H. Hendrichs, and W. McShea. 1993. Social and spatial organization of female white-tailed deer, *Odocoileus virginianus*, during the fawning season. Animal Behaviour 45:1007–1017.

Seip, D. R., and F. L. Bunnel. 1985. Foraging behaviour and food habits of Stone's sheep. Canadian Journal of Zoology 63:627–633.

Smith, P. G. 2003. Compos analysis, version 5.1 standard. Smith Ecology, Abergavenny, United Kingdom.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. W. H. Freeman, New York, New York, USA.

Stearns, S. R. 1992. The Evolution of Life Histories. Oxford University Press, Oxford, United Kingdom.

Svare, B. B. 1981. Maternal aggression in mammals. Pages 179–210 *in* D. A. Gubernick and P. H. Klopfer, editors. Parental care in mammals. Plenum Press, New York, New York, USA.

Swihart, R. K., and N. A. Slade. 1985. Testing for independence of observation in animal movements. Ecology 66:1176–1184.

Thompson, S. D., and M. E. Nicoll. 1986. Basal metabolic rate and energetic of reproduction in therian mammals. Nature 321:690–693.

Toigo, C. 1999. Vigilance behaviour in lactating female Alpine ibex. Canadian Journal of Zoology 77:1060–1063.

Tufto, J., R. Andersen, and J. Linnel. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology 65:715–724.

Villaret, J.-C., and R. Bon. 1995. Social and spatial segregation in Alpine ibex (*Capra ibex*) in Bargy, French Alps. Ethology 101:291–300.

Villaret, J. C., R. Bon, and A. Rivet. 1997. Sexual segregation of habitat by the Alpine ibex in the French Alps. Journal of Mammalogy 78:1273–1281.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, Florida, USA.

Wiersema, G. 1984. Seasonal use and quality assessment of ibex habitat. Acta Zoologica Fennica 172:89–90.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Associate Editor: Hudson.