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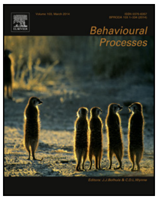

Cooperation improves the access of wild boars (*Sus scrofa*) to food sources

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ABSTRACT

Wild boar is a highly polycotous ungulate species, characterized by a complex and dynamical social organization based on the maintenance of long-term bonds between mother and daughters. The roots of this social organization have to be researched at the individual level, considering adaptations that improve fitness in hostile environments. We used information collected by camera-traps at artificial feeding sites, in two contrasting environments in Bulgaria (mountain habitat) and Italy (sub-Mediterranean habitat). We recorded 417 and 885 distinct groups on 7 and 11 foraging sites in Bulgaria and Italy, respectively. We computed (controlling for time range, study area and supplementary feeding site) an index of effective foraging time of the different social groups. We observed a positive and significant effect of the number of conspecifics of the same social group on the effective foraging time. The impact of the other social classes on effective foraging time is also positive, and males, yearlings, and juveniles benefited more from the presence of other social classes, while females were less affected. The access of the different social groups to foraging sites is not random. Males and yearlings play producers (i.e., search for food) and are prone to attend foraging sites before adult females and subadults, so attaining a larger foraging efficiency with respect to a situation where other groups are already present on the feeding site. Wild boars exhibit a more complex social organisation than previously believed, where cooperation prevails largely on competition. A rough division of labour is also present: yearlings, males, and juveniles use to play producers and assume a significant amount of risk determined by the presence of predators or hunters.

1. Introduction

Several studies have described the social structure of wild boar (Maselli et al., 2014; Rosell et al., 2004; Fernàndez-Llario et al., 1996; Nakatani and Ono 1995; Dardaillon, 1988). In this species, groups are characterized by phenological variations in size and composition, determined by the life-history cycle of the species. In particular, farrowing is considered the main cause of dissolution of social bonds between mother and offspring (Kaminski et al., 2005). Group size and the frequency of mixed-sex groups are typically larger in autumn-winter after weaning and during the rut.

It is necessary to discriminate ephemeral or occasional groups from more stable aggregations. Previous studies recognized that the basic social organization of wild boar is represented by families or matriarchal groups (Dardaillon, 1988; Nakatani and Ono, 1995; Rosell et al., 2004) where adult females are associated to their offspring (piglets and subadults). Both adult males and females may remain associated to form very large groups or sounders. Genetic studies (Podgórski et al., 2014a) have confirmed the presence of matriarchal groups for the Białowieża Primeval Forest (eastern Poland), while such a genetic structure of females was absent in the Alpe di Catenaia (central Italy) (Iacolina et al., 2009). Probably such a difference represents a side effect of hunting activity.

A large spatial association among females is determined by the fact that natal dispersal distance in wild boar is typically larger for males than for females (Truvé and Lemel, 2003; Keuling et al., 2010; Podgórski et al., 2014b). Wild boar is considered a polygynous species but a certain amount of promiscuity (multi-paternity within litters) has been recently demonstrated (Delgado et al., 2008; Poteaux et al., 2009).

Few studies have investigated the functional meaning of the very dynamical social patterns observed in wild boar. Kaminski

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et al. (2005), using a large number of individually-tagged animals, confirmed the presence of a long-term association among mother and daughters in the wild boar population of Chateauvillain-Arc-en-Barrois (eastern France). The maintenance of mother-daughters associations beyond the time of first reproduction, which in wild boar can be attained at as soon as one year of age, can incur in important fitness costs related to increased local resource competition in litters, which are much larger of those observed in other ungulates of similar body size (Servanty et al., 2009). Indeed Kaminski et al. (2005) showed an inverse dependence of social affinity between mother and daughters with the number of daughters, suggesting the presence of within-group competition. Iacolina et al., (2009) also showed the presence of non-kin individuals inside sounders. Such individuals would increase the cost of cooperation. Thus, to understand the dynamics of the social organization, it is relevant also to evaluate the benefits conferred by the formation of large and long-lasting social groups in wild boar. Several explanations can be proposed (Gardner and Foster, 2008). Protection against predators, according to the selfish herd mechanism (Hamilton, 1971) might be especially relevant where large predators are present. Beyond reducing predation probability, the formation of selfish herds can be also useful to improve foraging efficiency, by reducing per-individual vigilance time. Communal rearing of juveniles (piglet-sitting) may increase the reproductive success of females and their inclusive fitness and it has been demonstrated in highly-social species of mammals such as mole rats (*Bathyergidae*) (O'Riain and Faulkes, 2008) and meerkats (*Suricata suricatta*) (Clutton-Brock et al., 1999).

Foraging together for resources is a ubiquitous feature of group living, observed across *taxa*, but seldom all group members show the same, stereotyped behavior. In group foraging, cooperation and competition are strongly intermingled and the social group remain stable only if the former process prevails on the latter one. Observations on foraging sites suggest that large wild boar are able to dislodge smaller ones, albeit the extent of the reduction of forage intake for subordinate individuals remains unknown (Meynhardt, 1986).

Further, we expect that in a species characterized by a sophisticated behavioral repertoire and cognitive capacities such as the wild boar, group members, depending on their status (sex, age, phenotipic conditions), may exhibit different behavioral strategies. Theoretically, social interactions during foraging have to be framed in terms of the producer–scrounger game, in which individuals have the option either to produce (i.e., independently search for) resources or scrounge them from producers (Arbilly et al., 2014). Interestingly, when dispersal is impossible, Held et al. (2000) showed a complex foraging behavior in the domestic pigs with information exchanges among animals and where subordinates aimed to reduce exploitation by other group members.

It is impossible to study scrounger/producer interactions under natural conditions. Indeed most of the evidence about wild boar social interactions come from Meynhardt's (1986) study performed under controlled conditions. The aim of this paper is to investigate communal foraging behavior in wild boar within and among different groups using standardized observations by camera traps at artificial foraging sites. Camera traps are more and more used to investigate ecology and ethology of wild boar, because the method is cheap, easy-to-use and flexible. For instance, Sweitzer et al. (2000) and Morimando et al. (2008) used camera-traps for evaluating population parameters, Kuijper et al. (2014) investigated the "landscape of fear" of wild boar under potential wolf (*Canis lupus*) predation, while Maselli et al. (2014) studied its social behavior. In fact, only foraging sites make possible to record interactions among animals, which, for any other aspect, are fully wild.

For this study, we considered a seasonal period just before the onset of rut when juveniles are already weaned and females are motivated to exploit artificial feeds to recover from milking effort; males, conversely, have to improve their physical conditions in preparation for the rut. During this period sounders are large, increasing the opportunity of observing interactions among different social classes and sexes, without the strong disturbance determined by hunting which occurs later in the season. In order to enhance the generality of results, we compare two contrasting environments: the relatively poor mountain habitat in Bulgaria and the richer sub-Mediterranean habitat in Italy.

More specifically, we attempt to test whether or not the effective foraging time is affected by the study site, time range, and the presence of conspecifics of the same age/sex class or by individuals of other social classes.

2. Materials and methods

A description of the Bulgaria and Italian study areas was reported in Supplementary materials I. We used camera traps to record the activity of wild boar on the feeding site. The method of data collection and the approach used to determine the composition, residence time (RT), size (CLUSTER) and foraging time (FT) of social groups was described in Supplementary materials II and III.

The research did not imply any manipulation of animals. Forage was purchased to animals for different reasons than the present research and independently from it.

We used Generalized Linear Mixed Models (GLMM) (PROC GLIMMIX, SAS Institute, 2011) for hypotheses testing (Supplementary materials IV). We followed Bolker et al. (2008), for the selection of the appropriate distribution in GLMM analysis.

For each social class (adult males, adult females, yearlings, subadult males, subadult females and piglets) we developed a suite of models to explain the variance of FT. Model selection was performed using the AICc adopting the following approach. We assumed *a-priori* that FT is strongly influenced by the study location (Bulgaria, Italy) and by the time belt (Night: 0–6 h, Morning: 6–12 h, Afternoon: 12–18 h, Evening: 18–24 h). Then we tested the impact of CLUSTER, which shall be positive in cases of inter-individual facilitation and negative in cases of inter-individual competition. The potential impact of different social groups was computed as the average amount of minute-animal that remained in the FS when the group of interest was present. In other words, we assumed that the interaction between two groups is a linear function of the number of potential competitors and of the period of time the groups shared the FS. Whether estimated coefficients are significantly different from 0, we assumed the presence of competition (negative coefficients) or facilitation (positive coefficients). In model selection, we added sequentially adult males, subadult males, adult females, subadult females, yearlings, and piglets. Models were ranked in increasing AICc value and ΔAICc, Akaike weights, and evidence ratios were computed (Buckland et al., 1997). Finally, parameter averaging was computed using the widely accepted criterion of ΔAICc ≤ 4.

Further, we decided to develop a shorter-scale analysis focusing on wild boar behavior at the first arrival of the group on the FS. We assumed that a risk-prone social group would exploit a FS even in the absence of other animals (hereafter defined as producers), while a risk-adverse group would exploit the FS only in the presence of other animals which witnessed the absence of dangers (e.g., a hunter) in the FS (hereafter scroungers) (Arbilly et al., 2014). At the first arrival of a group on the FS, we recorded whether, and which, other social groups were present in the area. Finally, we investigated whether or not entering the FS in the absence of potential competitors influences the FT of the group of interest.