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TESI

**Cooperation, leadership and numerical assessment of opponents in
conflicts between groups of feral dogs (*Canis lupus familiaris*)**

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GENERAL INTRODUCTION

Domestic dogs (*Canis lupus familiaris*) were probably the first animals to be domesticated by human beings (Clutton-Brock 1995). It is now widely accepted that they evolved from group living wolves (*Canis lupus*), although over different time periods across the world and involving several wolves subspecies (Clutton-Brock 1995; Vilà et al. 1997). It has been suggested that the appearance of the permanent human settlements in the Neolithic period may have provided the first dogs with the possibility to adjust to a new ecological niche: dogs that were less scared of approaching human villages were possibly allowed to scavenge on abundant refuse and may have had their puppies found and raised by humans, thus increasing their reproductive success (reviewed in Coppinger & Schneider 1995). Direct selection by humans on tameness and for retention of juveniles' behaviour into adulthood may have increased dogs' behavioural plasticity and made them more trainable (Coppinger et al. 1987; Coppinger and Schneider 1995). Subsequently, artificial selection has furtherly modified dogs' morphology, physiology and behaviour to meet human requirements and to make dogs suitable for performing specific tasks (Coppinger & Schneider 1995). There is also some evidence that domestication may have increased dogs' cognitive abilities and made them particularly skilled at reading human communicative signals (Hare et al. 2002; Miklosi et al. 2003; Hare & Tomasello 2005; but see Udell et al. 2008). Thus, through a complex evolutionary process, dogs have become perfectly adapted for living in human society (Miklosi et al. 2004), although the effects of artificial selection and the relaxation of natural selection pressures have made them dependent on humans for survival.

However, dogs live in various degrees of association with people. There are dogs which have no limitations on their movements and activities placed by humans and thus are termed "free-ranging". Among these, dogs which are not socialized to human beings and avoid human contact are termed "feral" (Daniels & Bekoff 1989). Such dogs may form social bonds with their conspecifics and live in social groups in a manner which, to a certain degree, resembles the lifestyle of their wild ancestors, although sometimes they may still depend on the food provided indirectly or directly by

humans. Currently, the extent to which the behaviour of both free-ranging and feral dogs may be considered adaptive is still not known. Precisely, it is not known the extent to which domestication has altered their ability to form structured and organized social groups in comparison to wolves, and their capacity to adjust to ecological circumstances which are different from those traditionally experienced by dogs living in closer association with humans.

The first studies on free-ranging dogs in urban environments concluded that they formed non-structured and loose aggregations (Beck 1973). Other authors have found that urban free-ranging dogs were social and defended territories (Fox 1975; Font 1987). A feral dog population living in a mountainous region of Italy showed an interesting variability in social organization apparently matching local conditions of abundance and distribution of food resources (Macdonald & Carr 1995): dogs which had access to abundant human refuse lived in cohesive, territorial packs which competed successfully against smaller groups; dogs which subsisted on less abundant and predictable food, lived in social groups but spent most of the time alone. So the behaviour of these dogs appeared to be adaptive. However, other authors have emphasized that feral dogs populations are not reproductively self-sustaining, suffer from very high rates of density-independent juvenile mortality and depend on external recruitment of abandoned dogs to maintain a given group size (Boitani et al. 1995; Boitani & Ciucci 1995). Also, groups of feral dogs appear in some cases as aggregations of monogamous pairs without internal hierarchical structure (Boitani & Ciucci 1995). Unlike wolves, feral dogs do not exhibit cooperative hunting and communal rearing of puppies (Daniels & Bekoff 1989; Macdonald & Carr 1995; Pal 2005). Moreover, unlike wolves, reproduction within the group is not limited to a dominant breeding pair and the mating system is promiscuous (Daniels 1983; Pal et al. 1999). All these differences have often been attributed to the effect of artificial selection (Boitani et al. 1995).

During the period April 2005-May 2006, my colleague Simona Cafazzo has carried out a pioneering PhD research on the social organization and social dynamics of a feral dogs population living in a suburban environment at the periphery of Rome. Such dogs are not sociable to human

beings although they subsist entirely on the food provided daily by volunteer “dog caretakers”. She has found that dogs lived in packs of related individuals which travelled, rested and fed as a cohesive unit. Also they were highly cooperative in conflicts against strangers over access to food. Within a very large pack containing up to 42 individuals there was a linear dominance hierarchy which reliably predicted access to resources (food and mates). Also, dogs engaged frequently in ritualized greeting ceremonies and other affiliative behavioural patterns. There was some evidence of mate choice with both males and females preferring high-ranking partners. So, dogs showed a quite complex social structure which resembled that of wild canids with respect to several aspects, including well established dominance relationships, social bonds and cooperation against competitors.

In this thesis, I have continued the work of my colleague with the aim of further examining the possible adaptive value of feral dogs’ behaviour. To do this, I have used feral dogs as a model species for testing predictions based on evolutionary arguments and game theoretical models. I hope to show that, even if domesticated animals do not represent an ideal model for testing evolutionary hypotheses (Maynard Smith & Parker 1976; Price 1984), there is no a priori reason for assuming that their behaviour could not be adaptive. Since the dogs studied have been living under natural selection pressures for a few generations, I assume that every adaptive behaviour observed should have evolved in their wild ancestors before domestication.

The thesis is organized in three papers which are currently submitted for publication. In the first paper I focus on dogs’ intergroup conflicts and in particular on the relationship between intergroup agonistic behaviour and numerical cognition. It has been hypothesized that numerical competence in social animals has evolved to allow the assessment of relative group size during intergroup conflicts, and thus to allow animals to avoid becoming engaged in unwinnable contests against larger groups (McComb et al. 1994). Given the importance of group territoriality in wolves (Mech & Boitani 2003), it is conceivable that feral dogs may have retained the ability to assess relative group size. I test this hypothesis and also investigate the potential cognitive mechanisms involved in

such assessment. Studies on numerical cognition in animals have been almost exclusively carried out under laboratory conditions (see Hauser & Spelke 2004; Brannon 2005), and thus studies conducted in a more natural setting are urgently needed in order to clarify which selective pressures may have led to the evolution of numerical competence in animals.

In the second paper, I focus on collective movements during activity changes not involving intergroup contests, and I set the study within the very recent theoretical framework on leadership and group decision making in animals (Conradt & Roper 2003, 2005, 2007). I describe which individuals (leaders) within feral dog packs make collective decisions about the nature and timing of group activities, and how the number of decision makers vary according to the size of the group. I show how the pattern of group decision making emerge from the social relationships between pack members and, in particular, I test the hypothesis that individuals following leaders' decisions are those more in need of receiving social support from companions perceived as valuable social partners (Lamprecht 1992).

In the third paper I resume the topic of intergroup conflicts although, this time, I examine more specifically dogs' behaviour at individual level. Precisely, I investigate the pattern of individual participation in intergroup conflicts and try to unravel which evolutionary and proximate mechanisms may promote cooperation in feral dog packs. First, I test whether individuals modify their level of cooperation according to the odds of winning the conflict (which again imply the ability to assess relative group size). Then, I show how the social prestige enjoyed by dogs acting as leaders provide the opportunity to verify whether the handicap hypothesis (Zahavi & Zahavi 1997) may be a good explanation for the evolution of cooperation in animal societies. Finally, I test whether cooperation in dogs may be promoted by pattern of social affiliation and discuss the possible implications for dogs' social cognition.

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**1. Numerical cognition and assessment of opponents in conflicts
between groups of feral dogs (*Canis lupus familiaris*).**

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ABSTRACT

In conflicts between social groups, competitors should make the decision to attack/retreat according to the number of individuals in their own and the opposing group. We tested this hypothesis by recording naturally occurring conflicts in a population of feral dogs, *Canis lupus familiaris*, living in a sub-urban environment and controlling for the confounding effect of owner-intruder asymmetry. The overall probability of at least one pack members approaching aggressively opponents increased with decreasing the ratio of the number of rivals to that of the present pack members. Moreover, the probability of more than half the pack members withdrawing from a conflict increased with increasing such a ratio. The skill of dogs in correctly assessing relative group size appeared to improve with increasing the asymmetry in size between interacting packs in case large numbers (>4) were involved, and appeared less affected by size asymmetries when dogs had to compare small numbers. These results provide the first indications that, in domestic dogs, a representation of quantity based on noisy mental magnitudes may be involved in assessment of opponents in intergroup conflicts and that a more precise numerical system may operate when dealing with small numbers.

Keywords: natural intergroup conflicts, assessment of opponents, game theory, numerical cognition, noisy mental magnitudes, *Canis lupus familiaris*

INTRODUCTION

Classic game theoretical models predict that animals should be more willing to enter a conflict against a competitor when the benefit accrued from obtaining a contested resource (e.g. food and/or mates) are likely to outweigh the costs (Parker 1974). Costs in terms of injuries sustained are expected to increase, during a conflict, at rates that are inversely correlated with a competitor's resource holding potential (RHP) which is a measure of its fighting ability (Parker & Rubenstein 1981). Consequently, in order to reduce the costs of fighting, in asymmetric animal conflicts competitors should assess their own RHP relative to that of the opponent and make the decision to escalate a fight or retreating on the basis of such assessment (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982; Enquist & Leimar 1987).

Asymmetric conflicts will often involve social groups of animals which exhibit cooperative intergroup aggression. An array of observational studies have shown that in such intergroup conflicts victory usually goes to the side with the higher number of group members (several primates, Cheney 1987, Kitchen et al. 2004; barnacle geese, *Branta leucopsis*, Black & Owen 1989; territorial ants, *Atzecca trigona*, Adams 1990; lions, *Panthera leo*, Packer et al. 1990; spotted hyenas, *Crocuta crocuta*, Hofer & East 1993; feral dogs, Macdonald & Carr 1995; ethiopian wolves, *Canis simensis*, Sillero-Zubiri & Macdonald 1998; coyotes, *Canis latrans*, Gese 2001), thus strongly indicating that group size might be an approximate measure of one group's RHP. As a consequence, it may be hypothesized that in conflicts between social groups individuals should assess the number of conspecifics in their own and in the opposing group and adjust their cooperative agonistic behaviour accordingly. Studies testing such hypothesis in vertebrate species have often relied on playback experiments in which the presence of intruders has been simulated using species-specific recorded vocalization to elicit a territorial aggressive response in the tested animals. Thus, it has been demonstrated that female lions (McComb et al. 1994), male chimpanzee, *Pan troglodytes*, (Wilson et al. 2001), male black howler monkeys, *Alouatta pigra*, (Kitchen 2004) and wolves,

Canis lupus, (Harrington & Mech 1979) are more likely to approach aggressively simulated intruders when facing favourable odds, that is in situations in which their own group outnumbered intruders' group.

It has been suggested that the advantage of avoiding the costs of fighting against larger groups may have provided one of the main selective pressures leading to the evolution of numerical assessment skills in social species (McComb et al. 1994). Studies investigating the cognitive mechanism underlying numerical competence in animals have often involved discrimination tasks under laboratory conditions and have proved the ability to discriminate between the quantities of food items and other various objects of many different taxa including: rats, *Rattus norvegicus*, (Meck & Church 1983); tamarin monkeys, *Saguinus oedipus*, (Hauser et al. 2003); rhesus monkeys, *Macaca mulatta*, (Flombaum & Hauser 2005); orangutans, *Pongo pygmaeus*, (Call 2000); chimpanzee (Beran 2001, 2004); salamanders, *Plethodon cinereus*, (Uller et al. 2003); grey parrots, *Psittacus erithacus*, (Pepperberg 2006), and mosquitofishes, *Gambusia holbrooki*, (Agrillo et al. 2008). It has been suggested that non-human primates and possibly other among the above taxa share with human beings two distinct non verbal systems for representing numerosities, one representing precisely small numbers (up to 3-4) and the other representing approximately larger numerosities (Gallistel & Gelman 2000; Hauser & Spelke 2004; Brannon 2005). The large approximate number system is thought to represent discrete countable quantities as continuous mental magnitudes subject to scalar variability. This means that numbers are not represented as precise values but, instead, the signals encoding these magnitudes vary across different trials, with the variability being positively correlated to the size of the quantity to be estimated (Gallistel & Gelman 2000). Consequently, large magnitudes are more likely to be confused with similar quantities. Discriminability between different quantities follow the Weber's law: it becomes progressively easier as the ratio of the smaller quantity to the larger one decreases or when the difference between the larger and the smaller increases (Gallistel & Gelman 2000).

The small precise number system has been described by an object-file model (Feigenson et al. 2002). In this model each discrete item of a set to be enumerated is represented by a distinct symbol (object-file). Representations of numerosities are exact rather than approximated but, since the number of object-files available is small, they are limited to a set size of about 3-4 (reviewed in Brannon 2005). Discriminability of numerosities in this case does not follow the Weber's law.

However, up to now, very few studies have attempted at ascertaining the cognitive mechanism underlying assessment strategies in naturally occurring intergroup conflicts. This is not surprising given that such conflicts can be rarely observed in such a way to allow the collection of systematic data on behaviour and group size.

In this study, we investigated assessment of relative group size in naturally occurring conflicts between groups of feral dogs, which are much more abundant and accessible than wild animals, and tried to formulate predictions about dogs' intergroup agonistic behaviour based on both the cognitive and the game-theoretical approach.

In areas where they have access to abundant food resources directly or indirectly provided by human beings, feral dogs, i. e. those domestic dogs which are not socialized to humans (Daniels & Bekoff 1989a), live in packs formed by several males and females which have been described as territorial and highly cooperative in conflicts against strangers (Font 1987; Daniels & Bekoff 1989a, b; MacDonald & Carr 1995; Boitani et al. 1995; Boitani & Ciucci 1995; Pal et al. 1998; Cafazzo 2007), thus constituting a good model for testing hypotheses on group size assessment in intergroup conflicts.

Here, we recorded agonistic behaviour in conflicts between feral dogs packs which involved a much wider range of possible asymmetries in group size than that examined by previous experimental studies on this topic (see MacComb et al. 1994; Grinnell et al. 1995; Heinsohn 1997; Wilson et al. 2001; Kitchen 2004). In particular, we addressed the following questions. Firstly, we wanted to ascertain whether feral dogs are able to assess relative group size in intergroup conflicts and if they could use such information adaptively. We predict that, if feral dogs are adopting an

evolutionarily stable strategy as that proposed by some game theoretical models (Maynard Smith & Parker 1976; Parker & Rubenstein 1981) they should be more likely to behave aggressively towards opponents when they estimate their own group as being larger than the opposing group and, viceversa, should retreat from a conflict when they estimate their group as being smaller than the opposing group. Secondly, we sought to produce indications that assessment of relative group size in dogs may be accomplished using cognitive mechanisms similar to those that are supposed to operate in primates (see above). We predict that if the dogs' behaviour conforms to the Weber law, they should be more likely to make optimal decisions about whether or not attacking opponents (and whether or not retreating from a conflict) when the difference in size between the interacting packs is large and the ratio of the number of dogs in the smaller pack to the number of dogs in the larger one is small. This would provide indications that dogs are representing quantities as noisy mental magnitudes. On the other hand, if the performance of dogs in making optimal decisions drops drastically when the size of the interacting packs is higher than four, this would provide indications that assessment of relative group size is based on a system such as the object-file model.

The decision to enter a conflict may also be affected by asymmetries other than those in RHP, particularly asymmetries in resource value (Enquist & Leimar 1987) and arbitrary role asymmetries (Maynard Smith & Parker 1976; Leimar & Enquist 1984; Kokko et al. 2006). For instance, wolves are more likely to respond to human howling in the presence of a valuable resource as a recent kill (Harrington & Mech 1979). Moreover, the owners of a territory may value the contested resources more highly than the intruders (Krebs 1982; Tobias 1997; Johnsson & Forser 2002) and, thus, should be expected to be more motivated to fight. In order to control for these important complicating factors we considered the effect of the presence of food resources on dogs agonistic behaviour and tested the assumption of indirect defence of an area by mean of marking behaviour in feral dogs by recording the locations of scent marking activities.

MATERIALS AND METHODS

Study Area

The research was carried out in a sub-urban environment sited in the south-west periphery of Rome (Italy), an area traditionally called “Muratella”. The study area has a total surface of about 300 hectares and is delimited to the north, west and south sides by roads with heavy traffic and to the east side by cultivated areas. The area is crossed by another road which represents the main connection between the two more important lines in the south and in the west and that, at the same time, split the study area in two different sectors one in the south-west part and another in the north-east. The south-west sector is quite urbanized although not densely populated. It contains a recently built residence, a hotel, three large buildings with offices, four parking areas and an erecting yard. The north-east sector is mainly occupied by a natural reserve called “Tenuta dei Massimi”. The habitat in the reserve consists mainly of open grasslands, which are periodically ploughed, with interspersed wooded areas (*Quercus cerris* and *Quercus suber* were the prevailing plant species). Wild animals commonly observed in the reserve includes: pheasants (*Phasianus colchicus*), black kites (*Milvus migrans*), kestrels (*Falco tinnunculus*), herring gulls (*Larus argentatus*), carrion crows (*Corvus corone cornix*), green whipsnakes (*Coluber viridiflavus*), rats (*Rattus* spp.), crested porcupines (*Hystrix cristata*) and red foxes (*Vulpes vulpes*).

Feral dogs had free access to virtually every part of the study area. They used the reserve mainly to find resting sites, refuges and dens for puppies into the dense vegetation of the wooded areas. However, they frequently approached the central road crossing the study area, especially in the very early morning to feed on the food brought by volunteer dog caretakers. Food mainly consisted of pieces of meat taken in a slaughter-house, was placed, together with water, at some specific feeding sites all of which were virtually sited in the close vicinity of the road (see Fig 1).

Animals and packs' history

This study was part of a longer research project begun in April 2005 on the dog population living in the study area. A census of the population revealed that about 90-100 adult feral dogs inhabited the study area, leading to a very conservative estimate of density of about 30 animals/Km² (Cafazzo 2007). All dogs of the studied population were medium-large sized mongrels and there was not a recognizable predominant breeding type (Cafazzo 2007). Most dogs lived in groups which appeared to be composed to a wide extent by relatives. Dogs which travelled, rested and defended resources as a cohesive unit (Cafazzo 2007), thus fitting the definition of canid pack (Mech 1970), were considered as belonging to the same group.

With very few exceptions, dogs were not sociable to humans although they appear to be completely dependent on humans for food provision. The food provided by humans was abundant and it did not appear to be a limiting factor.

The studied populations was subject to control-management by the Rome Municipality which periodically trapped the animals, sterilized them and then released them back in the area. However, at the time when this research was conducted there were still many intact animals in the population. All the neutered dogs in the studied packs were sterilized between 6 and 12 months before the initiation of this data collection, except where indicated (see details below).

This research focused mainly on three of the eleven packs living in the area during the period May 2007-September 2008. These were selected because lived in a sector of the study area characterized by many wide open spaces and good observational points from which variables concerning intergroup interactions could be reliably recorded.

All individuals belonging to the studied packs were individually recognized on the basis of coat colour pattern and size, and sexed on the basis of genital morphology and body posture during urine-marking (males raises their hind leg higher than females; Bekoff 1979).

For the purposes of these research, individuals were assigned to broad age classes: they were considered as juveniles until the age of 11 months; subadults from one to two years of age and

adults afterwards. Age was precisely known for individuals that were born not before 2005, whereas all dogs born before that date were fully adult at the time when this research was conducted.

At the beginning of this study (May 2007) the “Corridoio pack” comprised 11 individuals: 4 intact males (1 adult and 3 subadults), 2 neutered males (1 adult and 1 subadult), 2 intact females (1 adult and 1 subadult) and 3 neutered females (1 adult and 1 subadult). In November 2007 another intact female rejoined the pack after a long period of separation.

The “Curva pack” consisted of 10 individuals: 1 intact adult female, 4 intact males (3 adults and 1 subadult), one neutered subadult male and 4 juveniles (3 females and 1 male). One month after the beginning of the study one of the males dispersed.

The “Piazza pack” included 4 individuals: 1 intact adult male, 1 neutered subadult male and 2 neutered females (1 adult and 1 subadult) both of which died during the course of the study.

In November 2007 the composition of the Curva pack changed, in that its members were joined by another pack consisting of 4 intact adult males and 2 intact adult females, and formed what we called the “Fused pack”. Between November 2007 and March 2008 two adult males and three adult females of this group were sterilized by the Rome municipality. Although there is no obvious reason to expect that sterilization would impair numerical competence in dogs, it seems to cause a decrease in aggression and marking behaviour (Maarschalkerweerd et al. 1997). To check whether the behaviour of this group, whose individuals were sterilized during the course of the study, was different from that of the other packs we included pack identity as a factor in a general linear model (see more details below).

Behavioural observations

Observations on dogs’ behaviour were conducted daily usually between 0600 hours and 1700 hours to cover, when possible, all the daylight period. To locate the dogs we walked on foot along a circuit and tried to observe each group on a rotational daily basis when possible. Upon locating a pack we first recorded the group composition, that is which individuals belonging to that pack were present at that time (sometimes the packs splitted and group members were not found all together at

any time), and monitored continuously group composition. Dogs were observed from distances ranging between 20 and 150 meters using a 10 x 50 binocular. If two packs were located within a few hundreds meters (or less) of each other so that we could reasonably expect an intergroup conflict between such packs to be imminent, we selected an observational point from which the behaviour of both packs and their composition could be recorded. Such observational point was always more elevated than the location where the conflict was expected to occur unless the dogs were so near to the observer that he could easily follow them on foot during their movements. Interactions were recorded ad libitum (Altmann 1974).

We assessed the size of the interacting packs on the basis of the number of adult and subadult individuals of both sexes that were within 50 meters of each other at the time when an intergroup conflict began. In practice, most dogs were often within 1-10 meters of the nearest companion during resting, and interindividual distance tended to further decrease during attacks against opposing groups. Distances were estimated visually by comparison with the measured distances separating several topographic landmarks.

An individual dog was defined as actively participating into an intergroup conflict if it approached opponents aggressively by moving forward at least 10 meters when the distance separating opposing packs at the time when the conflict initiated ranged between 20 and 100 meters, and if it lunged towards opponents in case the distance separating opposing packs was less than 20 meters. Such criterion was chosen because most intergroup interactions did not involve aggressive physical contact (with bites and/or scratches) but consisted of threatening displays in which group members ran together towards the opponents by barking furiously and snarling or walked towards opponents with a tense body posture by staring and keeping the tail raised. A pack was considered as behaving aggressively towards an opposing group when at least one of its members behave aggressively as described above.

An opposing pack reaction to a threat consisted of one of the following responses: retreating (walking away from opponents, or fleeing away); counterattacking (at least one group member

approaching aggressively as defined above); defensive barking but without any approach; simply ignoring the threat.

A pack was regarded as having lost an intergroup conflict whether the opposing pack was able to elicit a retreat response by more than half of its pack members or prevented all its pack members from having access to food, in the case that the contested resource was food. In turn, a conflict was regarded as occurring for access to food in one of the following cases: i) two packs were waiting for the food brought by people arriving around the same feeding site and a conflict took place once the food was placed; ii) a pack or single dog approached a feeding site where another pack was feeding and an agonistic interaction ensued; iii) a pack or single dog approached a feeding site in order to feed and was threatened by another pack that was already there but was not feeding.

An intergroup interaction ended when all individuals belonging to the pack involved stopped showing signs of aggression. Two consecutive agonistic interactions involving the same packs were regarded as two different events in one of the following cases: i) all individuals belonging to the interacting packs returned to their original starting locations as before the interaction took place and then another one ensued; ii) pack did not resume their original locations but at least 10 minutes elapsed between the end of the previous aggression and the beginning of the second one; iii) less than 10 minutes elapsed but the group composition had changed in the meanwhile.

Altogether, we spent in field 1147.2 hours during the period May 2007-September 2008, in which we observed 392 intergroup conflicts. We succeeded in collecting complete data about the size and the behaviour of the packs involved as well as about conflict outcome for 198 interactions involving the studied packs and other packs living in the area, or single individuals that were temporarily separated from their pack, or lone dogs which were not associated to any pack. At other times, dense vegetation or other obstacles either prevented us to ascertain which individuals were actually present or to see the outcome. Finally, interactions were discarded whether an oestrus female was present within 50 meters of any member of an interacting pack. This was done because, usually,

oestrus females were courted by males belonging to several different packs simultaneously and often more than two packs intermingled.

Defended areas

We defined a territory as a defended area from which competitors are excluded. To assess whether the packs studied were actually defending exclusive areas (territories), we recorded the locations of scent marking events (ad libitum sampling, Altmann 1974) on a 1: 1250 scaled map of the study area (to the nearest 20-30 meters). Scent marking consisted of raised-leg urinations by both males and females, a behavioural pattern that is involved in indirect territorial defence in canids (Peters & Mech 1975; Bradshaw & Nott 1995; Sillero-Zubiri & Macdonald 1998) and that we used to estimate the extent of areas defended by dogs independently of intergroup aggression. Precisely, we recorded marking events during travelling and feeding, excluding marking events occurring during intergroup conflicts, and during courting activities. We calculated the sizes of the defended areas by applying the minimum convex polygon method (Harris et al. 1990). The data for the Piazza pack collected before and after the change in group composition were pooled to have a set comparable to those of the other two packs.

We also recorded the locations of intergroup conflicts and regarded them as intrusions into other packs' defended areas if the stranger pack was more than 100 meters beyond the boundary of its own area.

Statistical analysis

Since we observed repeated interactions among a limited number of packs many of our data were not statistically independent. To control for such a dependency we operated as follows. First of all, for each recorded intergroup interaction we randomly selected one of the two interacting packs by tossing a coin, and included in the analysis only the data concerning the attacking/retreating behaviour of the selected pack. We refer to the selected pack as “random pack” and to the non selected one as “opposing pack”. Then, we used general backward stepwise regression models

(STATISTICA Release 7, StatSoft Inc., Tulsa, OK, U.S.A.) to investigate the effect of variables measuring numerical asymmetries between the packs on the probability of both aggressive approach and retreating response, and included the identity of both the random pack and the opposing pack as categorical factors in the models.

Aggressive approach by at least one pack member and losing the conflict (retreating by more than half of pack members or food deference) were both scored as dependent binary variables (“yes” and “no”) and we ran a different model for each dependent variable. Independent variables were the same for all the models: number of dogs present (referred to the random pack), number of opponents (referred to the opposing pack), ratio of the number of opponents to the number of present dogs, difference between number of opponents and number of present dogs, odds (scored as a categorical variable “favourable”, “unfavourable” and “even”), food presence (scored as a binary variable “yes” and “no”), and the above cited identities of the two interacting packs. We did not include a factor for owner-intruder asymmetry for the reasons explained below (see results). However, for the purposes of these analyses we included only the interactions involving the packs for which we had sufficient data on the extent of the defended areas which were 146.

To check whether the assessment ability of dogs was better when dealing with small numbers we carried out a post hoc conditioned analysis using three different subsets of the recorded interactions: the first subset consisted of the interactions in which the size of both packs was larger than 4; the second subset comprised the interactions in which the size of both packs was smaller than or equal to 4; the third subset included those interactions in which one pack was larger than 4 and the other one smaller than or equal to 4. We repeated the above described analyses on the three subsets and also used one-way ANOVA with the above dependent variables as factors and the ratio of the number of opponents to the number of present dogs as dependent continuous variable.

RESULTS

Defended areas

The spatial analysis of marking events ($n = 819$) seemed to indicate that dogs were not defending exclusive areas (Fig. 1). The degree of overlap between the areas marked by the Corridoio, the Piazza and the Curva/Fused packs was considerable, in the range 45-75 %, and overlapping mainly occurred in a sector containing three feeding sites. Such areas were small and very similar in size, varying between 26.6 and 28.1 hectares. Since all of the 146 observed interactions between the studied packs occurred within 100 meters of the overlapping areas, we did not further consider the effect of the owner-intruder asymmetry on aggressive behaviour in this study.

Intergroup conflicts

Out of 198 intergroup contests for which we had complete informations on group size and behaviour, 92 had a clear outcome. The larger group won 76 out of these 92 (82.6%), the smaller one was victorious in 13 interactions (14.1%) and in the remaining 3 cases (3.3%) the winner and the loser were equal in size. The pack which was the first to behave aggressively turned out as the winner in 80 of the interactions with a clear outcome (87%), whereas the pack which counterattacked was the winner in 8 interactions (8.7%). There were 3 interactions in which both the packs attacked each other approximately at the same time and one remaining in which a single dog fled away from a stranger pack before this actually attacked him. Finally, aggressive escalation with bites was recored in 9 out of 198 interactions (4.5%).

The general linear model (GLM) developed for the overall probability of aggressive approach by at least one pack member was significant ($R^2 = 0.35$, $F_{4,141} = 18.93$, $P < 0.0001$) and showed that, among the independent variables considered, the ratio of the number of opponents to the number of present dogs had the most significant effect (*coefficient* = -0.13 ± 0.02 , $T = -6.94$, $P < 0.0001$; Fig. 2a). Precisely, the predicted probability of aggression increased with decreasing such a ratio. Aggression was also dependent in some cases by opposing pack identity, with the Curva pack being

less likely to be attacked (*coefficient* = -0.25 ± 0.08 , $T = -3.18$, $P = 0.0018$) and the Piazza pack being more likely to be attacked (*coefficient* = 0.15 ± 0.07 , $T = 2.30$, $P = 0.02$).

The GLM of the binary variable “losing” or “non losing” was also significant ($R^2 = 0.30$, $F_{4,141} = 14.80$, $P = 0.0001$) and revealed exactly the opposite trend: the predicted probability of losing an intergroup conflict was significantly affected by the ratio of the number of opponents to the number of present dogs and decreased with increasing such a ratio (*coefficient* = 0.10 ± 0.02 , $T = 6.48$, $P < 0.0001$; Fig. 2b). Random packs were also more likely to lose when facing the Curva pack and less likely to lose when facing the Fused pack (whose members were sterilized during the study), although such effects were weaker (*coefficient* = 0.21 ± 0.07 , $T = 3.08$, $P = 0.0025$; *coefficient* = -0.13 ± 0.06 , $T = -2.30$, $P = 0.023$ respectively).

It was not possible to fit a model for the dependent variable losing/non losing when considering only the sub-set of interactions in which both the competing packs contained more than 4 dogs (mean ratio of the smaller to larger pack was 0.71 ± 0.02). The model of aggression approached significance but explained little variance ($R^2 = 0.20$, $F_{3,34} = 2.87$, $P = 0.051$). In this case, the probability of aggressive approach was negatively affected by “favourable odds” (*coefficient* = -0.32 ± 0.12 , $T = -2.68$, $P = 0.01$) and by random pack “Curva” (*coefficient* = -0.38 ± 0.18 , $T = -2.10$, $P = 0.04$). Altogether, the ratio of the number of opponents to the number of present dogs in interactions where the random pack attacked was not significantly different from that observed in interactions when the random pack did not attack (ANOVA: $F_{1,36} = 0.035$, $P = 0.85$; Fig. 3a). Similarly, such a ratio was not significantly different in interactions in which the random pack was defeated and in interactions in which it was not defeated (ANOVA: $F_{1,36} = 0.84$, $P = 0.37$; Fig 3b).

When considering the sub-set of interactions in which the size of both competing packs was smaller than or equal to 4 (mean ratio of the smaller pack to the larger one was 0.56 ± 0.04), we found that the GLM of the variables affecting the probability of aggression was significant ($R^2 = 0.63$, $F_{2,31} = 26.85$, $P < 0.0001$). Aggression was significantly affected only by the categorical

variable “odds” in that the predicted probability of attack was at its maximum with “favourable odds” (*coefficient* = 0.24 ± 0.07 , $T = 3.33$, $P = 0.0023$) and was close to zero with “unfavourable odds” (*coefficient* = -0.53 ± 0.08 , $T = -6.72$, $P < 0.0001$; Fig 4a). The GLM developed on the same subset of interactions for the probability of losing the conflict was also significant ($R^2 = 0.71$, $F_{8,25} = 7.53$, $P < 0.0001$). The ratio of the number of opponents to that of present dogs had, this time, the biggest impact on the dependent variable and the probability of losing increased with such a ratio (*coefficient* = 0.37 ± 0.06 , $T = 6.55$, $P < 0.0001$; Fig 4b). Food had also a significant effect in that random packs were more likely to retreat in the absence of food (*coefficient* = 0.19 ± 0.05 , $T = 3.60$, $P = 0.0014$). Finally, losing was dependent on the identity of several packs (random pack Curva: *coefficient* = 0.26 ± 0.09 , $T = 2.88$, $P = 0.008$; random pack Corridoio: *coefficient* = -0.34 ± 0.15 , $T = -2.20$, $P = 0.037$; opposing pack Curva: *coefficient* = 0.52 ± 0.17 , $T = 3.01$, $P = 0.006$; opposing pack Piazza: *coefficient* = 0.37 ± 0.13 , $T = 2.89$, $P = 0.008$; opposing pack Fused: *coefficient* = -0.97 ± 0.24 , $T = -3.98$, $P = 0.0005$).

The general linear models fitted for both the probability of aggression and that of losing on the subset of interaction when the size of one pack was larger than 4 and the size of the other was smaller than or equal to 4 (mean ratio of the smaller to the larger pack was 0.33 ± 0.02) were significant (for aggression: $R^2 = 0.45$, $F_{1,72} = 59.76$, $P < 0.0001$; for losing: $R^2 = 0.26$, $F_{1,72} = 25.51$, $P < 0.0001$), and revealed that in both cases the ratio of the number of opponents to that of present dogs was the only significant predictor (*coefficient* = -0.14 ± 0.02 , $T = -7.73$, $P < 0.0001$; *coefficient* = 0.09 ± 0.02 , $T = 5.05$, $P < 0.0001$ respectively). The probability of aggressive approach increased with decreasing the ratio and that of losing increased with increasing such a ratio (Fig 5 a,b).

DISCUSSION

Dogs have a very long history as domesticated animals (Clutton-Brock 1995), during which their morphology and behaviour have been altered through intensive selective breeding and relaxation of

natural selection pressures (Price 1984; Coppinger & Schneider 1995), thus every adaptive interpretation of their behaviour should be considered very cautiously. However, domestic dogs descended from group living wolves (Vilà et al. 1997) and there are evidences that they still retain important aspects of the social organization of their wild ancestors which evolved before domestication (Cafazzo 2007). However, in comparison to wolves which typically show very little home range overlap between different packs and quite frequently kill conspecifics (Mech & Boitani 2003), feral dogs of the studied population exhibited a fairly high degree of tolerance towards strangers, with very few intergroup interactions escalating into serious aggression. Such traits may be explained by a combination of factors including domestication, which may lead to a decrease in intraspecific aggression (Price 1984), abundance of food resources, which are known to cause a decrease in territoriality in several vertebrate species (Maher & Lott 2000) and in wolves as well (Peterson 1979), and relatedness between members of different packs (3 members of the Curva pack were previously members of the Corridoio pack). Nevertheless, interpack competition appeared to be still functional in order to defend space and acquire food.

In this study we have provided strong indications that, despite domestication, feral dogs are able to assess relative group size in intergroup conflicts and seem to use such information adaptively by making the decision to attack and/or retreat from a conflict on the basis of such assessment. Dogs living in packs were more likely to approach aggressively stranger packs the lower the ratio of the number of opponents to the number of present dogs, and were more likely to withdraw from a conflict the higher the ratio of the number of opponents to that of the present dogs. Our general backward stepwise regression models have shown that, altogether, such ratio was a better predictor of dogs' behaviour than other correlated variables such as the difference in size between the interacting packs and the absolute number of companions and rivals. Apparently, dogs were behaving in a manner resembling an evolutionarily stable strategy proposed by Maynard Smith & Parker (1976) for asymmetric animal contests such as: "attack when you estimate the RHP of your

pack as being higher than that of the opposing pack, and withdraw when you estimate the RHP of your pack as being lower than that of the opposing group”.

In our studied population there were no large asymmetries in the value of resources between competitors, since all packs were fed by humans everyday and roughly at the same time of the day. Nevertheless, dogs appeared to be sensitive to the presence of food, in that packs were less likely to retreat from conflicts when the food was the contested resource, and irrespective of relative group size (provided that the size of the interacting groups was small). Such results parallel those found in wolves which seem to be more ready to respond to a simulated intrusion in the presence of a kill (Harrington & Mech 1979), although in that study it was not possible to control for the effect of pack size.

In this study the probability of the dogs behaving aggressively towards opposing groups and of losing the ensuing conflict were predicted moderately well by relative group size. However, there were also cases where smaller packs attacked larger ones and won the contest, especially when both packs comprised more than 4 individuals. Game theoretical studies predict that aggression by competitors with the lower RHP should occur when the value of the contested resources is extraordinarily high so as to compensate for the costs of fighting a superior opponent (Parker & Rubenstein 1981; Austad 1983; Enquist & Leimar 1987; Bonanni et al. 2007). These arguments seem to apply to intergroup conflicts as well. For instance, male black howler monkeys responds to simulated intruders which outnumber them only in the presence of offspring that need to be protected from the risk of infanticide, suggesting that the value of winning may play an important role (Kitchen 2004). Moreover, male lions will approach aggressively simulated same sexed intruders even when facing overwhelming odds due to a very low probability of gaining tenure in an alternative pride in case they are evicted by rivals (Grinnell et al. 1995).

However, in our study food resources were abundant and of relatively low value if compared to the potential costs of an escalated fight. Under such conditions, aggression by the smaller competitors may be theoretically expected if they have some chance of winning the contest (Morrell

et al. 2005) as when, in our study, asymmetry in size between two interacting packs is small. On the other hand, aggression by smaller dogs packs might have been, in some cases, due to mistakes in relative group size assessment. We have found that, when analysis of data was restricted to the subset of interactions in which both interacting groups had a size larger than 4 individuals, the ratio of the number of opponents to the number of present dogs had no effect on either the probability of attacking opponents or that of losing the contest. Thus, apparently, dogs were not able to correctly assess relative group size and make optimal decision about their intergroup agonistic behaviour with numbers higher than four. An apparent set size limit of about 3-4 in quantity discrimination ability would be predicted by the object-file model of quantity representation. However, it should be noted that in such sub-set of interactions dogs had to compare group sizes, in order to make the decision to attack or retreat, that differed by a relatively high mean ratio of the smaller to the larger (0.71). In interactions in which one of the interacting groups comprised more than 4 individuals and the other one less than 4, dogs had to estimate large numerosities and discriminate the larger from the smaller group size in order to make optimal decision about their intergroup agonistic behaviour, but they had also to compare group sizes that differed by a much smaller mean ratio (0.33). The results have shown that, in this case, the agonistic behaviour of dogs was significantly predicted by the ratio of the number of rivals to that of companions (probability of aggression increased with decreasing such a ratio, and that of losing increased with increasing such a ratio), indicating that dogs were able to represent large numerosities and discriminate the larger group size from the smaller one when dealing with group sizes differing by a small ratio. An improvement in numerical performance with decreasing of the ratio of the smaller group size to the larger one is exactly what would be predicted by the Weber law, suggesting that dogs' numerical competence conforms to such a law and that dogs represent number of conspecifics, both those larger and smaller than 4, as noisy mental magnitudes subject to scalar variability. The typical Weber law signature of a system for quantity representation based on approximate magnitudes has already been found in a study on domestic dogs in which animals had to choose the larger versus the smaller quantity of food items

(Ward & Smuts 2007). Many other studies on a wide range of taxa support the view that animals represent numbers as approximate mental magnitudes (rats, Platt & Johnson 1971; monkeys, Flombaum & Hauser 2005; apes, Call 2000, Beran 2004; fishes, Agrillo et al. 2008), suggesting that such approximate number system may be phylogenetically very old. However, to our knowledge, this is the first study providing indications that a system for quantity representation based on noisy mental magnitudes may actually underlie numerical assessment of competitors in naturally occurring intergroup conflicts, supporting the hypothesis that the need to reduce the costs of intergroup aggression might have favoured the evolution of numerical cognitive abilities. Moreover, our results and those of Ward & Smuts (2007) taken together also show that the ability of dogs to assess quantities is context independent, that is the same system based on approximate magnitudes seems to operate to quantify both conspecifics and food items.

Feral dogs appeared to correctly assess relative group size also in situations when both the interacting packs comprised a number of individual smaller than or equal to 4, despite having to compare group sizes which differed by a greater mean ratio (0.56) than that recorded in interactions where one of the group sizes was larger than 4. As indicated by the better goodness of fit of our models (see results), assessment of relative group size appeared to be even more precise in this case. Moreover, the predicted probability of intergroup aggression did not increase linearly with the ratio of the number of opponents to that of the present dogs this time, but rather dogs virtually always attacked opponents when facing favourable or even odds and never attacked in cases odds were not favourable. In particular, dogs approached aggressively with roughly the same probability when they outnumbered opponents by a ratio 2/1 as when the ratio was 3/2 or 4/3 (see Fig 4a), indicating that, with small numbers, they discriminated the larger from the smaller group size equally well irrespective of the ratio. This is in contrast with the results of the study by Ward & Smuts (2007) in which many dogs failed to discriminate the larger from the smaller quantity of food when these differed by one item. Apparently, this may indicate that, in our study, feral dogs might have been discriminating small group sizes using a system such as the object-file model in which

representation of small numbers is precise and does not follow the Weber law (Hauser et al. 2000; Feigenson et al. 2002; Brannon 2005). However, we have also found that the predicted probability of losing the contest (retreating), with both group sizes smaller than 4, increased linearly with the ratio of the number of opponents to that of present dogs (see Fig. 4b), thus suggesting that even discrimination of small group sizes may become easier with more extreme numerical imbalances. Another possibility is simply that larger unfavourable numerical asymmetries between packs are required to elicit a retreat response than the asymmetries required to elicit an aggressive response. Nevertheless, even if our results do not clearly support an object-file model for representing small numbers in feral dogs, it remains possible that two different systems may be involved in the representation of small and large numbers respectively in feral dogs, the first being more precise and the other being based on noisy mental magnitudes.

Support for the object-file system comes mainly from studies on human infants (Feigenson et al. 2002) and rhesus monkeys (Hauser et al. 2000) in which subjects could successfully compare small quantities of food items which differed by relatively large ratios (e. g. 3 vs 4) but failed when the comparison of quantities included any value greater than 4. Conversely, studies on apes have found an effect of the ratio on quantities discrimination performance even with animals dealing with small numbers (Call 2000; Beran 2004).

It has been suggested that domestic dogs are able to form and remember mental representations of quantity (Ward & Smuts 2007) and also to operate over such representations by performing very simple additions (West & Young 2002). However, in this study, we have not implied an ability of the dogs to count. Moreover, it is possible that, in our study, feral dogs were not actually representing numbers, but instead continuous variables which covaried with number such as total surface occupied by pack members or density. Continuous variables may in some cases allow an easier and quicker assessment of the relative strength of the interacting groups and enable animals to escape from stronger opponents in a reasonable time. Estimation of quantity based on continuous variables seem to represent a common phenomenon in animals. For instance, female mosquitofishes

seem to assess shoal size on the basis of both total area and amount of movement of the fishes (Agrillo et al. 2008). It has been suggested that both discrete countable quantities and continuous uncountable quantities should be represented with the same continuous mental magnitudes because there are many natural situations in which the two kinds of quantities must be arithmetically combined (Gallistel & Gelman 2000).

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Figure 1. Areas scent marked by the studied packs. Arrows indicate the locations of the feeding sites used by the packs.

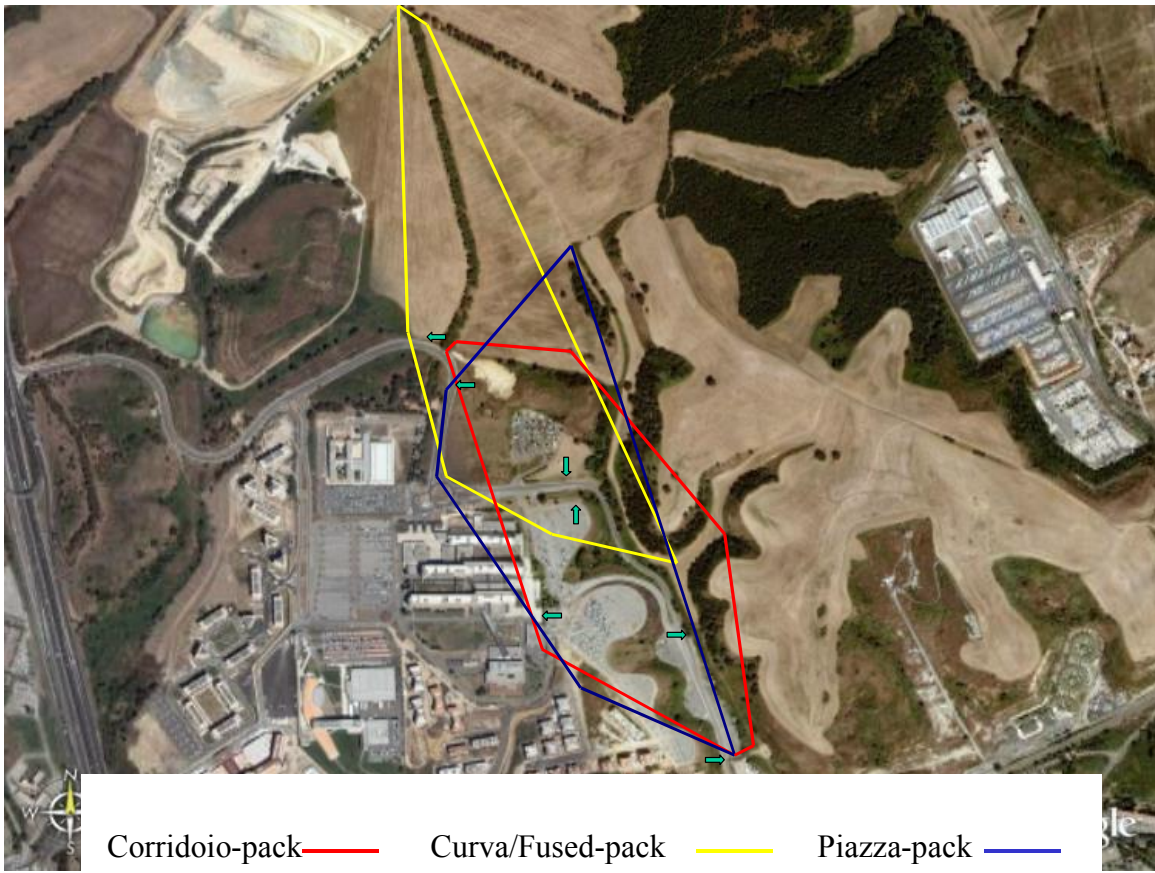
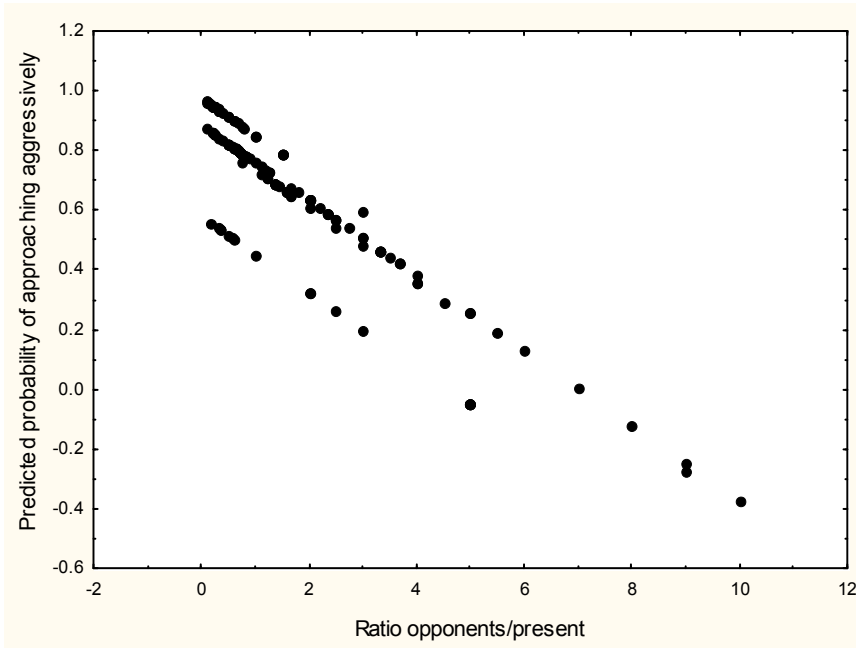


Figure 2. Predicted probability of approaching aggressively by at least one pack member (a) and of losing an intergroup conflict (b) versus the observed ratio of the number of opponents to that of present dogs (all interactions).

(a)



(b)

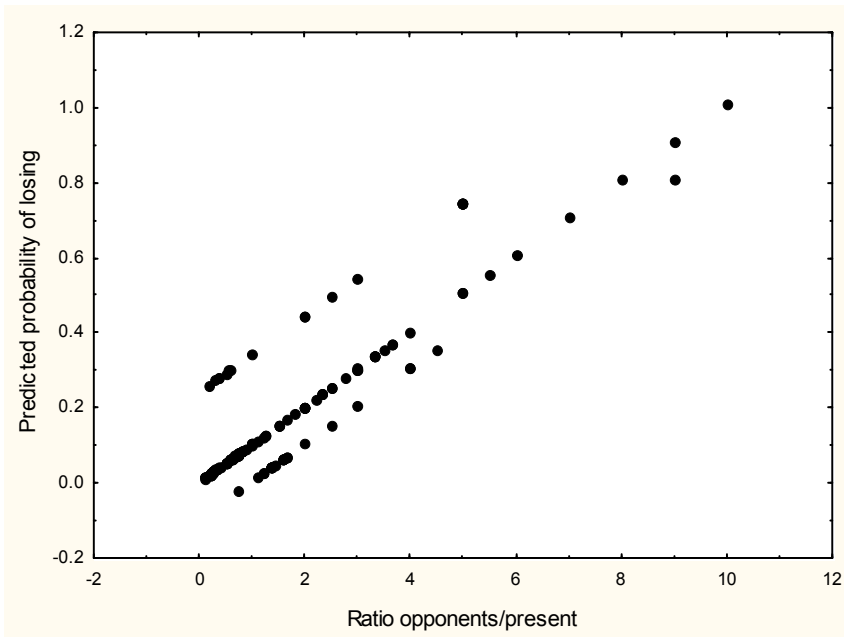
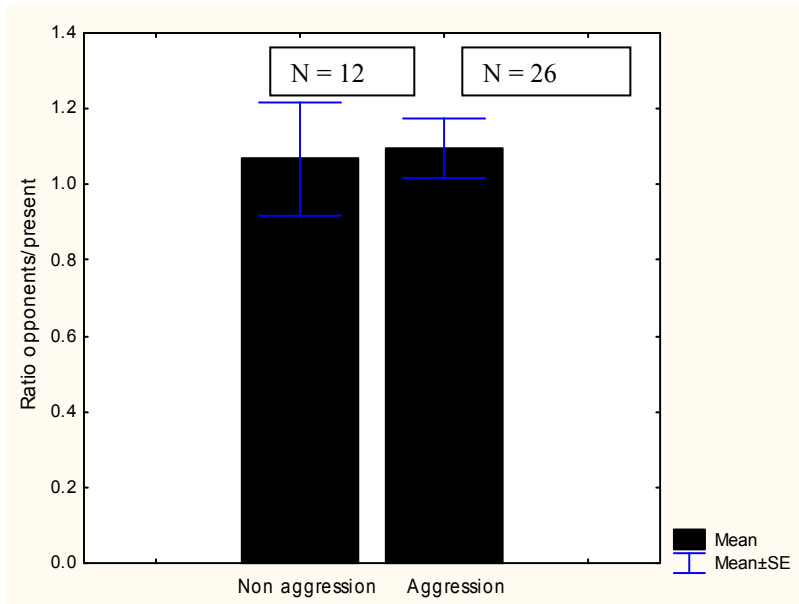


Figure 3. Effect of the ratio of the number of opponents to that present dogs on the probability of aggressive approach by at least one pack member (a) and of losing an intergroup conflict (b) in interactions where both the interacting packs comprised more than 4 individuals.

(a)



(b)

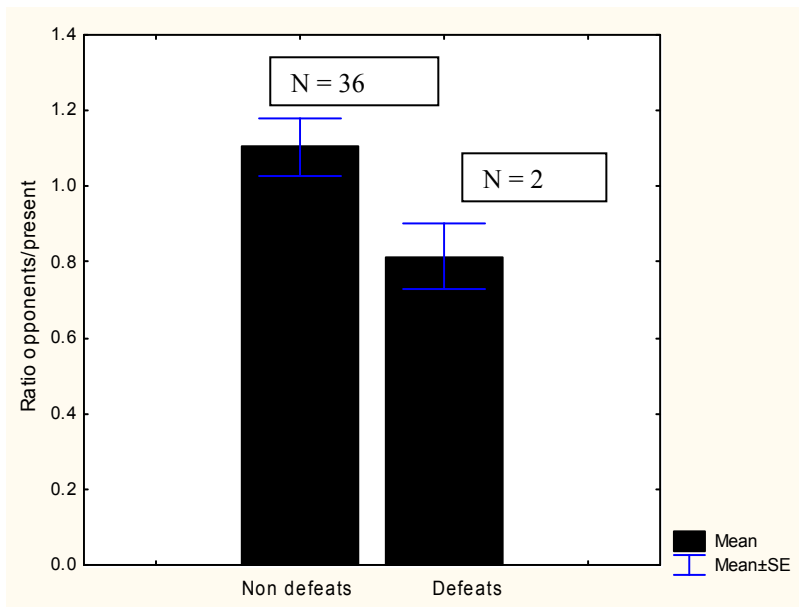
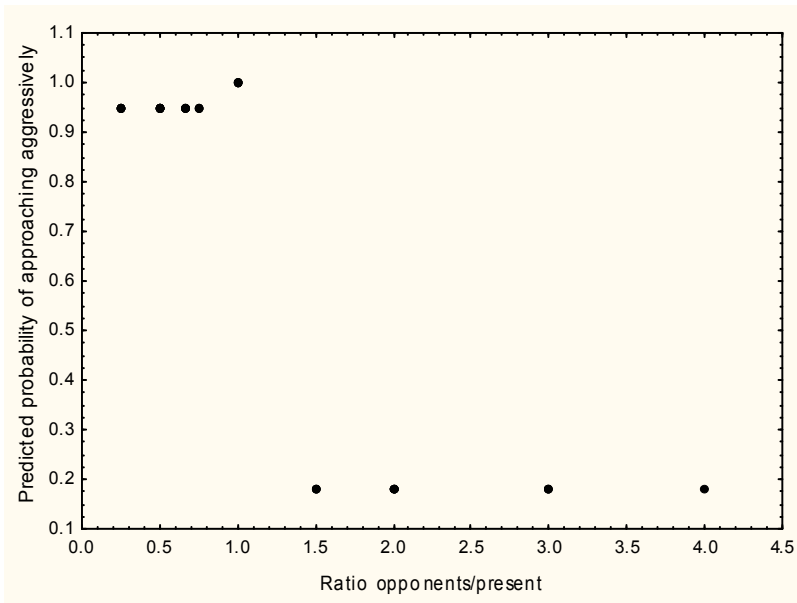


Figure 4. Predicted probability of approaching aggressively by at least one pack member (a) and of losing an intergroup conflict (b) versus the observed ratio of the number of opponents to that of present dogs in interactions when both interacting packs comprised a number of individuals smaller than or equal to 4.

(a)



(b)

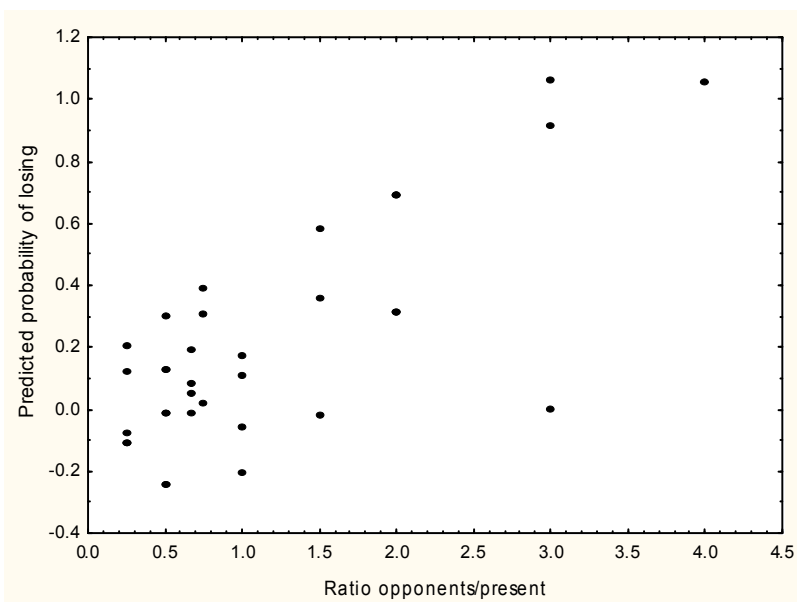
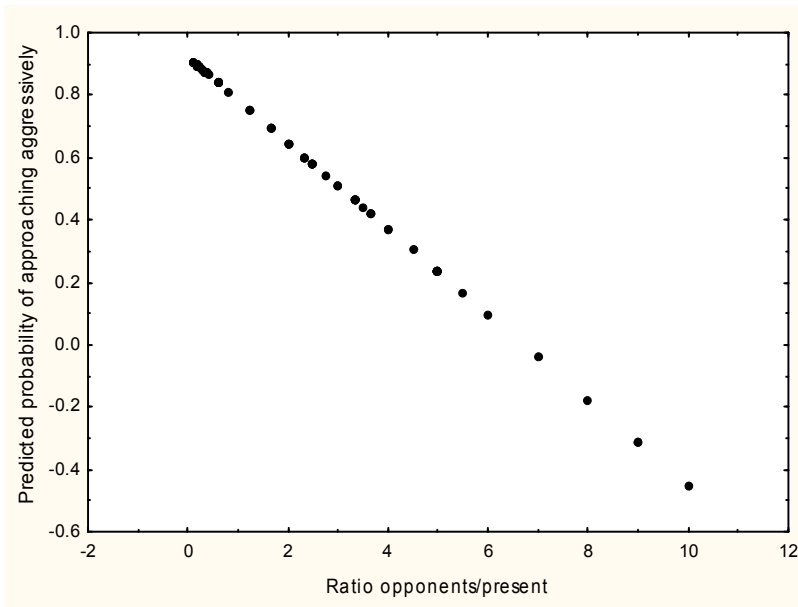
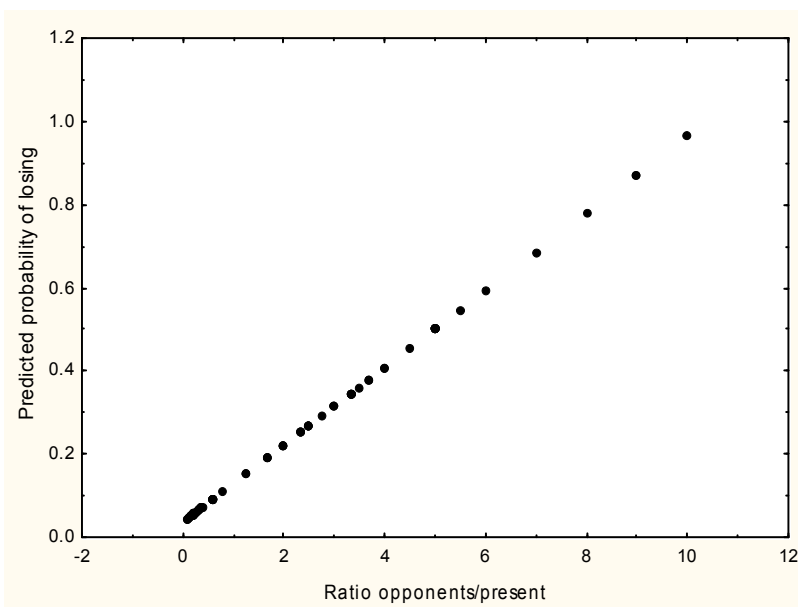


Figure 5. Predicted probability of approaching aggressively by at least one pack member (a) and of losing an intergroup conflict (b) versus the observed ratio of the number of opponents to that of present dogs in interactions when one pack comprised a number of individuals higher than 4 and the other one smaller than or equal to 4.

(a)



(b)



2. Effect of group size, dominance rank and social bonding on leadership behaviour in feral dogs (*Canis lupus familiaris*).

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ABSTRACT

Consensus decisions about the nature and timing of group activities allow animals to maintain group cohesion, but also entail costs due to the fact that individuals often differ with respect to their optimal activity budgets. Two mechanisms whereby animals reach a consensus include consistent leadership, in which one single dominant individual make the decisions, and variable leadership in which several group members contribute to the decision outcome. Sharing of consensus decisions is expected to reduce consensus costs to most group members especially in large groups. Both patterns are supposed to emerge from the complexity of social relationships of group members. We investigated the distribution of leadership in a population of feral dogs (*Canis lupus familiaris*), highly social carnivores, and tested how variables such as group size, dominance rank, gender and number of greeting partners affect such distribution between individuals. Although leadership was in no case concentrated on a single group member, most packs were characterized by a limited number of habitual leaders. In the largest pack the number of habitual leaders decreased after its size had shrunk. Individual variation in leadership was significantly predicted by dominance rank, gender and number of greeting partners with the last variable being the most consistent predictor. These results suggest that in social species collective movements may arise from the need of subordinates to maintain close proximity with specific valuable social partners.

Keywords: Individual variation in leadership; consensus decisions; consensus costs; group size; social bonds; *Canis lupus familiaris*

INTRODUCTION

Group-living in animals entails several benefits to individuals such as improved defence against predators, cooperation in conflicts against conspecifics, cooperative hunting and exchange of informations about location of resources (Packer et al. 1990; Sterck et al. 1997; Creel 1997; Franks et al. 2002). However, in order to get the advantages of sociality animals need to maintain their social group cohesive, that is they have to synchronize their movements and activities so that most group members will remain in the same place at the same time (Conradt & Roper 2000). In other words, animals belonging to the same group need often to make collective decisions about which activities to perform and when to perform them (Conradt & Roper 2003). Specifically, such group decisions are termed “consensus decisions” in case individuals of a social group choose together between two mutually exclusive actions with the aim to reach a consensus (Conradt & Roper 2005). Consensus decisions usually concern movement direction, travel destination and activity duration (Conradt & Roper 2005). Two extreme mechanisms that have been proposed to allow animals to reach consensus decisions are “consistent leadership” and “variable leadership” respectively (Conradt & Roper 2003, 2005). Leaders (or decision makers) are those individuals that, even when animals decide collectively, are more influential in affecting the decision outcome whereas the others will simply accept their decision. Precisely, consistent leadership (also termed “despotic”, or “unshared leadership”) refers to the same individual, usually the highest ranking or the oldest and most experienced member of a social group, being the one which always lead group actions (Conradt & Roper 2005). Conversely, variable leadership (also termed “democratic” or “shared leadership”) refers to social situations where different group members contribute to the decision outcome on different or on the same occasion (Conradt & Roper 2005). Empirical examples of consistent leadership are provided by studies on mountain gorillas (*Gorilla gorilla beringei*), in which the male silverback is the highest ranking member of the social group and seem to determine most decisions about travelling direction (Schaller 1963; but see Stewart & Harcourt 1994). Also, in a cooperative breeding carnivore such as the dwarf mongoose (*Helogale parvula*), the breeding and

dominant female determines foraging initiation, route taken, distance travelled and selection of resting sites of all the group (Rasa 1987). Variable leadership can be found in white-faced capuchin monkeys (*Cebus capuchinus*) in which virtually all group members can successfully initiate a collective movement (Leca et al. 2003) or in bar-headed geese (*Anser indicus*) where members of different age/sex classes lead the group at the different times of the year (Lamprecht 1992). Variable leadership can involve either “equally shared consensus decision”, where all group members contribute to the decision outcome, or “partially shared consensus decision” in which a given proportion of group members, usually a demographic subset, contribute to decision outcome (Conradt & Roper 2005). Examples of the last pattern may be represented by another cooperative breeding carnivore such as the wolf (*Canis lupus*) in which group activities are predominantly led by both members of the dominant breeding pair (Mech 2000; Peterson et al. 2002), or by primate species such as hamadryas (*Papio hamadryas hamadryas*) and chacma baboons (*Papio hamadryas ursinus*) in which adult males make all or most decisions about travelling initiation respectively (Kummer 1968; Stueckle & Zinner 2008).

However, consensus decisions often involve considerable conflict of interest between group members, termed consensus costs (Conradt & Roper 2000), due to the fact that individuals, and especially those belonging to different age/sex classes, usually differ with respect to their optimal activity duration, or their preferred travel destination, and thus the actual group decision outcome may differ from some individual’s optimal decision outcome (Gompper 1996; Ruckstuhl 1999; Conradt & Roper 2000). For instance, in some ungulate species the optimal duration of foraging bouts differs between individuals of different sex and the costs of activity synchronization may be so high that they contribute to cause the social segregation of the sexes (Ruckstuhl & Neuhaus 2000; Conradt & Roper 2000). Consensus costs will be also affected by which group members contribute to the decision outcome: theoretical models suggest that for most group members equally shared consensus decisions should result in lower synchronization costs than unshared decisions (Conradt & Roper 2003). Subordinates should benefit by accepting a despotic decision of

a single dominant and experienced leader only in case group size is small and there is a large asymmetry in information concerning the environment (e. g. location of resources, predation risks) between the dominant leader and the subordinates themselves (Conradt & Roper 2003). Consequently, it may be hypothesized that shared decision making would be more likely to occur in large groups given that many subordinates together can invest more energy in resisting a despot's decision than a single despot can invest in coercion (Conradt & Roper 2003, 2005). More recently, it has been shown how both equally shared decision making and unshared decision making can evolve as evolutionarily stable strategies through individual natural selection (Conradt & Roper 2007). A game theory model has revealed that equally shared decision making can evolve under a wider variety of conditions and specifically when: groups are heterogeneous in composition, including different age/sex classes; alternative decision outcomes differ in consensus costs; groups are close to, or above optimal group size; consensus costs are high relative to (but not higher than) grouping benefits (Conradt & Roper 2007).

In species in which consensus decisions are not equally shared, individual variation in leadership is not a simple function of social dominance or experience. It is now widely recognized that group decision making and movements arise from complex interactions and social relationships between group members (Wrangham 1980; Dunbar 1983; Lamprecht 1992; Byrne 2000; Couzin & Krause 2003; Couzin et al. 2005; Fischhoff et al. 2007). It has been suggested that group members which follow leaders' decisions are those more in need of receiving social support and protection by leaders themselves which are regarded as valuable social partners, that is those which are of high social rank and/or have knowledge about location of resources (Lamprecht 1992). Since affiliative behaviour in many social species helps individuals to develop strong social bonds with valuable social partners (Seyfarth 1977; East et al. 1993; Schino 2001), it appears that investigating the relationship between leadership and affiliative behaviour in social animals may prove useful to the aim of understanding more about both proximate mechanisms and functional consequences of leadership. For instance, in a group of chacma baboons, it was found that the leader male was not

the highest ranking individual but the one which received more affiliative behaviour by adult females and he acted to protect both females and juveniles from harassment by more dominant individuals (Byrne et al. 1990).

Individual variation in leadership may also be affected by gender, independently of dominance rank. For instance, in species where reproduction increases the energy and water demands of females, females may be more motivated than males to initiate group movements so as to arrive at food and water sources first and fulfill their requirements (e. g. several lemuriformes, Erhart & Overdorff 1999, Overdorff et al. 2005; zebras, *Equus burchellii*, Fischhoff et al. 2007).

In this study we investigated the pattern of individual variation in leadership in a population of feral dogs living in a suburban environment and how such variation was affected by variables such as group size, dominance rank, gender, age and social affiliation. Feral dogs are those domestic dogs which are not socialized to humans (Daniels & Bekoff 1989a). In some areas where abundant food resources are made available by humans, they form packs which are quite heterogeneous in composition comprising individuals belonging to different age/sex classes (Font 1987; Daniels & Bekoff 1989a, b; MacDonald & Carr 1995; Boitani et al. 1995; Boitani & Ciucci 1995; Pal et al. 1998; Cafazzo 2007). Recent studies have demonstrated that, despite a very long history as domesticated animals (Clutton-Brock 1995), they show a complex level of social organization with hierarchical social structure, ritualized greeting ceremonies and post-conflict affiliation (Cafazzo 2007; Cools et al. 2008). Most importantly, consensus making decisions appears to constitute a basic feature of the dogs' social organization since packs travel as cohesive units and are highly cooperative in conflicts against conspecifics (Cafazzo 2007; Bonanni et al. submitted). Keeping the pack cohesive would be functional since large packs dominate smaller ones in intergroup conflicts and lone dogs which are temporarily separated from their own pack are the most likely to be attacked by strangers (Bonanni et al. submitted).

Here, we aimed firstly at describing the pattern of leadership during activity changes in feral dog packs ranging in size from 3 to 27 individuals and placed it along the continuum from unshared, via

partially shared, to equally shared decision making. We tested whether leadership was evenly or unevenly distributed within each pack and if it was more evenly distributed in larger packs; then, we tried to explain individual variation in leadership using variable such as dominance rank, gender and age; clearly, equally shared decision making will imply even distribution of leadership and no significant effect of dominance rank. We also assessed the amount of affiliative behaviour received by each individual; we predicted that if leaders are followed because they are regarded as valuable social partners by other group members, then they should receive more affiliative behaviour than non-leaders.

MATERIALS AND METHODS

Study area

The research was carried out in a sub-urban environment sited in the south-west periphery of Rome (Italy), an area traditionally called “Muratella”. The study area has a total surface of about 300 hectares and is delimited to the north, west and south sides by roads with heavy traffic and to the east side by cultivated areas. The area is crossed by another road which represents the main connection between the two more important lines in the south and in the west and that, at the same time, splits the study area in two different sectors one in the south-west part and another in the north-east. The south-west sector is quite urbanized although not densely populated. It contains a recently built residence, a hotel, three large buildings with offices, four parking areas and an erecting yard. The north-east sector is mainly occupied by a natural reserve called “Tenuta dei Massimi”. The habitat in the reserve consists mainly of open grasslands, which are periodically ploughed, with interspersed wooded areas (*Quercus cerris* and *Quercus suber* are the prevailing plant species). Wild animals commonly observed in the reserve include: pheasants (*Phasianus colchicus*), black kites (*Milvus migrans*), kestrels (*Falco tinnunculus*), herring gulls (*Larus argentatus*), carrion crows (*Corvus corone cornix*), green whipsnakes (*Coluber viridiflavus*), rats (*Rattus* spp.), crested porcupines (*Hystrix cristata*) and red foxes (*Vulpes vulpes*).

Feral dogs had free access to virtually every part of the study area. They used the reserve mainly to find resting sites, refuges and dens for puppies into the dense vegetation of the wooded areas. However, they frequently approached the central road crossing the study area, especially in the very early morning to feed on the food brought everyday by volunteer dog caretaker. Food, mainly consisting of pieces of meat taken in a slaughter-house, was placed, together with water, at some specific feeding sites all of which were virtually sited in the close vicinity of the road. So the food was abundant and predictable both in space and time and there was no asymmetry in information about location of food between individual dogs.

Packs studied

Dogs studied belonged to a population of about 100 animals inhabiting the study area. All dogs were medium-large sized mongrels and there was not a recognizable predominant breeding type (Cafazzo 2007). Most dogs of the population lived in groups which appeared to be composed to a wide extent by relatives. Dogs which travelled, rested and defended resources as a cohesive unit (Cfazzo 2007), thus fitting the definition of canid pack (Mech 1970), were considered as belonging to the same group. With very few exceptions, dogs were not socialized to humans although they appear to be completely dependent on humans for food provision. The food provided by humans was abundant and it did not appear to be a limiting factor.

All dogs of the packs studied were individually recognized on the basis of coat colour and pattern and sexed on the basis on genital morphology and body posture during urine-marking (males raises their hind leg higher than females; Bekoff 1979).

The studied populations was subject to control-management by the Rome Municipality which periodically trapped the animals, sterilized them and then released them back in the area. However, at the time when this research was conducted there were still many intact animals in the population. All the neutered dogs included in the data collection were sterilized between 6 and 12 months before the initiation of the study.

The research was conducted in two phases. In the first part, which encompassed the period April 2005-May 2006, we focused on a group called the “Corridoio pack” whose size ranged from 40 to 25 individuals throughout the study period. However, for the purposes of this study data were collected for 27 individuals that were: 6 adult males, 5 adult females, 4 sub-adult males, 1 sub-adult female, 6 juveniles males, and 5 juveniles females. We defined adult dogs as those which were at least two years old, sub-adult dogs as those that were between one and two years old and juveniles as those that were younger than one year (see details on age estimation below). All these dogs were intact with the exception of a female.

In the second part of the study, which encompassed the period May 2007-September 2008, we focused on three packs, including the Corridoio pack as well, whose size had considerably shrunk in the meanwhile (Corridoio pack II henceforth). Nine dogs (6 males and 3 females) that were members of the Corridoio pack during the first phase of the study were still in the same pack during the second phase, whereas two males and a female had dispersed in the “Curva pack” and another neutered female had dispersed into the “Piazza pack” (see below).

In May 2007 the Corridoio pack II comprised 11 individuals: 4 intact males (1 adult and 3 subadults), 2 neutered males (1 adult and 1 subadult), 2 intact females (1 adult and 1 subadult) and 3 neutered females (1 adult and 1 subadult). In November 2007 another intact female rejoined the pack after a long period of separation.

The Curva pack consisted of 10 individuals: 1 intact adult female, 4 intact males (3 adults and 1 subadult), one neutered subadult male and 4 juveniles (3 females and 1 male). One month after the beginning of the study one of the males dispersed. Between November 2007 and March 2008 two adult males and three adult females of this group were sterilized by the Rome municipality. Given the individual changes in behaviour that sterilization is likely to provoke (Maarschalkerweerd et al. 1997), we did not analyze at individual level the data collected, for this pack, after October 2007.

The Piazza pack included 4 individuals: 1 intact adult male, 1 neutered subadult male and 2 neutered females (1 adult and 1 subadult) both of which died during the course of the study. Both

the sterilization of members of the Curva pack and the death of members of the Piazza pack greatly reduced the data set available for these two packs on leadership behaviour.

Leadership

Observations on dogs' behaviour were conducted daily usually between 0600 hours and 1700 hours to cover, when possible, all the daylight period. To locate the dogs we walked on foot along a circuit and tried to observe each group on a rotational daily basis when possible. Dogs were observed from distances ranging between 20 and 150 meters using a 10 x 50 binocular. Data on leadership were collected *ad libitum* (Altmann 1974) while monitoring all group members simultaneously. Altogether 630.4 hours of observation in the field were totalized in the first part of the study and 1147.2 in the second.

When a leadership bout began we recorded the behaviour of all individuals belonging to the same pack that were within 50 meters of each other. Everytime we observed a dogs which initiated to move so as to leave all other group members behind itself, we checked if at least other two dogs moved in the same direction within 10 minutes; if this was the case we recorded the initiator as a leader and the other as followers. Followers were regarded as walking in the same direction as the leader if they moved following directly the initiator, or if they converged towards it, or if they walked in a direction parallel with and not more than 10 meters distant from that of the initiator. Collective movements concerned the following activity changes: from resting to travelling; from resting to feeding or drinking; from resting in an area exposed to the sun to a shaded area; from resting in an open area to resting into the dense vegetation. With the exception of the first, all activity changes involved sometimes short distance movements (10-50 meters). In this case, followers had to move for at least half the distance travelled by the leader for their behaviour being scored as following. We did not include here neither collective movements related to conflicts against other packs (because these were examined in another paper), nor movements occurring during courting activities (because leading in this case was biased in favour of the oestrus female). Successive movements were scored as independent if they were separated by an activity change

lasting at least 10 minutes (for instance, two different travelling bouts separated by resting for 10 minutes). We did not assume that every movement away from other pack members was an attempt at initiating a collective movement. We calculated for each individual a “leadership score” as follows: for each dog within its pack we divided the total number of times it behaved as a leader by the sum of the total number of times it behaved as follower and the total number of time it behaved as leader.

Assessment of social bonds

To assess whether the establishment of social bonds affected consensus decision making, we recorded ad libitum two behavioural patterns displayed by dogs during ritualized greeting ceremonies: licking the muzzle of another dog (or simply pushing the muzzle of the other dog with the nose) and wagging the tail while holding the tail itself down. Both the behavioural patterns convey components of both submission and affiliative intentions and were defined by Schenkel (1967) as active submission: “the impulse and effort of the inferior towards friendly harmonic social integration”. Although these behavioural patterns are not independent because are often displayed by the same dog at the same time, we considered them separately here because muzzle-licking seem to have a higher directional consistency index and a closer association with dominance rank (Cafazzo 2007; Cafazzo et al. submitted). For each dog we calculated the number of companions by which it received at least one instance of muzzle-licking and tail-wagging and divided it by the total number of available companions in its pack to allow comparison between individuals belonging to packs of different size.

Assessment of dominance rank

To assess dominance rank we also recorded ad libitum all submissions showed by dogs in response to aggressions and dominance displays. These were called here non-active submissions and included: avoiding eye contact, lowering the head, lowering the tail between the hind legs, laying down on the back, yelping, fleeing, withdrawing, interruption of feeding (in the feeding context). Aggressive behaviour included: threats (lunging, pointing, staring at, curling of the lips, baring of

the canines, raising the hackles, snarling, growling, barking), chasing, biting, hitting with paws, fighting. Dominance displays included: upright and stiff body posture with the head and tail held high, putting the muzzle or a paw on conspecific's back.

For each pack, we ranked all the occurrences of both muzzle-licking and non-active submissions into squared matrices with performers on one axis and recipients on the other one. To arrange individuals into a dominance rank order that was most consistent with a linear dominance hierarchy we applied the method developed by de Vries (1998) which minimize the number of inconsistencies (dominance reversals) and the strength of inconsistencies. We also tested the transitivity of dominance relationships within each pack by applying an improved test of linearity (de Vries 1995) that is based on Landau's linearity index but takes into account unknown and tied relationship between group members. Both tests were performed using MatMan 1.1 (Noldus Information Technology, Wageningen, The Netherlands).

In order to compare dominance rank across packs of different size, individuals were assigned a standardized rank following the procedure illustrated in East & Hofer (2001). Ranks were evenly distributed between the highest rank (standardized rank +1) and the lowest rank (standardized rank -1), with the median rank being scored as 0.

Statistical analysis

When possible, we tested whether the distribution of leadership across individuals within packs deviated significantly from an even distribution using a chi-square test (Siegel & Castellan 1988). Since the total number of observed collective movements varied across individuals we calculated the expected frequencies as follows: we built a $N \times 2$ table with all individuals within a pack as lines and the total number of times a given individual behaved as leader and follower as columns respectively. For each cell into the table the expected frequency was calculated as the total score of the corresponding line multiplied by the total score of the corresponding column and divided by the total of all the scores entered in the table.

1 To explain individual variation in leadership we ran general backward stepwise regression models (STATISTICA Release 7, StatSoft Inc., Tulsa, OK, U.S.A.) with “leadership score” as described above as dependent variable. When the model was applied to the Corridoio pack during the first phase of the study the independent variables were: standardized dominance rank, age, proportion of group companions by which each dogs received at least one instance of muzzle-licking, and gender. When the model was applied to individual dogs studied during the second part of the study two additional independent categorical variables were considered: pack identity and the binary factor intact/sterilized. Such analyses were also repeated after replacing “muzzle-licking received” with “tail-wagging received” to check which variable was the best predictor.

Dogs were assigned to different age classes: the first class included two individual dogs that showed obvious signs of old age (presence of gray muzzle hair and worn theet); the second class included dogs that were fully grown at the time when the study began (April 2005) but did not show signs of old age; the third class comprised individuals that were juveniles at the beginning of the study (on the basis of allometry and body size) and thus were presumably born in 2004; the other classes comprised dogs that were observed to be born in 2005, 2006 and 2007 respectively.

Interobserver reliability

Interobserver reliability was assessed between two of us (R. B. & S. C.) by calculating “leadership scores” as described above for eight dogs belonging to the Corridoio pack (that was studied by both observers) across twelve collective movements. Pearson correlation between the leadership scores obtained by the two observers was $R = 0.98$.

RESULTS

Distribution of leadership within packs

In the Corridoio pack leadership was clearly not restricted to a single dog ($n = 133$ collective movements). As shown in Figure 1a, every adult and subadult individual could be successful in recruiting at least two followers, whereas juveniles never behaved as leaders. However individual

differences in the frequency of leadership were significantly greater than expected by chance even when restricting the analysis to adults and subadults ($\chi^2 = 84.94$, $df = 15$, $P < 0.0001$).

Leadership was also variable in the Corridoio pack II ($n = 94$ collective movements) but the individual differences in the tendency to lead again deviated significantly from an even distribution ($\chi^2 = 241.55$, $df = 10$, $P < 0.0001$). However, in this case, there was just one dog (the highest ranking male) out of 11 (9 %) which behaved more frequently as leader than he behaved as follower, whereas in the first phase there were 6 out of 27 dogs (22.2 %) which behaved more frequently as leaders (Figure 1a, b).

In the Curva pack ($n = 17$ collective movements) a male was the consistent leader before his dispersal from the pack one month after the beginning of the study (Figure 2a). After such dispersal event (the male was excluded from the subsequent analyses due to insufficient informations on its social status and relationships), leadership was variable although a female was the only dog which behaved more frequently as leader than she behaved as follower (Figure 2b). Such female had dependent puppies and did not travel with the pack during the period in which it was led by the mentioned male.

In the Piazza pack ($n = 11$ collective movements) leadership was equally shared between two males which led much more frequently than a female in poor physical condition (Figure 3).

In both the Curva and the Piazza pack, the chi-square test could not be applied due to the fact that more than 20% of the expected frequencies were smaller than 5 (see Siegel & Castellan 1988).

Dominance hierarchies

For the Corridoio pack a significantly linear dominance hierarchy based on direction of submissive behaviour was detected both in the first and in the second part of the study (Improved linearity test: $h' = 0.65$, $P = 0.0001$; $h' = 0.74$, $P = 0.001$ respectively; Tables 1-2). Conversely, for the Curva pack we found a hierarchy which was not significantly linear (Improved linearity test: $h' = 0.58$, $P = 0.09$). However, since there were no dominance reversals in this hierarchy (Table 3), the lack of transitivity was certainly due to missing interactions between some individuals. The hierarchy of the

Piazza pack was perfectly linear although it contained just three dogs that were not enough to reach a statistical level of significance (Table 4).

Individual variation in leadership

The general linear model of the variable “leadership score” for the Corridoio pack was significant and showed a very good fit ($R^2 = 0.86$, $F_{3, 23} = 45.62$, $P < 0.0001$). Among the independent variables considered dominance rank had the most significant effect (*coefficient* = 0.32 ± 0.06 , $T = 5.66$, $P < 0.0001$): the higher was a dog’s social status, the more frequently such dog behaved as leader (Figure 4a). Leadership was also positively and significantly affected by the proportion of group companions by which each dog received muzzle-licking (*coefficient* = 0.53 ± 0.17 , $T = 3.17$, $P = 0.004$; Figure 4b). Gender had also a significant although weaker effect: females led more frequently than males when the rank and the number of greeting partners were kept equal (*coefficient* = 0.057 ± 0.02 , $T = 2.37$, $P = 0.027$).

The general linear model of leadership score developed for the packs studied during the second part of the study was also significant ($R^2 = 0.62$, $F_{1, 21} = 34.78$, $P < 0.0001$) and showed that the proportion of companions by which each dog received muzzle licking was, this time, the only significant predictor variable (*coefficient* = 0.60 ± 0.10 , $T = 5.90$, $P < 0.0001$): dogs which were greeted by many partners behaved more frequently as leaders (Figure 5).

When we replaced muzzle-licking received with tail-wagging received, the general linear models were still significant and yielded quite similar results, although the goodness of fit (R^2) decreased slightly. Tail-wagging received was a less significant predictor of leadership than dominance and gender in the first part, but was the only positive and significant predictor in the model referring to the second part of the study.

Finally, leadership scores of 13 dogs that were studied during both phases of the research were not significantly correlated ($r_P = 0.21$, $P = 0.49$).

DISCUSSION

In this study we have found that in feral dog packs leadership during activity changes was not concentrated on a single individual. Every adult and subadult individual within a given pack could successfully initiate a collective movement involving a minimum of three animals, whereas dogs younger than one year rarely succeeded in doing so. However, in all packs studied, but the smallest, some individuals behaved as habitual leaders (i. e. they behaved more frequently as leaders than they behaved as followers) and other as habitual followers. In the two packs for which testing was possible, the distribution of leadership among individuals was significantly different from an even one. Thus, consensus decision making in feral dogs may be characterized as “partially shared” according to the terminology introduced by Conradt & Roper (2005). Nevertheless, unlike other species which seem to fit such definition (e. g. spotted hyenas, *Crocuta crocuta*, and lions, *Panthera leo*, in which most decisions about group travelling direction are taken by females; Schaller 1972; Holekamp et al. 2000) in feral dogs there was not an easily recognizable specific demographic subset which contributed to most group decisions but, rather, the individual probability to lead the group increased linearly with the dominance rank and the number of greeting partners.

Another indication that a limited number of individuals, usually, contributed to the decision making process may come from the general pattern of communication observed among group members during activity changes. It has been suggested that the more numerous are the individuals involved in the decision process and the more communication signals are likely to be needed to coordinate the movement (Leca et al. 2003). Thus, many species have evolved specific vocalizations and intention movements to signal the willingness to depart and increase the probability of recruiting followers (e. g. several primates, Boinski 2000; dwarf mongooses, Rasa 1987; domestic geese, *Anser domesticus*, Ramseyer et al. in press). However, there was not obvious signal used by the dogs in our population to signal the intention to depart; rather an individual started moving in a given direction and the companions could adhere or not to the proposition. A

female sometimes barked upon initiating movements as if she was trying to draw the attention of potential followers but this was not the typical pattern. However, initiators often gave glances backwards to companions until all the pack eventually began to follow or sometimes came back if were not followed by anyone. Habitual leaders were often the first dogs that aroused when all the pack members were resting and many other members began to arouse immediately after as if they were carefully attending the leaders' activities.

Although the number of packs studied is too small to fully evaluate the effect of group size on the distribution of leadership between individuals, some indications are provided by the comparison of the pattern observed in the Corridoio pack during the first and the second phase of the study. There were six habitual leaders in such a pack during a period when its size ranged from 40 to 25 individuals, whereas there was just one single habitual leader in the same pack at the time when its size was 8-12 individuals. This result may provide some support for theoretical models predicting that shared decision making would be more likely to occur in relatively large groups based on the argument that a single despot should invest less energy in enforcing a decision than many subordinates together should invest in resisting (Conradt & Roper 2003, 2007). It is noteworthy, however, that even in dog packs where leadership was more unevenly distributed (e. g. Corridoio pack II) we have never observed coercion in form of herding of subordinates as occur in baboons (Kummer 1968; Byrne et al. 1990) or in equids (Rubenstein 1994). Nevertheless, it remains theoretically possible that dominants could manipulate subordinates' behaviour using more subtle means such as punishment.

Since the assessment of leadership in both the Curva and the Piazza pack was based on a smaller data set, any conclusion should be considered much more cautiously. In the Curva pack the pattern of consensus decision making appeared to be quite similar to that found in the Corridoio pack II with just one habitual leader (after the dispersal of one male, his role as predominant leader apparently was taken over by a female) and other individuals leading group activity changes occasionally. Conversely, in the Piazza pack, that was the smallest group studied comprising just 3 individuals for

most of the study period, two males with a clear dominant-subordinate relationship were equally likely to initiate group movements whereas a female often lagged behind almost certainly because was in poor physical condition.

The Corridoio pack that we have studied during the first part of this research was one of the largest canid packs ever observed. Its size was close, for example, to that of the largest wolf packs observed in the wild that comprised about 30-40 individuals (reviewed in Mech & Boitani 2003). Although we lack information about the optimal size of dog packs (the size that maximize the average fitness of individual members, Sibly 1983), such group was presumably above optimal size and also included animals belonging to different age-sex classes which, conceivably, differed with respect to their optimal activity budget. These are exactly two among the most important conditions favouring the evolution of equally shared decision making according to the game theoretical model developed by Conradt & Roper (2007). Since group size above optimal decrease the benefits of group-living and, since group heterogeneity acts to increase consensus costs to group members, both the conditions should destabilize group cohesion. Also, equally shared decision making appears to be of great importance for the evolution of stable social groups (Conradt & Roper 2007). However, we have shown in this study that consensus decisions were not equally shared in such large group and this may indicate that equally shared decisions making may not be the only possible evolutionary stable strategy played by a population in which groups are close or above optimal group size. It may be argued that domesticated animals such as dogs may not represent an evolutionarily stable population due to the effects of artificial selection (Maynard Smith & Parker 1976). Moreover, the strategy played will also depend on the population starting point. Since domestic dogs descended from wolves (Vilà et al. 1997), it seems plausible that they have inherited and still to a large extent retain the pattern of group decision making of their wild ancestors. However, there are some important differences between the social organization of wolves and that of feral dogs. For instance, Mech (1999) emphasized that the social structure of most wolf packs is not properly described as a dominance hierarchy but, instead, as a family including a breeding pair

and their offspring of the previous years. According to this view, breeding wolves lead group activities simply because offspring tend to follow their parents' initiatives (Mech 1999; 2000). In comparison to wolves, dog packs comprise several adult breeding females (Macdonald & Carr 1995; Pal et al. 1999; Cafazzo 2007) and those of our studied population, in particular, included adult offspring of the previous years and showed a linear dominance hierarchy which predicted access to resources (Cafazzo 2007; this study). Perhaps the social structure of dogs and their leadership pattern might be more easily compared to those of the few wolf packs which include multiple breeders, and in which an actual distinction could be made between dominant and subordinate breeders. Data on collective movements in such large wolf packs seem to confirm that social dominance is the strongest predictor of leadership during travelling and foraging (Peterson et al. 2002). Moreover, the highest frequency of leadership by subordinate breeders and nonbreeding wolves has been recorded in the largest of the packs studied which included 14-23 animals (Peterson et al. 2002). Thus, the results in wolf packs with multiple breeders appear to be similar to those we have found in dogs with respect to both the relationship between leadership and dominance and the less uneven distribution of leadership in larger groups.

A weak but significant effect of gender on leadership was found in the Corridoio pack during the first part of the study, in that females led more than males when dominance rank and the number of greeting partners were kept equal (females tend to be subordinate to males in dog packs, see Tables 1-4). The fact that we did not find such an effect of gender in the second part of the study, when most females were sterilized, suggest that higher leading may be linked to female reproductive state and, in particular, to the need of pregnant females to initiate travelling to reach first feeding locations (lactating females typically did not travel together with the rest of the pack possibly due to high consensus costs at that time). Three females for which we have sufficient data had, indeed, a higher leadership score during pregnancy if compared to non-reproductive periods.

In wolves the tendency to lead by females seem to decrease during pregnancy (Peterson et al. 2002). However, in comparison to female wolves, female dogs receive typically a much more

limited assistance by the males during the reproductive periods (Pal 2005) and, thus, their energetic requirements may be particularly demanding.

Relationship between leadership and greeting ceremonies

In this study we have found that the number of partners from which active submission was received during greeting ceremonies was a significant predictor of leadership, together with dominance rank, during the first part of the study and was the only significant predictor in the second phase. Thus, it seems that, altogether, active submission received during greeting was a more consistent predictor of leadership than dominance rank itself throughout the study period. Also, among the behavioural patterns displayed during greeting ceremonies muzzle-licking received functioned better than tail-wagging received as predictor of leadership. Muzzle-licking is a behavioural pattern ontogenetically derived from the food-begging behaviour of puppies (Schenkel 1967) and, indeed, “following a leader” may also be traced back to a situation of an infant following the mother: thus, “muzzle-licking” and “following” may be both ontogenetically and functionally linked.

Active submission by subordinates appears to confirm the asymmetry in social status between greeting partners (de Waal 1982; de Waal & Luttrell 1985; East et al. 1993; Wittig & Boesch 2003) and imply a friendly disposition by the dominant animals in favor of the social integration of the subordinates (Schenkel 1967). Greeting may, thus, provide a mechanism whereby individuals of different social status resolve conflicts within the group (East et al. 1993) and, since both conflict-resolution mechanisms and leadership should promote group cohesion in social animals, an association between these two variables does not seem surprising. Thus, one interpretation of our results is that dogs which habitually behaved as leaders were high-ranking individuals with which subordinate followers had developed strong social bonds. In this study, there were high-ranking dogs which were not greeted by companions and rarely, if at all, behaved as leaders. This results support the view that collective movements in highly social species, such as the domestic dog, may result from the effort of individuals which are more in need of social support to maintain close

proximity with specific valuable social partners (high-ranking individuals and/or kin) with which, in turn, have developed affiliative relationships.

About the kind of social support that would be needed by followers, it is well known, for instance, that affiliative behaviour may promote cooperative relationships between individuals in order to compete jointly against opponents both within their own group and against other groups in primates (Seyfarth & Cheney 1984; Wilson et al. 2001) and carnivores (de Villiers et al. 2003). In feral dogs cooperation in conflicts against other packs is common (Bonanni et al. submitted); coalitionary support in intra-pack agonistic interactions also occurs and association indexes (which are a good measure of affiliative relationships, Hill & van Hooff 1994) between coalition partners are significantly higher than those between coalition partners and the targets of the coalitionary attack (Bonanni et al. unpublished).

To ascertain whether and to which extent social bonds between leaders and followers may provide an explanation of the proximate mechanisms underlying consensus decision making in social animals more data will be obviously needed. Up to now, few studies have provided quantitative data on both leadership and affiliative relationships within social groups. However, some support for the above presented hypothesis may come from the following examples: in typical wolf packs both the members of the breeding pair share leadership and are the focus of greeting by their offspring (Mech 1999); in dwarf mongooses males compete to groom the dominant and leader female (Rasa 1987); in domestic geese it seems that leaders recruit a higher number of followers when they have a higher number of neighbours before departures and these are their preferential association partners (Ramseyer et al. in press); in chacma baboons lactating females often follow the movements of specific males with which they have developed a friendly relationship and which presumably may protect their offspring from infanticidal males (Stueckle & Zinner 2008; see also Byrne et al. 1990). In an influential paper Wrangham (1980) pointed out that among female-bonded primate species (in which females are the philopatric sex) females are often more influential than males in determining group movements, whereas males control more group movements in non

female-bonded species (in which males are the philopatric sex). This has sometimes be related to the fact that the philopatric sex has a knowledge of the home range which is superior to that of the immigrant sex (Erhart & Overdorff 1999; Leca et al. 2003). However, an alternative explanation for this pattern is that, since intrasexual social bonds are stronger among females in female-bonded species and among males in non-female bonded species (Wrangham 1980), individuals belonging to the sex with the higher number of affiliative partners may be those which affect more group movements.

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Table 1. Corridoio pack: submissive interactions.

Dogs	MER	GAS	PIP	LEO	GOL	LAN	MAM	NAN	ISO	DIA	SIM	PON	SEM	KIM	MOR	STE	CUC	DOT	GON	MAL	HAN	GRE	BRO	EOL	EMY	MAG	PIS	Totp
MER																												0
GAS	95																											95
PIP	37	49																										86
LEO	13		3																									16
GOL	23	13	10	6			1		2		3		1															59
LAN	7	10	14		5																							36
MAM	5	2	5	1	1	3		1					1															19
NAN	8		1				3																					12
ISO	2	2	1		3	5	1	2																				16
DIA	1				1				1				10	1														14
SIM	59	32	25	16	19	18	8	6	1	3		12				1												200
PON	14	30	26	4	13	9	7	1	3	1	13		1	3	2									1				128
SEM	20	23	34		26	18	9	3	23		98	8		5	2			3										272
KIM	1	4	10	3	3	10	16	3	2		3	4	5															64
MOR	15	5	7		1	7	7	3	7			1	3	1														57
STE	11		2		2	3	10		8			1		3														40
CUC	5	4	3		5	8	16		9		5		10	9	11	2								4				91
<i>DOT</i>	12	9	2		17	30	10		12		4	1	15	2	4		9				3							130
<i>GON</i>	12	1	8	1	5	27	10		7		13	3	13	4	13		6	4		1	1							129
<i>MAL</i>	4	5	3	3	6	9	11	1	8		1	2	15		6	1	8		2								2	87
<i>HAN</i>	13	8	10	11	4	5	7	7		1	9	6		3	3	2	2	1	3							1		96
GRE	11				2	4	4	12			2	5						1		1	1							43
<i>BRO</i>	12		4		9	4	9	1	8		4	1	7	1	7	1	4	7	9	3								91
<i>EOL</i>	16	5	6	3	12	19	11	1	19		4	1	8	4	6	1	4	5	5	4	3		5					142
EMY	2				11	10	5		12		4		10		4	2	1	1	2	1	1		2	7				75
MAG	3	4	1		3	11	8		15		3	1	33	2	3	1	2	4	1						11			106
PIS	6		2	3	6	5	11	3	8			2	8	2	7		2	1	1	4	1	1	2	5				80
Totr	407	206	177	51	154	205	164	44	145	5	166	48	140	40	68	11	38	27	23	17	12	1	9	26	0	0	0	

Bold type: females; standard type: males; italic type: juveniles

Totp = total submissions performed, Totr = total submission received

Table 2. Corridoio pack II. Submissive interactions.

Dogs	GOL	DOT	LAN	MAM	ISO	GON	EOL	BRO	SAS	MON	MAG	Totp
GOL			2							1		3
DOT	4											4
LAN	4	1										5
MAM	1			1								2
ISO	1											1
GON	2	36	2									40
EOL	6	5	5	3			1					20
BRO	5	13	6			2	29					55
SAS	2	2	2	1			1	4	1		1	14
MON	3	3		1			1	3	2	5		18
MAG	17	2	5	1	6			2		1		34
Totr	45	64	21	6	8	32	9	3	7	1	0	

Bold type: females; standard type: males

Totp = total submissions performed, Totr = total submission received

Table 3. Curva pack: submissive interactions

Dogs	GAS	MOR	MUS	NER	JOS	FRA	DAN	PAS	GIO	Totp
GAS										0
MOR	1									1
MUS	2	1								3
NER	1	4								5
JOS	1	7	14	1						23
FRA		3	1			2				6
DAN	1	1	3	2	2					9
PAS		3				2				5
GIO		6		5	3	1				15
Totr	6	25	18	8	9	1	0	0	0	

Bold type: females; standard type: males; italic type: juveniles

Totp = total submissions performed, Totr = total submission received

Table 4. Piazza pack: submissive interactions

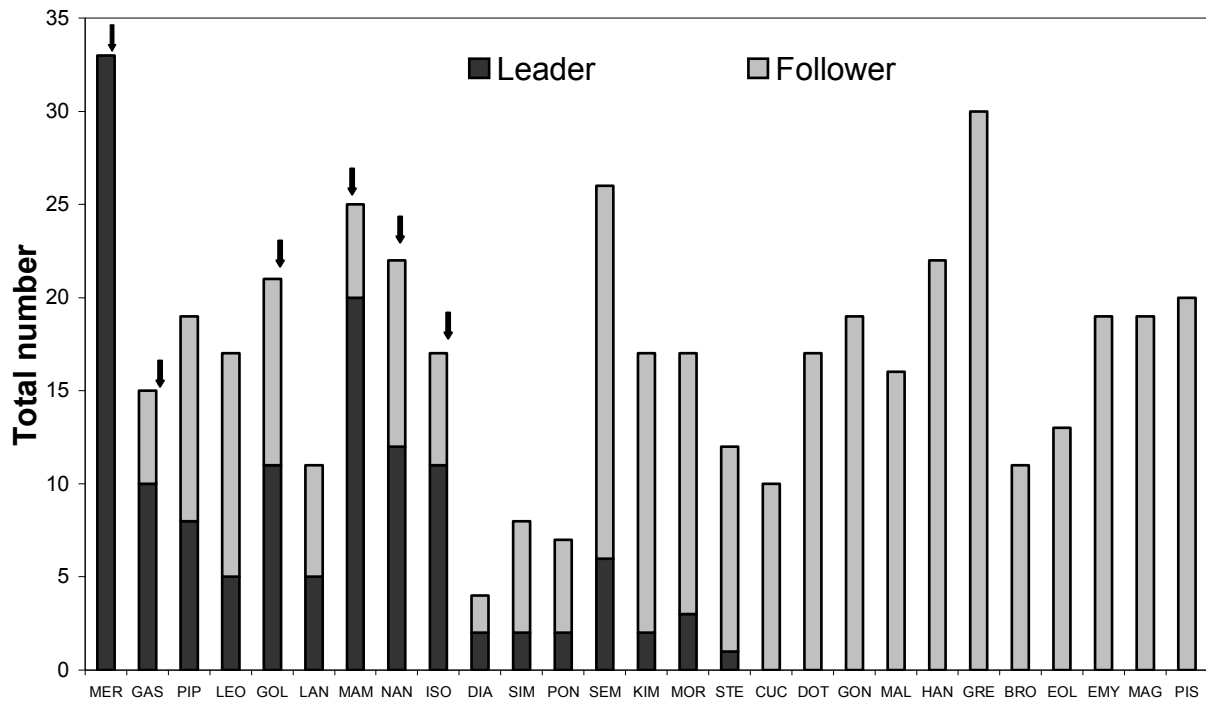
Dogs	MAT	OTT	STE	Totp
MAT				0
OTT		13		13
STE		4	1	5
Totr		17	1	0

Bold type: females; standard type: males; italic type: juveniles

Totp = total submissions performed, Totr = total submission received

Figure 1. Corridoio pack: total number of events in which each dog behaved as leader and follower respectively during the first (a) and the second (b) phases of the study. In (a) all individuals from CUC to PIS are juveniles. Black arrows indicate habitual leaders.

(a)



(b)

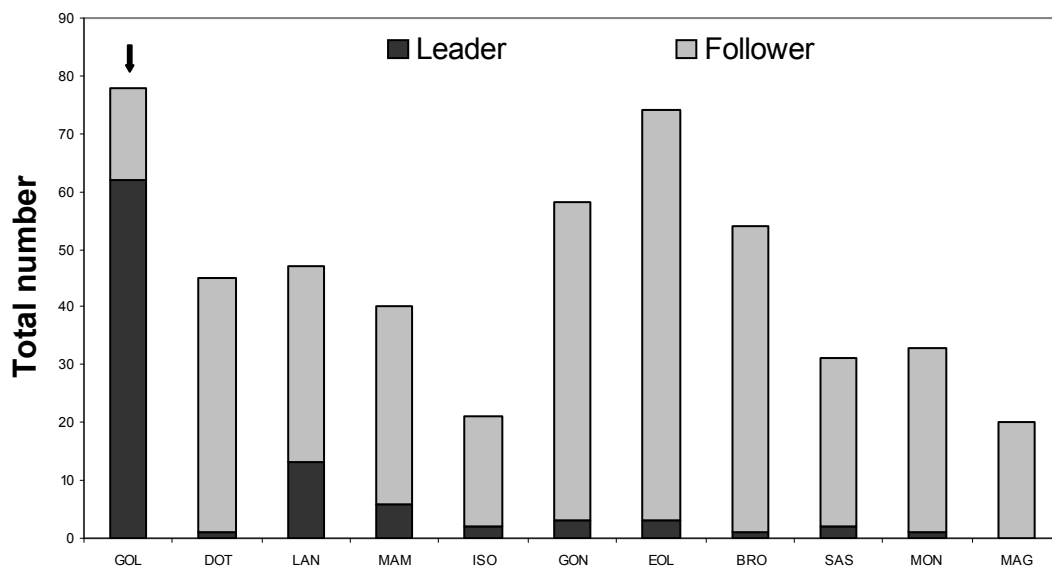
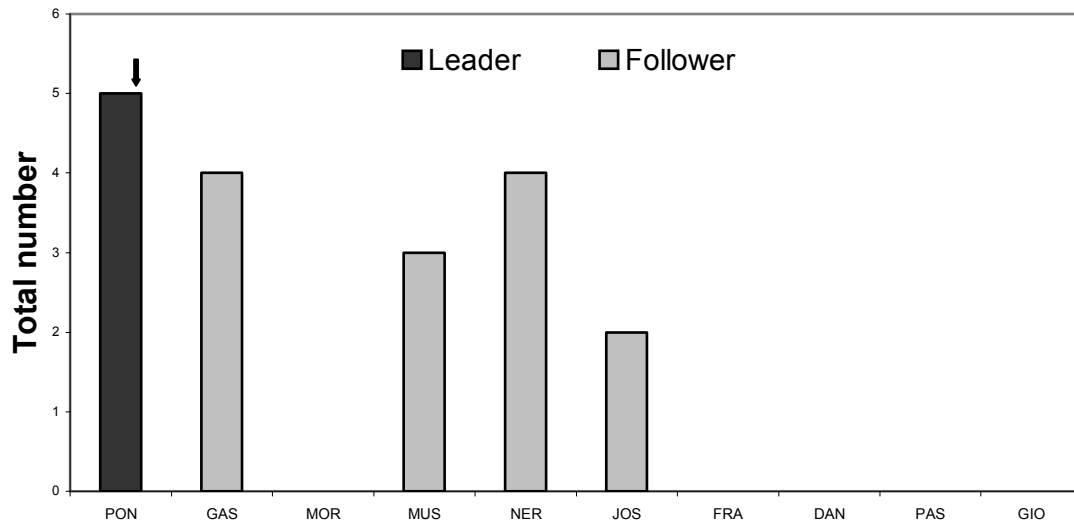


Figure 2. Curva pack: total number of events in which each dog behaved as leader and follower before (a) and after (b) the dispersal of the male PON. All individual from FRA to GIO are juveniles. Black arrows indicate habitual leaders.

(a)



(b)

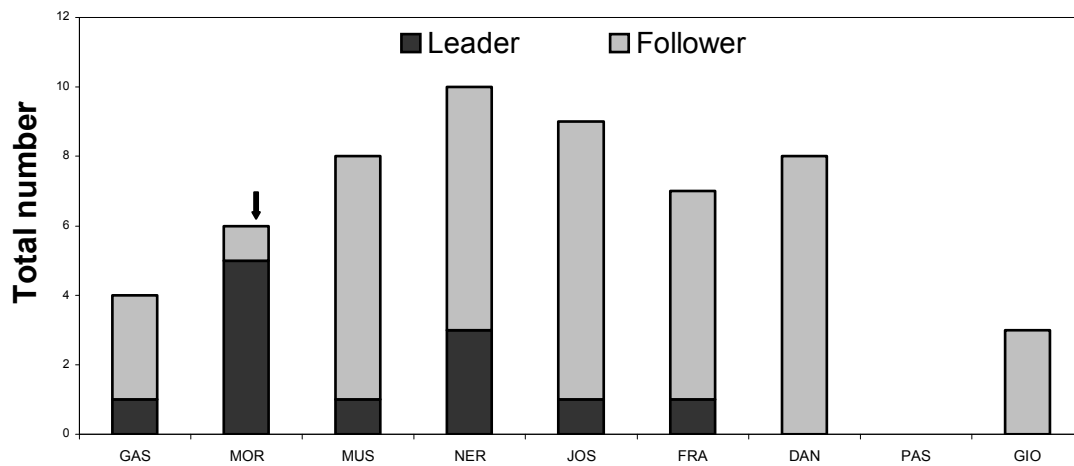


Figure 3. Piazza pack: total number of events in which each dog behaved as leader and follower

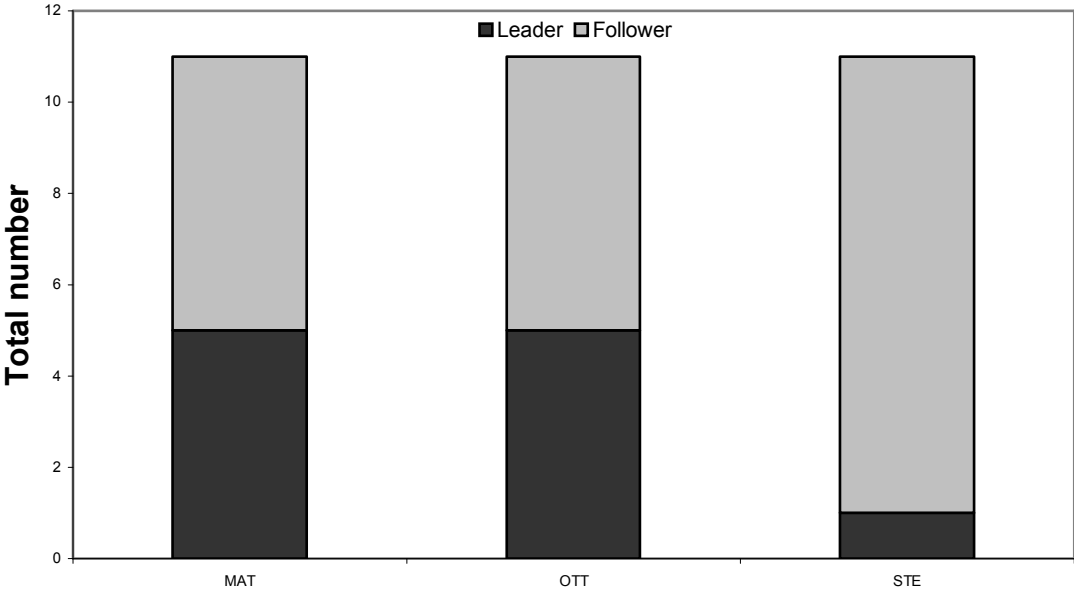
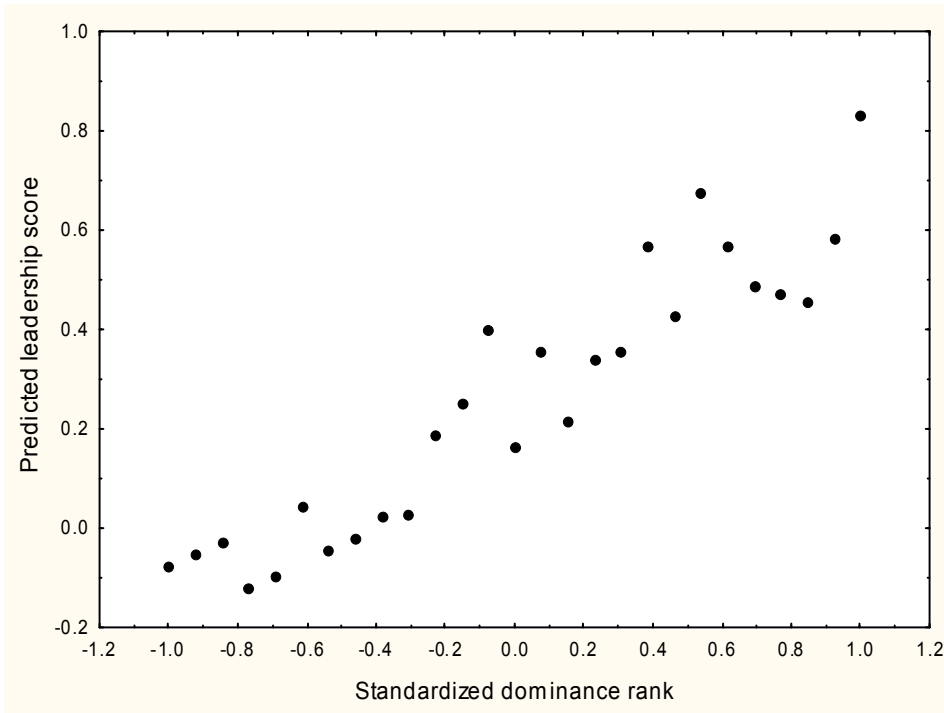


Figure 4. Corridoio pack: predicted leadership in relation to standardized dominance rank (a) and proportion of group members from which each dog received active submission in greeting ceremonies (b).

(a)



(b)

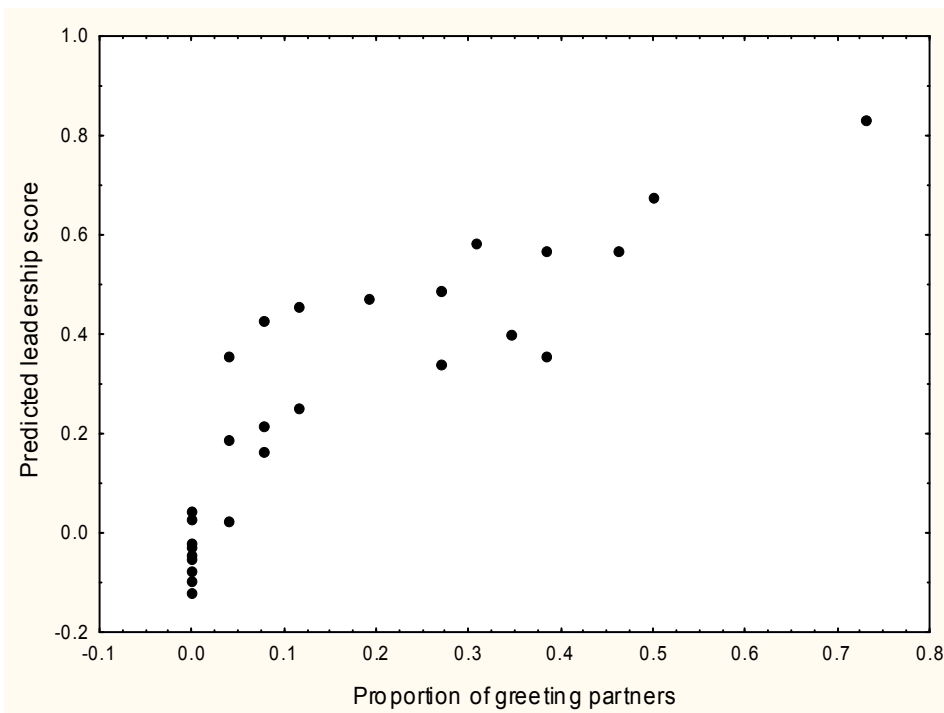
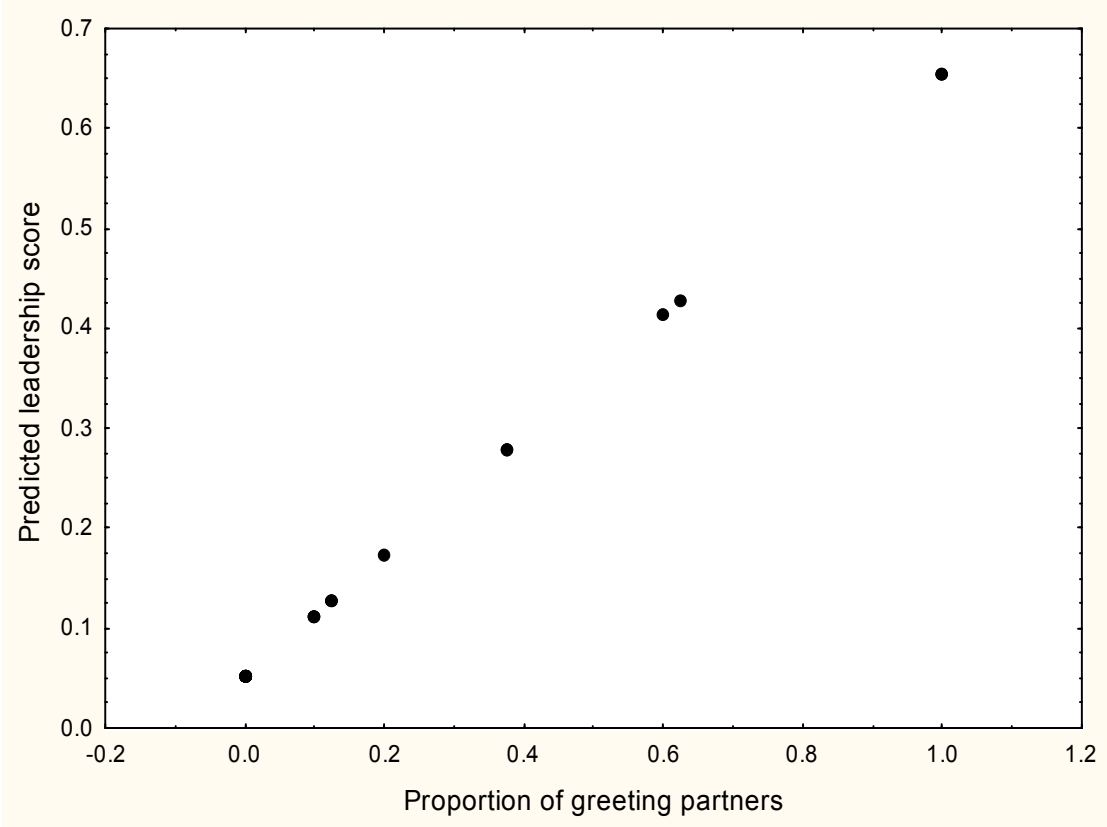


Figure 5. Predicted leadership score in relation to proportion of group members from which each dog received active submission in greeting ceremonies: dogs of all packs studied during the second phase of the study.



**3. Patterns of individual participation and cheating in conflicts
between groups of feral dogs (*Canis lupus familiaris*).**

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ABSTRACT

Cooperative intergroup aggression provide an example of a costly cooperative behaviour whose benefits spill over non-cooperative animals as well. Consequently, investigating factors which promote individual participation in intergroup contests should prove useful in order to understand how cooperation may persist in animal societies despite cheating. Here, we examined variables affecting individual participation in naturally occurring conflicts between groups of feral dogs, highly social carnivores which are much more abundant and accessible than their wild counterparts. The study focused on three packs, ranging in size from 3 to 11 individuals, and the analysis was based on 198 intergroup conflicts. The overall proportion of cooperating animals decreased significantly with increasing the number of group companions, while keeping the number of opponents equal. In one pack, the individual probability of active participation decreased significantly in case such pack had a numerical advantage over opponents. Dogs belonging to the smallest pack tended to be more cooperative than those belonging to larger groups. Social prestige (measured as the amount of active submissions received) did not appear to be a consequence of cooperative behaviour. Individual variation in cooperation was mainly accounted for by variation in the number of affiliative partners. Young and high ranking dogs tended to cooperate more when their group was outnumbered by opponents but did not stay at the front of the pack during conflicts. These results emphasize the greater opportunity for cheating in larger groups and the importance of both mutualistic benefits and affiliative relationships in promoting cooperation.

Keywords: natural intergroup conflicts, cooperation, cheating, mutualism, handicap principle, affiliative relationships, *Canis lupus familiaris*

INTRODUCTION

In animal social groups, cooperation has been broadly defined as a joint action by two or more individuals which is carried out to achieve a common goal (reviewed in Boesch & Boesch 1989). Since cooperative behaviour is usually costly to group members which actively participate into the collective action and the resulting benefits may often spill over group members which have not participated, from an evolutionary standpoint cooperation may be destabilized by the threat of “cheating” (or “free-riding” or “defecting”); (Dugatkin 1997; Nunn 2000; Nunn & Lewis 2001). So one of the central questions in behavioural biology remains how cooperation in animals could evolve and remain stable despite the fact that some individuals can benefit more by exploiting other individuals’ cooperative actions and avoiding to pay any costs, than they would benefit by cooperating.

Several evolutionary mechanisms have been supposed to stabilize cooperation in animal societies: in kin selection (Hamilton 1964; Lehmann & Keller 2006), cooperation is stable in case the recipients of the benefits of the cooperative actions are close relatives of the cooperating individuals and even if such recipients do not incur the costs of such cooperative actions; in mutualism (Mesterton-Gibbons & Dugatkin 1992; Clements & Stephens 1995; Lehmann & Keller 2006), cooperation pays more than defection in terms of fitness and thus individuals cooperate to gain immediate individual benefits that outweigh the costs paid; in reciprocal altruism, or reciprocity, (Trivers 1971; Axelrod & Hamilton 1981; Olendorf et al. 2004), cooperation may be stable in repeated interactions between the same individuals if they play a strategy such as “tit for tat” (always cooperate during the first interaction and then retaliate against cheating by withholding further cooperation); finally, in the handicap principle

(Zahavi & Zahavi 1997; Roberts 1998; Lotem et al. 2003), individuals are supposed to gain social prestige, and thus to increase their direct fitness, by cooperating.

Free-riding is expected to undermine cooperation especially in sizeable groups where reciprocity is much less likely to evolve (Boyd & Richerson 1988, 1992) and relatedness between group members is usually lower (Frank 1995). Moreover, Nunn (2000) and Nunn & Lewis (2001) pointed out that even mutualistic benefits may be limited as groups become larger given that a smaller proportion of group members would be required to provide efficiently a collective good, thus leading to some level of free-riding.

Cooperation during intergroup conflicts in social species provides an example of a cooperative behaviour which is costly to participants, because it involves considerable expenditure of energy and risk of injury, and which often results in benefits to both cooperating and non-cooperating group members in terms of increased access to contested resources (Nunn & Deaner 2004). These are exactly the conditions under which cheating is expected to destabilize cooperation and, consequently, it is important to understand which factors may explain individual variation in cooperation and cheating in intergroup conflicts. Studies investigating patterns of individual participation and cheating in cooperative intergroup aggression have often carried out experiments using playbacks of recorded intruders' vocalizations to simulate territorial intrusions (e. g. lions, *Panthera leo*, Grinnell et al. 1995, Heinsohn & Packer 1995, Heinsohn et al. 1996; chimpanzees, *Pan troglodytes*, Wilson et al. 2001; black howler monkeys, *Alouatta pigra*, Kitchen 2004) or have studied animals living in semi-free ranging conditions (e. g. ringtailed lemurs, *Lemur catta*, Nunn & Deaner 2004) due to the rarity of natural intrusions. All of these studies have documented consistent individual differences in the extent of active participation in intergroup conflicts.

For instance, in a very influential study, Heinsohn & Packer (1995) concluded that female lions could be classified according to four different cooperative strategies: “unconditional cooperators” which always lead the group response to the simulated territorial intrusion (stay at the front of the group thus bearing the costs of fighting); “unconditional laggards” which always stay at the rear of the group, thus avoiding the risks of fighting; “conditional cooperators” which lead only when the group is outnumbered by the simulated opponents, that is when their cooperation is most needed; and “conditional laggards” which lag even farthest when their group is outnumbered. The authors suggested that “leaders” and “laggards” (or “cooperators” and “free-riders”) may coexist in a mixed evolutionarily stable strategy. Such individual variation was not explained by variables such as body size (a measure of fighting ability), age or kinship but it could have been related to differences in temperament with “bold” animals at the front of the group and “shy” individuals at the rear.

However, in other species individual variation in the level of cooperation may be explained by asymmetries in the benefits accrued from an intergroup conflict and in the costs incurred (Nunn 2000; Nunn & Lewis 2001; Nunn & Deaner 2004). For instance, in species with dominance hierarchies high-ranking individuals often enjoy priority of access to resources (food and mates), and thus may be more motivated than subordinates to defend such resources against opposing groups, or, alternatively, may simply experience fewer costs of fighting strangers due to their better fighting ability (Nunn 2000; Nunn & Lewis 2001; Nunn & Deaner 2004).

Further insights on the factors underlying individual variation in cooperation may come from laboratory studies which have focused on the proximate mechanisms of cooperation. Several studies on primates (capuchin monkeys, *Cebus apella*, Chalmeau et al. 1997;

chimpanzees, Melis et al. 2006; bonobos, *Pan paniscus*, Hare et al. 2007) and birds (e. g. rooks, *Corvus frugileus*, Seed et al. 2008) have shown that successful performance in solving a cooperative task by pairs of individuals (pulling two ropes simultaneously to gain access to food) is positively correlated to within pair social tolerance and affiliation as measured by the tendency to share food. Thus, if the development of affiliative relationships is a prerequisite for successful cooperation, then individual variation in cooperation within social groups may be partly explained by how many affiliative partners each individual has within the group.

In this study, we investigated the mechanism underlying cooperation and the pattern of individual participation and defection during conflicts between groups of feral dogs (*Canis lupus familiaris*) ranging in size between 3 and 11 individuals. Unlike most previous studies on cooperative intergroup aggression (see above) we did not use playback experiments to simulate intrusions but, instead, exploited the abundance and accessibility of dogs to record naturally occurring conflicts and assessed individuals' contribution on the basis of a much higher number of interactions if compared to playback studies.

Feral dogs are those domestic dogs which are not socialized to human beings (Daniels & Bekoff 1989a). In areas where they have access to abundant food resources directly or indirectly provided by humans they live in packs constituted by multiple breeding males and females which are highly cooperative in conflicts against strangers (Font 1987; Daniels & Bekoff 1989a, b; Macdonald & Carr 1995; Boitani et al. 1995; Boitani & Ciucci 1995; Pal et al. 1998; Cafazzo 2007). Although their morphology, physiology and behaviour have been modified during domestication (Clutton-Brock 1995, Coppinger & Schneider 1995), they still exhibit a complex social organization with a hierarchical structure which predict intrapack access to resources (Cafazzo 2007). Also, they seem to be able to assess relative group size in

intergroup conflicts and to adjust their intergroup agonistic behaviour according to the odds of winning, meaning that they are more likely to attack opposing groups the lower the ratio of the number of opponents to that of companions (Bonanni et al. submitted a).

Here, we first tested whether some of the evolutionary mechanisms assumed to stabilize cooperation in wild species may apply to domesticated animals such as feral dogs, and assumed that every adaptive behaviour observed in dogs in the context of conflicts against conspecifics would have evolved in wolves (*Canis lupus*), that are the dogs' wild ancestors (Vilà et al. 1997), before domestication.

We expect that if cooperation during intergroup conflicts in dogs is based on mutualism, then individuals dogs should be more likely to participate in conflicts when the individual benefits of cooperating are higher, that is when the participation of an additional animal is likely to increase substantially the probability of winning. Consequently, we predict that: individuals should be more likely to cooperate when attacking an opposing pack which outnumber their own pack in comparison to when attacking an opposing pack which is smaller than their own pack; the proportion of cooperating animals should increase when the aggressive behaviour is directed towards larger packs (or should decrease when the aggressive behaviour is directed to smaller packs); individuals belonging to smaller packs should be on average more cooperative than those belonging to larger packs.

Moreover, we predict that if cooperation in dogs is based on the handicap principle, then the amount of social prestige obtained by each individual (defined as the degree to which dominance rank is recognized by companions, Zahavi & Zahavi 1997) should be positively correlated with the amount of costly cooperative behaviour performed, i. e. cooperation

during conflicts against larger packs and frequency of staying at the front of the pack during conflicts.

As regards reciprocity, a rigorous test would require that animals do not exchange informations about their choice of cooperating or defecting during each round of an Iterated Prisoner Dilemma (Legge 1996; Noe 2006). However, since we believe that such condition is unlikely to be fulfilled in natural intergroup conflicts among feral dogs, during which group members have the possibility to communicate extensively with companions, we do not further consider reciprocity in this paper.

Subsequently, we attempted at explaining individual variation in cooperative behaviour during intergroup conflicts using variables such as dominance rank, leadership, age, gender and number of affiliative partners. Finally, we checked whether individual dogs modified their level of active participation in conflicts in which their own pack was outnumbered by opponents, as observed in female lions (see above).

MATERIALS AND METHODS

Study Area

The research was carried out in a sub-urban environment sited in the south-west periphery of Rome (Italy), an area traditionally called “Muratella”. The study area has a total surface of about 300 hectares and is delimited to the north, west and south sides by roads with heavy traffic and to the east side by cultivated areas. The area is crossed by another road which represents the main connection between the two more important lines in the south and in the west and that, at the same time, split the study area in two different sectors one in the south-west part and another in the north-east. The south-west sector is quite urbanized although not

densely populated. It contains a recently built residence, a hotel, three large buildings with offices, four parking areas and an erecting yard. The north-east sector is mainly occupied by a natural reserve called “Tenuta dei Massimi”. The habitat in the reserve consists mainly of open grasslands, which are periodically ploughed, with interspersed wooded areas (*Quercus cerris* and *Quercus suber* were the prevailing plant species). Wild animals commonly observed in the reserve includes: pheasants (*Phasianus colchicus*), black kites (*Milvus migrans*), kestrels (*Falco tinnunculus*), herring gulls (*Larus argentatus*), carrion crows (*Corvus corone cornix*), green whipsnakes (*Coluber viridiflavus*), rats (*Rattus* spp.), crested porcupines (*Hystrix cristata*) and red foxes (*Vulpes vulpes*).

Feral dogs had free access to virtually every part of the study area. They used the reserve mainly to find resting sites, refuges and dens for puppies into the dense vegetation of the wooded areas. However, they frequently approached the central road crossing the study area, especially in the very early morning to feed on the food brought by volunteer dog caretakers. Food mainly consisted of pieces of meat taken in a slaughter-house, was placed, together with water, at some specific feeding sites all of which were virtually sited in the close vicinity of the road.

Animals and packs' history

This study was part of a longer research project begun in April 2005 on the dog population living in the study area that consisted of about 100 animals. All dogs were medium-large sized mongrels and there was not a recognizable predominant breeding type (Cafazzo 2007). Dogs which travelled, rested and defended resources as a cohesive unit (Cafazzo 2007), thus fitting the definition of canid pack (Mech 1970), were considered as belonging to the same group.

With very few exceptions, dogs were not sociable to humans although they appear to be completely dependent on humans for food provision. The food provided by humans was abundant and it did not appear to be a limiting factor.

The studied populations was subject to control-management by the Rome Municipality which periodically trapped the animals, sterilized them and then released them back in the area. However, at the time when this research was conducted there were still many intact animals in the population. All the neutered dogs in the studied packs which we included in the analysis of individual cooperative behaviour were sterilized between 6 and 12 months before the initiation of the study (see details below).

This research focused mainly on three of the eleven packs living in the area during the period May 2007-September 2008. These were selected because lived in a sector of the study area characterized by many wide open spaces and good observational points from which variables concerning intergroup interactions could be reliably recorded.

All individuals belonging to the studied packs were individually recognized on the basis of coat colour pattern and size, and sexed on the basis of genital morphology and body posture during urine-marking (males raises their hind leg higher than females; Bekoff 1979).

We defined adult dogs as those which were at least two years old, sub-adult dogs as those that were between one and two years old and juveniles as those that were younger than one year (see more details on age estimation below). Age was precisely known for individuals that were born not before 2005, whereas all dogs born before that date were fully adult at the time when this research was conducted.

At the beginning of this study (May 2007) the “Corridoio pack” comprised 11 adult and subadult individuals: 4 intact males, 2 neutered males, 2 intact females and 3 neutered females.

The “Curva pack” consisted of 6 adult and subadult individuals (1 intact female, 4 intact males and one neutered male) and 4 juveniles (3 females and 1 male). One month after the beginning of the study one of the males dispersed.

The “Piazza pack” included 4 adults and subadults individuals: 1 intact male, 1 neutered male and 2 neutered females both of which died during the course of the study.

In November 2007 the composition of the Curva pack changed, in that its members were joined by another pack consisting of 4 intact adult males and 2 intact adult females, and formed what we called the “Fused pack”. Between November 2007 and March 2008 two adult males and three adult females of this group were sterilized by the Rome municipality. Given that sterilization seems to cause a decrease in aggression and marking behaviour in dogs (Maarschalkerweerd et al. 1997), changes in the dominance relationships and periods of social instability were highly expected in this pack. For this reason we did not analyse the behaviour of the Fused pack at individual level. However, we carried out an analysis at group level in which we checked whether the behaviour of the Fused pack during intergroup conflicts was different from that of the other packs, whose members were not sterilized during the course of the study, by including pack identity as a factor in a general linear model (see more details below).

Behaviour during intergroup conflicts and variables measured

Observations on dogs’ behaviour were conducted daily usually between 0600 hours and 1700 hours to cover, when possible, all the daylight period. To locate the dogs we walked on foot

along a circuit and tried to observe each group on a rotational daily basis when possible. Upon locating a pack we first recorded the group composition, that is which individuals belonging to that pack were present at that time (sometimes the packs splitted and group members were not found all together at any time), and monitored continuously group composition. Dogs were observed from distances ranging between 20 and 150 meters using a 10 x 50 binocular. If two packs were located within a few hundreds meters (or less) of each other so that we could reasonably expect an intergroup conflict between such packs to be imminent, we selected an observational point from which the behaviour of both packs and their composition could be recorded. Such observational point was always more elevated than the location where the conflict was expected to occur unless the dogs were so near to the observer that he could easily follow them on foot during their movements. Interactions were recorded ad libitum (Altmann 1974).

We assessed group size during intergroup conflicts on the basis of the number of adult and subadult individuals that were within 50 meters of each other at the time when an intergroup conflict began. In practice, most dogs were often within 1-10 meters of the nearest companion during resting and interindividual distance tended to further decrease during attacks against opposing groups. We recorded the cooperative agonistic behaviour of all adults, subadults and juveniles belonging to the two interacting packs. Distances were estimated visually by comparison with the measured distances separating several topographic landmarks.

An individual dog was defined as actively participating into an intergroup conflict (or “cooperating”) if it approached opponents aggressively by moving forward at least 10 meters when the distance separating opposing packs at the time when the conflict initiated ranged between 20 and 100 meters, and if it simply lunged towards opponents in case the distance

separating opposing packs was less than 20 meters. Such criterion was chosen because most intergroup interactions did not involve aggressive physical contact (with bites and/or scratches) but consisted of threatening displays in which group members ran together towards the opponents by barking furiously and snarling or walked towards opponents with a tense body posture by staring and keeping the tail raised. We recorded a dog as “cooperating” even if it was the only individual of its pack to behave aggressively toward opponents. Although our definition of cooperation requires a joint action by at least two animals, we agree with Mesterton-Gibbons & Dugatkin (1992) that a single individual will behave cooperatively if it acts in such a way to render the cooperation possible, even though the cooperation will not actually be realized unless other group members also behave cooperatively.

We defined an individual dog as “defecting” if it was present within 50 meters of companions at the time when a conflict began and it did not approach aggressively opponents while at least one companion was approaching. So, there could not be defection without cooperative behaviour by at least one companion. Individuals which approached opponents after the end of the conflict and without showing signs of aggressiveness were also scored as defecting.

We defined an individual dog as “leader-conflict” if it reached a closer proximity to the opponents than all its companions during an intergroup interaction (with the next closest dog at least half body-length behind the leader), or if it was the only group member to eventually reach a physical contact with opponents. A leader-conflict was actually non-discernable in about half of the recorded interactions. This is because several of the approaching dogs often stopped moving forward roughly at the same distance from the opposing group (especially when the approaching dogs encircled a single opponent).

An intergroup interaction ended when all individuals belonging to the pack involved stopped showing signs of aggression. Two consecutive agonistic interactions involving the same packs were regarded as two different events in one of the following cases: all individuals belonging to the interacting packs returned to their original starting locations as before the interaction took place and then another one ensued; pack did not resume their original locations but at least 10 minutes elapsed between the end of the previous aggression and the beginning of the second one; less than 10 minutes elapsed but the group composition had changed in the meanwhile.

We calculated for each individual dog a “cooperation score” as follows: for each dog within its pack we divided the total number of times it behaved cooperatively by the sum of the total number of times it defected on cooperating and the total number of times it behaved cooperatively. We also calculated a “cooperation score with favourable odds” and a “cooperation score with unfavourable odds” depending on whether the cooperative aggressive behaviour was directed towards a smaller or larger pack respectively.

Finally, we calculated for each dog a “leadership-conflict score”: again, for each dog we divided the total number of times it behaved as leader during a conflict by the total number of times it was present in an interaction in which a leader was detected for that dog’s pack. This was intended as an approximate measure of the frequency of being at the front of the pack during intergroup conflicts.

Altogether, we spent in field 1147.2 hours during the period May 2007-September 2008, in which we observed 392 intergroup conflicts. We succeeded in collecting complete data about the size and the behaviour of the packs involved for 198 interactions involving the studied packs and other packs living in the area, or single individuals that were temporarily separated

from their pack, or lone dogs which were not associated to any pack. All the interactions included in the analysis concerned conflicts over food resources or conflicts occurring in absence of any obvious source of competition. Interactions were discarded whether an oestrus female was present within 50 meters of any member of an interacting pack. This was done because, usually, oestrus females were courted by males belonging to several different packs simultaneously and often more than two packs intermingled.

Assessment of dominance rank and social prestige

The assessment of dominance rank was based on the direction of submissive behavioural patterns recorded ad libitum. This included both active submissions (licking the muzzle of another dog or pushing the muzzle of the other dog with the nose) and non-active submissions (avoiding eye contact, lowering the head, lowering the tail between the hind legs, laying down on the back, yelping, fleeing, withdrawing, interruption of feeding).

For each pack, we ranked all the occurrences of both muzzle-licking and non-active submissions into squared matrices with performers on one axis and recipients on the other one. To arrange individuals into a dominance rank order that was most consistent with a linear dominance hierarchy we applied the method developed by de Vries (1998) which minimize the number of inconsistencies (dominance reversals) and the strength of inconsistencies. Such test was performed using MatMan 1.1 (Noldus Information Technology, Wageningen, The Netherlands).

In order to compare dominance rank across packs of different size, individuals were assigned a standardized rank following the procedure illustrated in East & Hofer (2001). Ranks were evenly distributed between the highest rank (standardized rank +1) and the lowest rank (standardized rank -1), with the median rank being scored as 0.

In order to measure the social prestige we used the amount of active submission received by each dog during greeting ceremonies, a behavioural pattern which conveys components of both submission and social affiliation (Schenkel 1967) and which is a strong predictor of leadership during collective activity changes in feral dogs (Bonanni et al. submitted b). Consequently, it should indicate the extent to which individuals are regarded as valuable social partners by companions. In brief, for each dog we calculated the number of companions by which it received at least one instance of muzzle-licking during greeting ceremonies and divided it by the total number of available companions in its pack to allow comparison between individuals belonging to packs of different size.

Assessment of social affiliation

Affiliative behaviour was recorded ad libitum and included the following: tail-wagging, muzzle-licking, playing, play-invitation, allogrooming and resting in physical contact. Both tail-wagging and muzzle-licking are displayed during greeting ceremonies and, although they function to confirm asymmetries in social status, they also imply a friendly disposition by the dominant animal in favour of the social integration of the subordinate and thus the establishment of a strong social bonds between the two interacting animals (Schenkel 1967). Everytime we observed an affiliative interaction between two dogs, we regarded both the interacting dogs as having an affiliative partner irrespective of the directionality of the behaviour within the dyad. We calculated an “affiliative score” for each dog as the number of its affiliative partners divided by the total number of available companions within its pack. By not taking into account the directionality of the behaviour we built a variable that was markedly different from that used to measure social prestige.

Leadership during activity changes

We defined a “leader-travelling” during those collective activity changes which did not involve intergroup conflicts as the first dog which moved along the direction followed by at least two companions within 10 minutes (see Bonanni et al. submitted b for more details). A “leadership-travelling score” was calculated as follows: for each dog within its pack we divided the total number of times it behaved as a leader by the sum of the total number of times it behaved as follower and the total number of time it behaved as leader.

Statistical analysis

To test whether cooperation in dogs was based on mutualism we conducted three different kind of analysis. We first carried out an analysis at group level. Precisely, for each intergroup conflict we considered the proportion of cooperating dogs of the pack which behaved aggressively (a pack behaved aggressively towards the opponents when at least one of its members approached aggressively opponents) and included it as a dependent variable in a general backward stepwise regression model (STATISTICA Release 7, StatSoft Inc., Tulsa, OK, U.S.A.). When both the interacting packs attacked each other during the course of the same interaction, we randomly selected one of them by tossing a coin. The independent variable included in the model were: number of present dogs (referred to the attacking pack or the randomly selected pack), number of opponents (referred to the non-attacking or to the non-randomly selected pack), ratio of the number of opponents to the number of present dogs, difference between the number of opponents and present dogs, odds (scored as a categorical variable “favourable”, “unfavourable” and “even”), food presence (scored as a binary variable “yes” and “no”), and the identities of the interacting packs scored as categorical variables. We did not include a factor for owner-intruder asymmetry for two reasons: first of all, the packs

studied did not appear to defend exclusive areas (see Bonanni et al. submitted a); secondly, all intergroup conflicts included in the analysis occurred within the area usually scent-marked by the attacking group. So, the attacking packs were always “owners” within their marked area.

At individual level we tested if the “cooperation score with favourable odds” was significantly different from the “cooperation score with unfavourable odds” using a T-test for dependent samples. We also used one-way ANOVA with “total cooperation score” as a dependent variable and “pack” as a factor.

We tested whether individual differences in the level of cooperation (cooperation score) were significant using a chi-square test (Siegel & Castellan 1988). Since the total number of intergroup conflicts to which individuals took part varied, we calculated the expected frequencies as follows: we built a Nx2 table with all individuals within a pack as lines and the total number of times a given individual behaved cooperatively and defected as columns respectively. For each cell into the table the expected frequency was calculated as the total score of the corresponding line multiplied by the total score of the corresponding column and divided by the total of all the scores entered in the table.

To test for the handicap principle we ran a general backward stepwise regression model with social prestige (measured as explained above) as dependent variable and the following independent variables: cooperation score with unfavourable odds, leadership-conflict score, age and gender. Dominance rank was not included here given that it was not possible to assess it independently of active submissions received.

To investigate individual variation in the level of cooperation we considered three different measures of cooperation: “cooperation score with favourable odds”, “cooperation score with unfavourable odds” and “leadership-conflict”. Since such variables were correlated we

applied a Principal Component Analysis (PCA) in order to replace them with two new uncorrelated component variables, linear combinations of the original variables, called principal components which explained most of the variation in the data. We then ran general backward stepwise regression models using the principal components (factors) as dependent variables. In these models the independent variables were: age, standardized dominance rank, leadership-travelling, affiliative score and gender. For all the analysis conducted at individual level, except where specified, we considered all adult, subadult and juvenile dogs but excluded two adult females in poor physical conditions.

Dogs were assigned to different age classes: the first class included individual dogs that showed obvious signs of old age (presence of gray muzzle hair and worn theet); the second class included dogs that were fully grown at the time when the project began (April 2005) but did not show signs of old age; the third class comprised individuals that were juveniles at the beginning of the project (on the basis of allometry and body size) and thus were presumably born in 2004; the other classes comprised dogs that were observed to be born in 2005, 2006 and 2007 respectively.

RESULTS

Tests for mutualism

The general linear model developed for the “proportion of cooperating dogs” was significant although it explained little variance ($R^2 = 0.22$, $F_{17, 173} = 2.78$, $P < 0.0004$). The most significant predictor was the total number of present dogs (referred to the attacking pack) which had a negative effect (*coefficient* = -0.021 ± 0.007 , $T = -3.195$, $P = 0.0017$; Fig. 1). In other words, by keeping the number of opponents equal, the proportion of dogs that actively participated into the conflict decreased with increasing the number of dogs that were present

in the attacking pack (or the number of companions). The identity of the opposing pack had in one case a significant effect: the proportion of cooperating dogs decreased when the Piazza pack was the target of the attack (*coefficient* = -0.120 ± 0.054 , $T = -2.220$, $P = 0.028$).

For the Corridoio pack the individual “cooperation score with favourable odds” was not significantly different from the “cooperation score with unfavourable odds” ($T = -0.155$, $df = 9$, $P = 0.881$; mean scores: 0.65 ± 0.12 , 0.66 ± 0.17 respectively; Fig. 2a). Conversely, for the Curva pack the individual “cooperation score with favourable odds” was significantly smaller than the individual “cooperation score with unfavourable odds” ($T = -3.53$, $df = 8$, $P < 0.008$; mean scores: 0.56 ± 0.28 , 0.80 ± 0.17 respectively; Fig. 2b). As regards the Piazza pack, one individual had the same cooperation score irrespective of the odds, whereas the remaining two animals were indeed more likely to cooperate when facing favourable odds (Fig. 2c).

Pack identity had a nearly significant effect on the total individual cooperation score with the individuals belonging to the smallest pack (Piazza pack) being the most cooperative (ANOVA: $F_{2, 18} = 3.18$, $P = 0.066$; mean scores: Corridoio pack = 0.67 ± 0.03 , Curva pack = 0.63 ± 0.09 , Piazza pack = 0.99 ± 0.02).

Test for “cheating”

Individual differences in the level of cooperation were significant within both the Corridoio pack ($\chi^2 = 23.03$, $df = 9$, $P = 0.006$; observed attacks = 100; Fig. 3a) and the Curva pack ($\chi^2 = 77.99$, $df = 8$, $P < 0.0001$; observed attacks = 57; Fig. 3b). In the Corridoio pack this held even after removing from the analysis one emaciated female which had a very low cooperation score. In the Piazza pack the chi-square test could not be applied due to the fact that more than 20% of the expected frequencies were smaller than 5 (see Siegel & Castellan

1988). However, in this pack the two males had a nearly equal cooperation score whereas an emaciated adult female was much less cooperative (observed attacks = 37; Fig 3c).

Test for the handicap principle

The general linear model for the variables affecting “social prestige” was significant ($R^2 = 0.36$, $F_{1, 19} = 10.77$, $P = 0.0039$) and age was the only significant predictor variable (*coefficient* = 0.140 ± 0.043 , $T = 3.281$, $P = 0.0039$), i. e. older dogs received active submissions during greeting ceremonies from a higher number of social partners. Figure 4 shows the relationship between our measure of social prestige and two different measures of cooperation.

Individual variation in cooperation

The first factor of the PCA on our three measures of cooperation explained alone 62.3% of the total variance in the data and was highly and negatively correlated to all of the three original variables (Fig. 5a): dogs characterised by high negative scores on the first factor of the PCA were the most cooperative both in intergroup conflicts in which the odds were favourable (i. e. when their pack outnumbered the opposing pack) and in conflicts in which the odds were unfavourable (i. e. when their own pack was outnumbered by the opposing pack). Moreover, they stayed often at the front of the pack during a conflict (Fig 5b). Conversely, the second factor of the PCA, which explained alone 22.6% of the total variance in the data, was negatively correlated with “cooperation score with unfavourable odds” and positively correlated with “leadership-conflict” (Fig. 5a,b): dogs which had high negative values on the second factor cooperated often in conflicts when their pack was outnumbered by the opposing group but they rarely occupied the most advanced position of the pack.

The general linear model developed for the first factor of the PCA was significant ($R^2 = 0.33$, $F 1, 19 = 9.29$, $P = 0.0066$) and showed that “affiliative score” was the only significant predictor variable (*coefficient* = -3.13 ± 1.03 , $T = -3.05$, $P = 0.066$; Fig. 6). So, dogs which had a higher number of affiliative partners were the most likely to cooperate in all situations and the most likely to stay at the front of the pack during intergroup conflicts.

The model of the second factor of the PCA was also significant ($R^2 = 0.38$, $F 2, 18 = 5.58$, $P = 0.013$). Such factor was positively and significantly affected by age (*coefficient* = 0.57 ± 0.17 , $T = 3.33$, $P = 0.0037$; Fig 7a) and negatively affected by dominance rank (*coefficient* = -0.97 ± 0.35 , $T = -2.73$, $P = 0.014$; Fig. 7b), although the effects of both variables were weak. In other words, high ranking and young dogs tended to cooperate more often when their pack attacked a larger group but they did not stay at the front of the group.

DISCUSSION

Mechanisms of cooperation

In an another paper (Bonanni et al. submitted a) we have shown that in the feral dogs of the population studied the probability of at least one pack member approaching aggressively opposing groups increases with decreasing the ratio of the number of opponents to the number of companions. This will usually result in dog packs attacking smaller opposing packs more frequently than larger ones. However, attacks against larger packs may still occur in case the ratio of the number of opponents to that of companions is not very high, i. e. when the conflict is not unwinnable. In the present study, we have extended this analysis to show that the proportion of approaching animals within a given pack also seems to change according to relative group size. At group level we have found that, while keeping the number of

opponents equal, the proportion of cooperating animals within packs tended to decrease with increasing the size of the packs themselves. At individual level, we have found that the probability of active participation within one of the packs studied decreased significantly in case the aggression was directed towards smaller opposing packs in comparison to when the aggression was directed to larger packs. Moreover individuals belonging to the smallest of the group studied tended to be more cooperative than individuals belonging to other packs, although such tendency was not significant.

We suggest that all these results taken together may point to the same general conclusion: cooperation in conflicts between group of feral dogs seems to slightly decrease with decreasing the difficulty of winning the conflict: i. e. there is less cooperation when there are many companions present and when aggression is directed to small opposing packs because in such circumstances winning the conflict (and thus getting the contested resources) is easier and the same outcome may be obtained by a smaller proportion of cooperating animals. So the general pattern of intergroup aggression in feral dogs which emerges from our studies appear to be much more complicated than one could expect: generally packs are more likely to approach aggressively small opposing packs, but there is a tendency for a higher proportion of group members becoming engaged in cooperation in case the aggression is directed to large packs. Individuals belonging to very small packs possibly need to be more cooperative given that the active participation of all group members may be required to overcome even solitary opponents. Such pattern may be consistent with cooperation based on mutualism in which individuals cooperate to get individual benefits which overcome the costs in cases the participation of an additional member would increase substantially the probability of a successful outcome (Packer & Rutten 1988). As predicted by Nunn (2000) and Nunn & Lewis

(2001), the level of free-riding in this study tended to increase with increasing the size of the group.

Mesterton-Gibbons & Dugatkin (1992, 1997) identified two mechanisms which characterize mutualism and whose removal will select for non-cooperative behaviour: the “common enemy of an adverse environment” and the “boomerang factor”. In the case of intergroup conflicts the common enemy may be represented by the size of the opposing group: lone opponents may be easily outcompeted by two or three group members, whereas participation by a higher number of individuals would be required to outcompete a pack. The boomerang factor is “any uncertainty which increases the probability that a defector will be the victim of its own cheating”. This may apply to the case of intergroup conflicts if failure to cooperate during a conflict against a large group is likely due to cause defeat and loss of important resources, thus harming cheaters. Mutualism is thought to be the evolutionary mechanism underlying cooperation in territorial defence in male lions (Grinnell et al. 1995), male chimpanzee (Wilson et al. 2001), female ringtailed lemurs (Nunn & Deaner 2004) and also cooperative hunting in several carnivore species (Packer & Rutan 1988). In these cases it may be possible that both size of the opposing group and size of the prey to catch represent the common enemy of the adverse environment.

In species where individual fitness is positively correlated with group size the payoffs to each group member in each cooperative bout are likely to not be independent from the payoffs to its companions (Lima 1989; Grinnell et al. 1995; Heinsohn & Packer 1995; Roberts 2005). This is likely to apply to feral dogs as well given that larger groups tend to dominate smaller ones in intergroup conflicts (Bonanni et al. submitted a). In this situation, individuals need to have many companions to outcompete rival groups and thus should benefit from increasing

their companions' survival and reproductive success (which in turn would lead to group augmentation). Such "cooperation through interdependence" or "stakeholder altruism" (Roberts 2005) is expected to be evolutionarily stable when the increase in fitness arising from increasing the fitness of companions is such that it outweighs the costs of cooperation (Roberts 2005). Whereas in mutualism the primary benefit of cooperation is to the cooperating individual itself and the benefits to others are secondary, in stakeholder altruism the direct benefits go to companions and the benefits to the actor are a secondary consequence (Roberts 2005). However, this kind of cooperation would lead to similar predictions as mutualism concerning participation in intergroup conflicts: individuals should cooperate more when the odds are unfavourable in order to not place their companions at too much risk during a contest against a stronger pack (see Heinsohn & Packer 1995).

In this study we have found significant individual differences in the level of cooperation provided within the two largest packs studied: some dogs consistently defected on cooperating more often than others. Theoretical models (Boyd & Richerson 1992; Clutton-Brock & Parker 1995; Frank 1995) suggest that cooperation in sizeable groups may be stabilized by punishing defectors through active aggression (this differs from the strategy *tit for tat* which reacts to defection simply by withholding further cooperation and thus actually punishes both defectors and cooperators). However, in this study we have never observed cooperating dogs attacking individuals which had not participated in a conflict. Aggressive behaviour among the members of the same pack did indeed occur at a considerable rate only in feeding and mating competitive situations.

One candidate hypothesis to explain individual variation in cooperation and altruism is the handicap principle according to which costly cooperative behaviour may be used as an honest

signal of quality and competitive ability (Zahavi & Zahavi 1997; Roberts 1998). Individuals which gain social status by demonstrating the ability to bear the costs of cooperation, rather than through direct aggression to rivals should be more likely to be regarded as valuable collaborators by other group members (Carlisle & Zahavi 1986). Theoretical work has also shown that altruism as a signal can evolve and be evolutionarily stable (Gintis et al. 2001; Lotem et al. 2003).

Empirical support for the handicap hypothesis comes mainly from studies on arabian babblers (*Turdoides squamiceps*). Carlisle & Zahavi (1986) have reported evidences that, in these cooperatively breeding birds, helpers seem to compete for performing the altruistic action of feeding nestlings and usually interfere with the provisioning efforts of subordinate birds. In that study, positive correlations between helpers' dominance rank and frequency of nestling-feeding were observed in circumstances in which there was a high potential for interference between helpers (for instance when nests were already attended by a dominant helper) but not at other times. Moreover, Zahavi & Zahavi (1997) suggested that sentinel behaviour in the same species may also have evolved as a signal of quality given that dominant birds often interfere with the subordinates' efforts of behaving as sentinels. However, more recent studies conducted on the same species, and including a larger sample of both helpers and parents, did not find any evidence of competitive interferences, nor correlations between dominance rank and the behavioural patterns supposed to function as costly signals (Wright 1997; Wright et al. 2001).

In another paper (Bonanni et al. submitted b) we have found that feral dogs receiving active submissions from many partners are those which more frequently initiate collective movements (leaders), and have hypothesized that such group movements would result from

an attempt by subordinate dogs at maintaining close proximity with those individuals which are regarded as valuable social partners. One possible reason why habitual leaders are recognized as an important resource by followers, or in other words why they have gained such a social prestige, is that their cooperative behaviour is needed in order to overcome rival groups in contests for food or other resources. However, in the present work we have not found any evidence that social prestige is a direct consequence of costly cooperative behaviour performed during intergroup conflicts. Dogs which received more active submissions in greeting were not more likely to reach the closest proximity to the opponents (thus taking more risk), nor were more often engaged in contests against larger groups (which should require a greater effort and thus be more costly). Thus, if the amount of active submission received is a good measure of social prestige, as we believe, the handicap hypothesis is not supported by our study. It may be, of course, possible that our measures of cooperation are too simple and do not adequately represent the complexity of dogs cooperative behaviour. More sophisticated measures may be required to adequately assess the costs incurred by individuals, i. e. scoring all the dogs which reach close proximity to the opponents and not just the most advanced individual, or uncovering the possible presence of complementary cooperative roles which may differ with respect to the costs incurred by individuals which play them (see below). An alternative hypothesis which await testing is that leaders provide coalitionary support in intrapack agonistic interactions, although such coalitionary interactions do not occur frequently and a much more extended study period would be required for testing.

Individual variation in cooperation

The first factor of the PCA, which explained more than 60% of the variance in the data, showed that our three measures of cooperation in intergroup conflicts were positively correlated. So, individuals which were the most likely to be cooperative when their pack had a numerical advantage over opponents were still the most cooperative when their pack was outnumbered by opponents and the most likely to occupy an advanced position within the pack. Although our measures of cooperation differ from those used in the study by Heinsohn & Packer (1995), it seems that feral dogs exhibit a much smaller variety of cooperative strategies in comparison to female lions. However, the relation of both age and dominance rank to the second factor of the PCA, explaining more than 20% of the total variance, revealed an apparent conditional cooperative strategy by juveniles and high ranking dogs which tended to cooperate more when their presence was most needed, although they did not necessarily occupy the most advanced position of the pack. So, although high ranking dogs enjoy priority of access to resources (Cafazzo 2007), they apparently do not invest more energy than subordinates in resource defence against strangers unless a great effort is required to defeat a large opposing pack. Conversely, studies on the territorial behaviour of wild canids (e. g. wolves, Harrington & Mech 1979, Mech 1993; ethiopian wolves, *Canis simensis*, Sillero-Zubiri & Macdonald 1998; coyotes, *Canis latrans*, Gese 2001) seem to indicate that the members of the dominant breeding pair, and especially the male, contribute more to resource defence than helpers and puppies.

Most of the individual variation in cooperative behaviour in this study was explained by patterns of social affiliation among pack members (the variable “affiliative score” was the only significant predictor of the first factor of the PCA). Dogs which were more likely to

actively participate in intergroup contests were those with the higher number of affiliative partners. If feral dogs establish affiliative relationship preferentially with closely related individuals, as occurs in other species (Parker et al. 1995; Schino 2001), then this result would indicate that kin selection may play a role in promoting cooperation in dogs. However, preliminary analysis of genetic relatedness, based on microsatellite DNA extracted from faecal samples, indicate that most dogs of the pack studied may be related as closely as siblings (Francesco Nonnis Marzano personal communication), and thus it is possible that kinship cannot explain individual variation in the number of affiliative partners in this dog population. Differential affiliation may be instead explained by individual variation in temperament (Weinstein & Capitanio 2008).

Affiliative behaviour is known to promote cooperation in both primates (Seyfarth & Cheney 1984; Mitani et al. 2000) and social carnivores (de Villiers et al. 2003). From a functional perspective, animals may decide to cooperate with their preferred social partners because they need to be confident that their collaborators will not defect at a critical moment during a cooperative bout (Gilby et al. 2008). So, one possible interpretation of our results is that feral dogs which are more likely to actively participate into an intergroup conflict are those which expect to be supported by their preferred social partners. Such interpretation imply that dogs would have the cognitive ability to adjust their cooperative behaviour to that of their companions and to understand that a joint action is necessary to achieve a goal, or specifically that the partners' collaboration is necessary to defeat an opposing group. We believe that cognitively complex cooperation may be conceivable in dogs for several reasons: first we have observed dogs giving glances to their companions apparently as if they were waiting for their support before attacking opponents, although systematic data collection on such subtle

communicative behaviour is prohibitively difficult in natural conflicts. Secondly, we have sometimes observed feral dogs encircling opponents during conflicts, a collective action requiring some degree of division of labour and complementary roles performed by different individuals (see Boesch & Boesch 1989). Such “collaboration” would not be possible without taking into account the behaviour of others (Boesch 2002). Wolves, from which dogs descends, are also able to perform different complementary roles during cooperative hunting (Mech 1970). Third, under controlled conditions dogs have been shown to possess “human-like cognitive abilities”: they are more skillful than great apes at reading human communicative signals indicating the location of hidden food, and seem even to know what human beings can see in a number of different contexts (reviewed in Hare & Tomasello 2005). Some authors have suggested that the complex cognitive abilities of dogs have initially evolved during domestication as a by-product of selection for tame behaviour (Hare & Tomasello 2005). This is because a tolerant “human-like” temperament would be a necessary prerequisite for the evolution of complex forms of social cognition and cooperation: (comprehension of others’ behaviour and mental states would be useless when cooperating if individuals are not able to share the rewards of joint cooperative efforts, Hare & Tomasello 2005). However, a more recent study has shown that wolves are as skillful as dogs at reading human signals given the appropriated rearing conditions and experimental settings (Udell et al. 2008). So domestication may not be a prerequisite for human-like social cognition in canids. Whichever the right evolutionary scenario, our results may add further support to the view that higher sociability and tolerance to conspecifics facilitate cooperation in social species.

In conclusion, the results of the present study may shed some further lights on both the evolutionary and proximate mechanisms underlying cooperation in sizeable groups and stress the importance of both mutualistic benefits and affiliative relationships in promoting cooperation in social animals. We hope that our results could stimulate further studies on dogs cooperation and cognition under more controlled conditions.

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Figure 1. Predicted proportion of cooperating dogs in relation of the total number of pack members present.

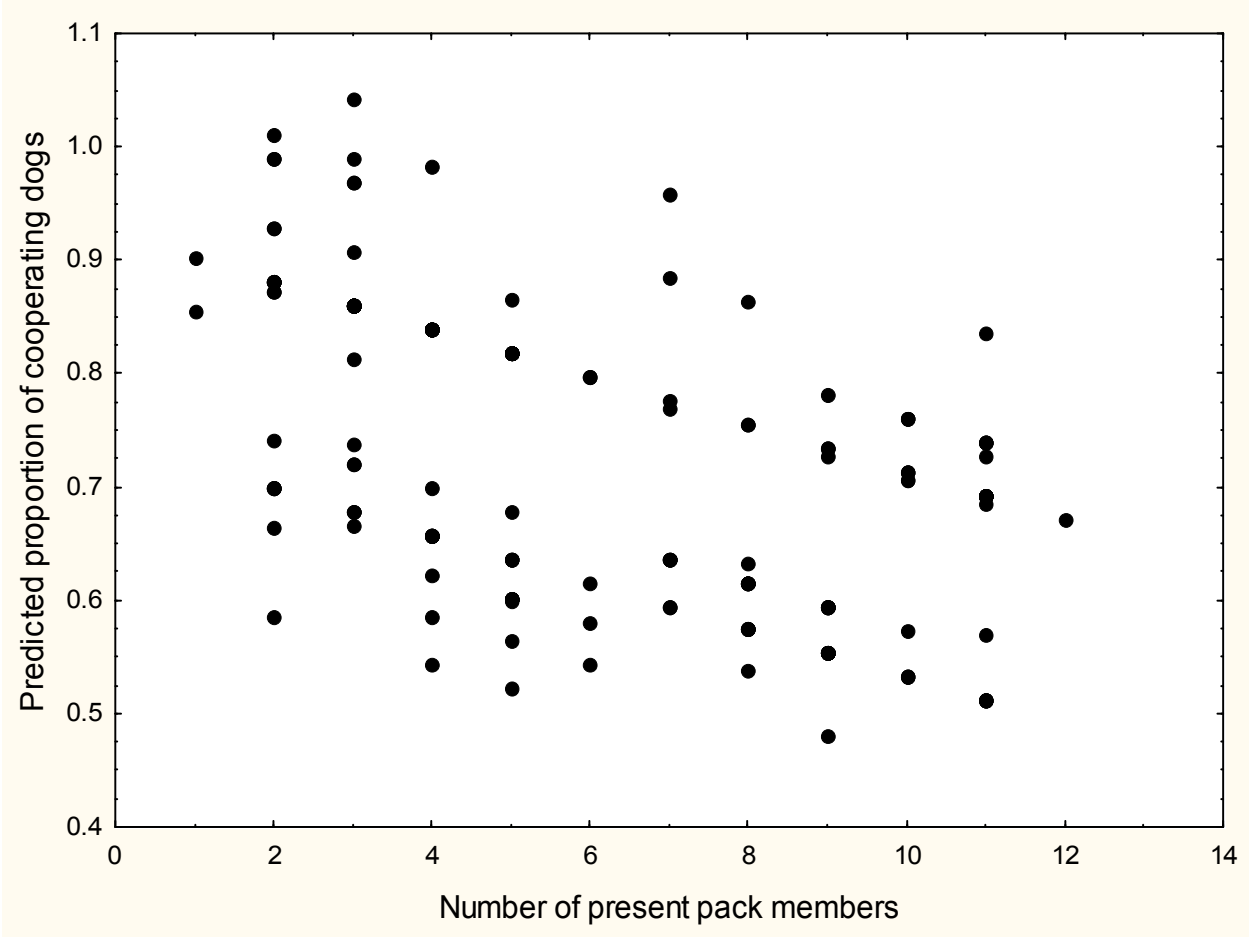
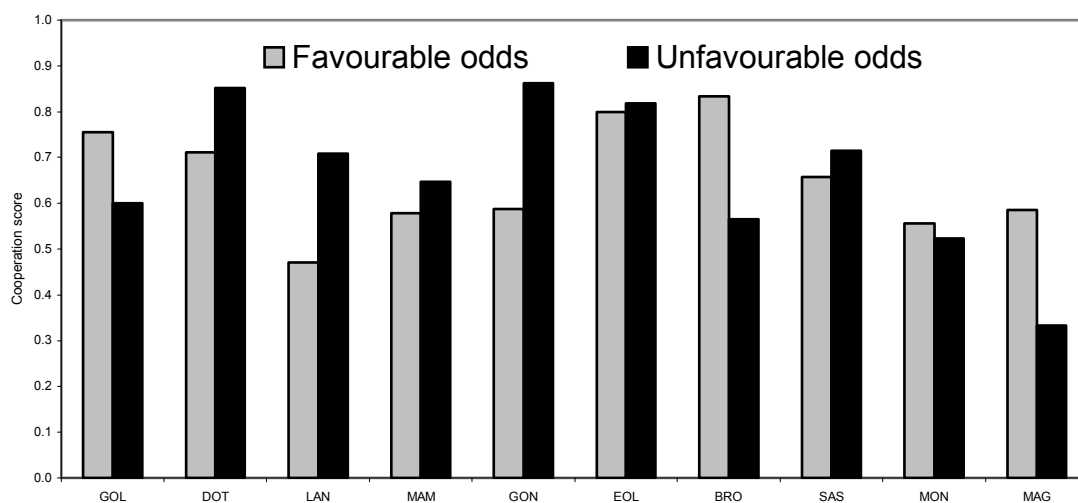
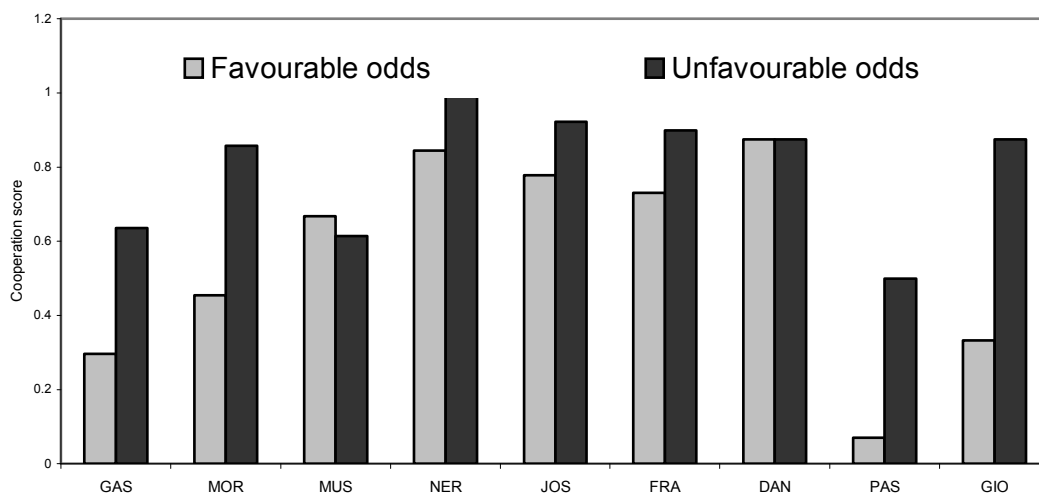


Figure 2. Individual cooperation scores with odds favourable and unfavourable respectively for the dogs of the (a) Corridoio, (b) Curva and (c) Piazza packs respectively. Differences between the two conditions are significant only for the Curva pack (see text for more explanations).

(a)



(b)



(c)

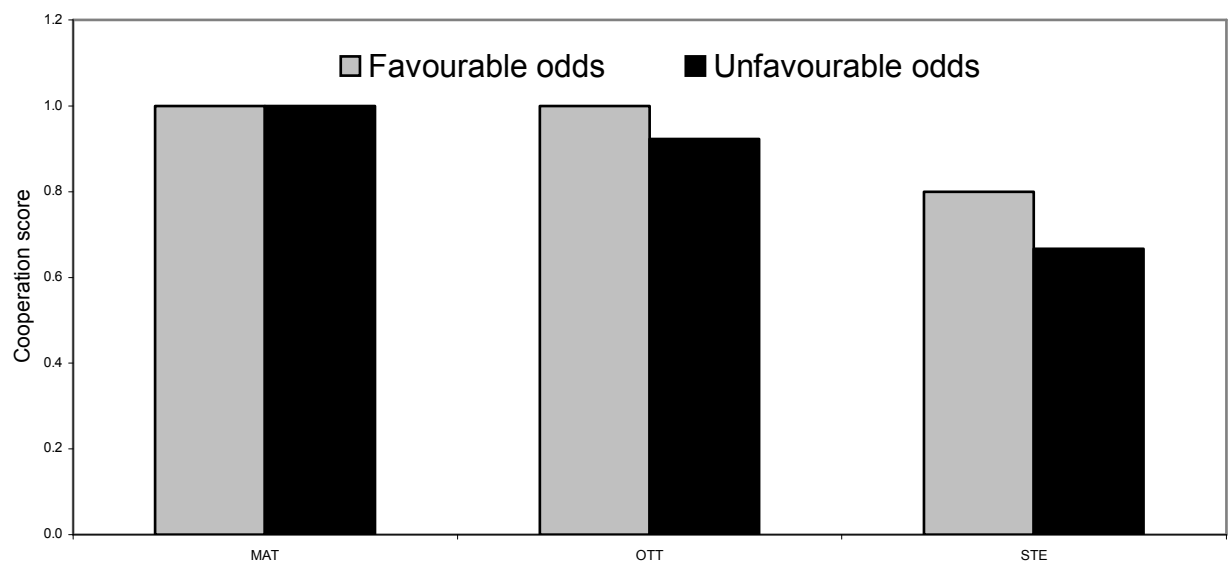
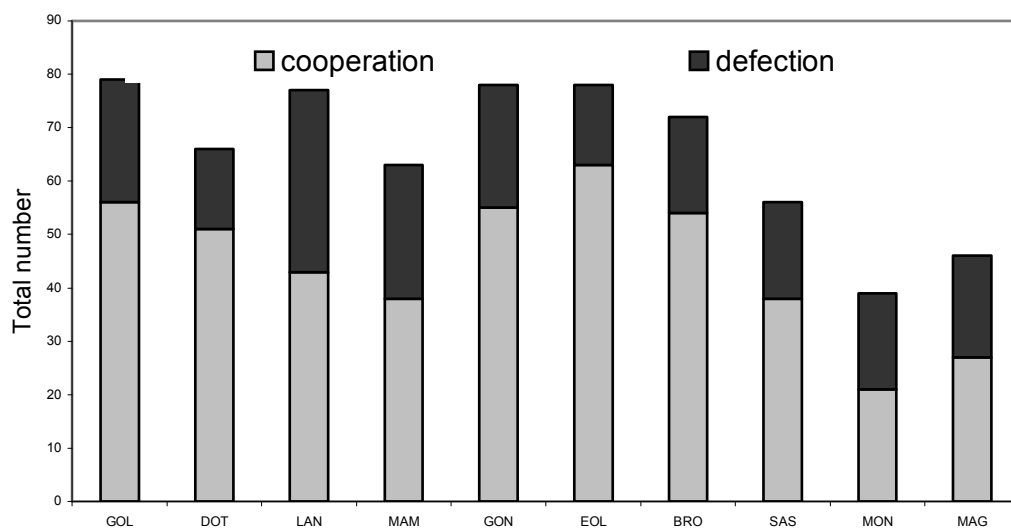
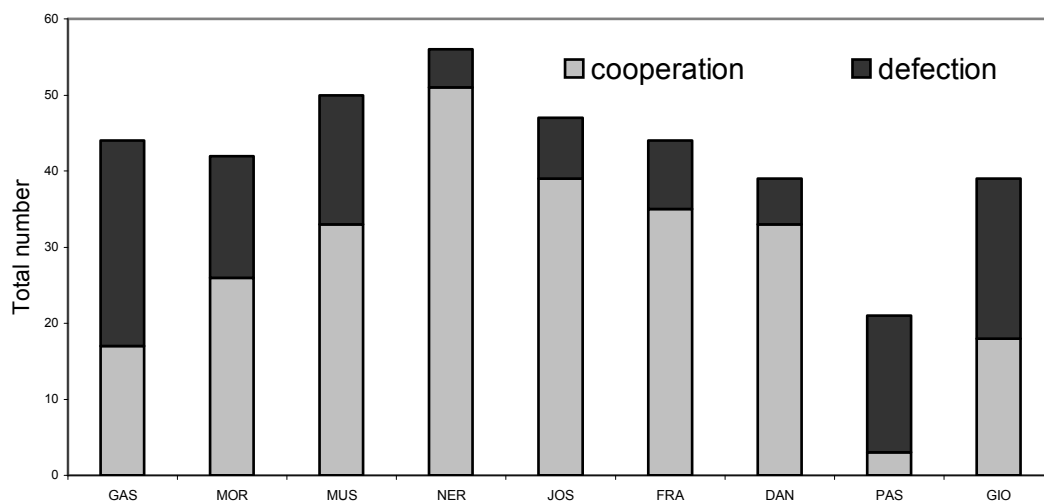


Figure 3. Total number of intergrup conflicts in which each dog has cooperated and defected respectively, within (a) the Corridoio, (b) the Curva and (c) thePiazza packs.

(a)



(b)



(c)

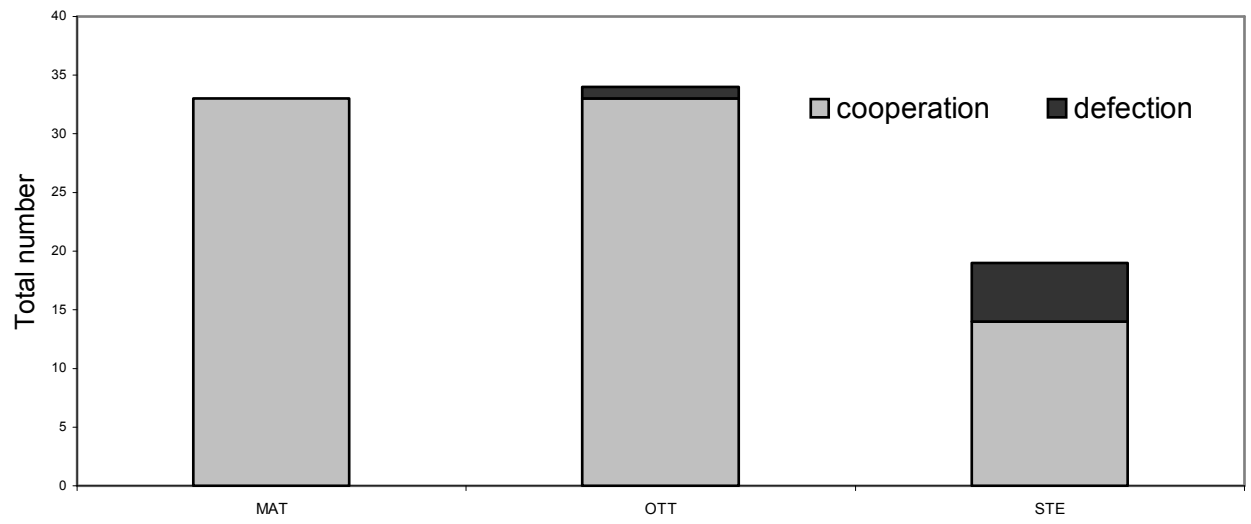
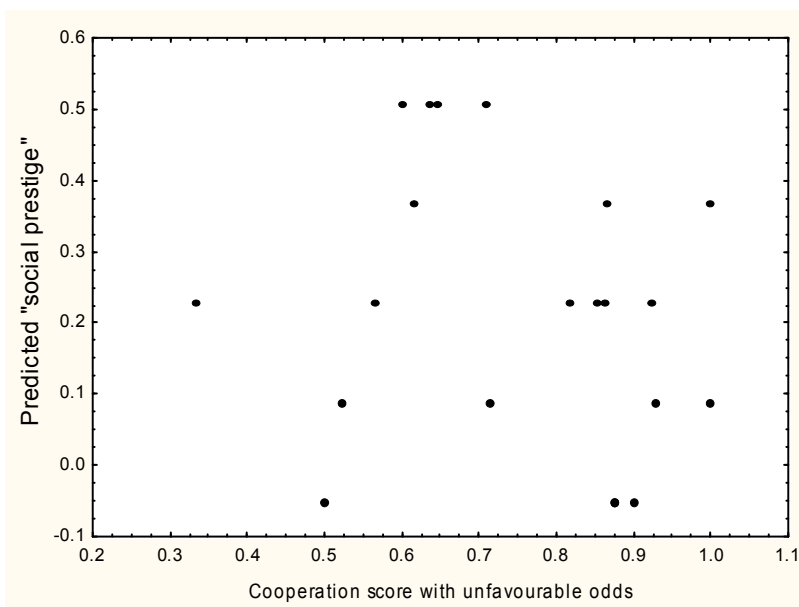


Figure 4. Predicted “social prestige” (proportion of group companions from which each dog has received at least one instance of active submission) in relation to: (a) cooperation score with unfavourable odds; (b) leadership during intergroup conflicts (see text for more explanations).

(a)



(b)

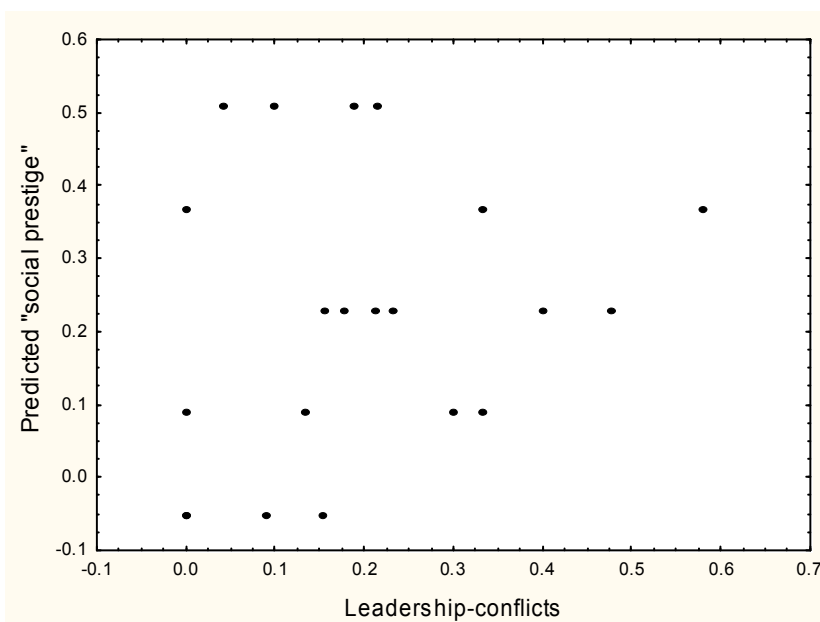
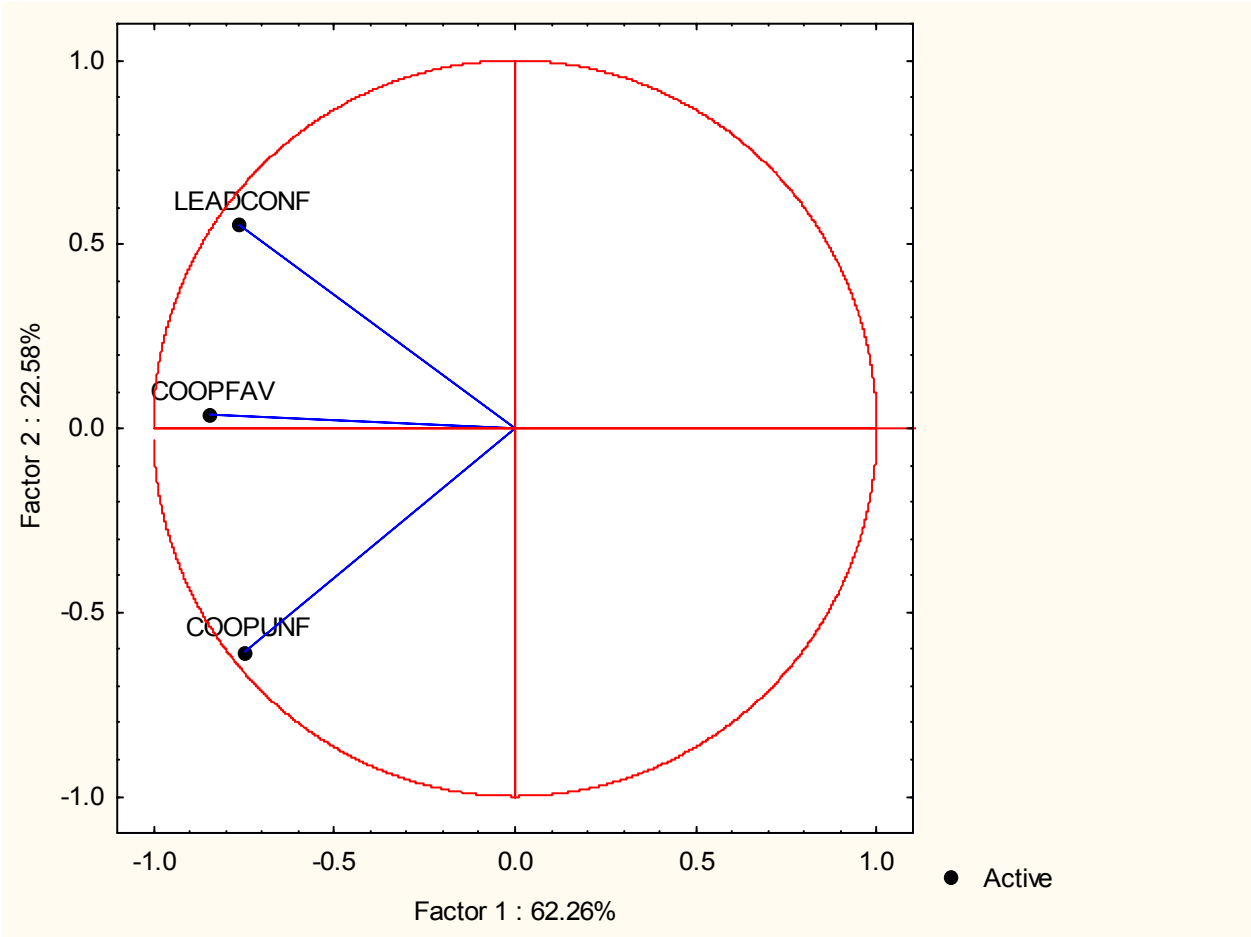


Figure 5. Principal Component Analysis (PCA) on three measures of cooperation in intergroup conflicts. The circle (a) shows the correlation between the initial variables and the new two components. The scatter plot (b) shows the position of the dogs on the plain and can be interpreted that can be interpreted in relation to the corresponding position of the variables on the correlation circle. LEADCONF = Leadership-conflict; COOPFAV = Cooperation score with favourable odds; COOPUNF = Cooperation score with unfavourable odds.

(a)



(b)

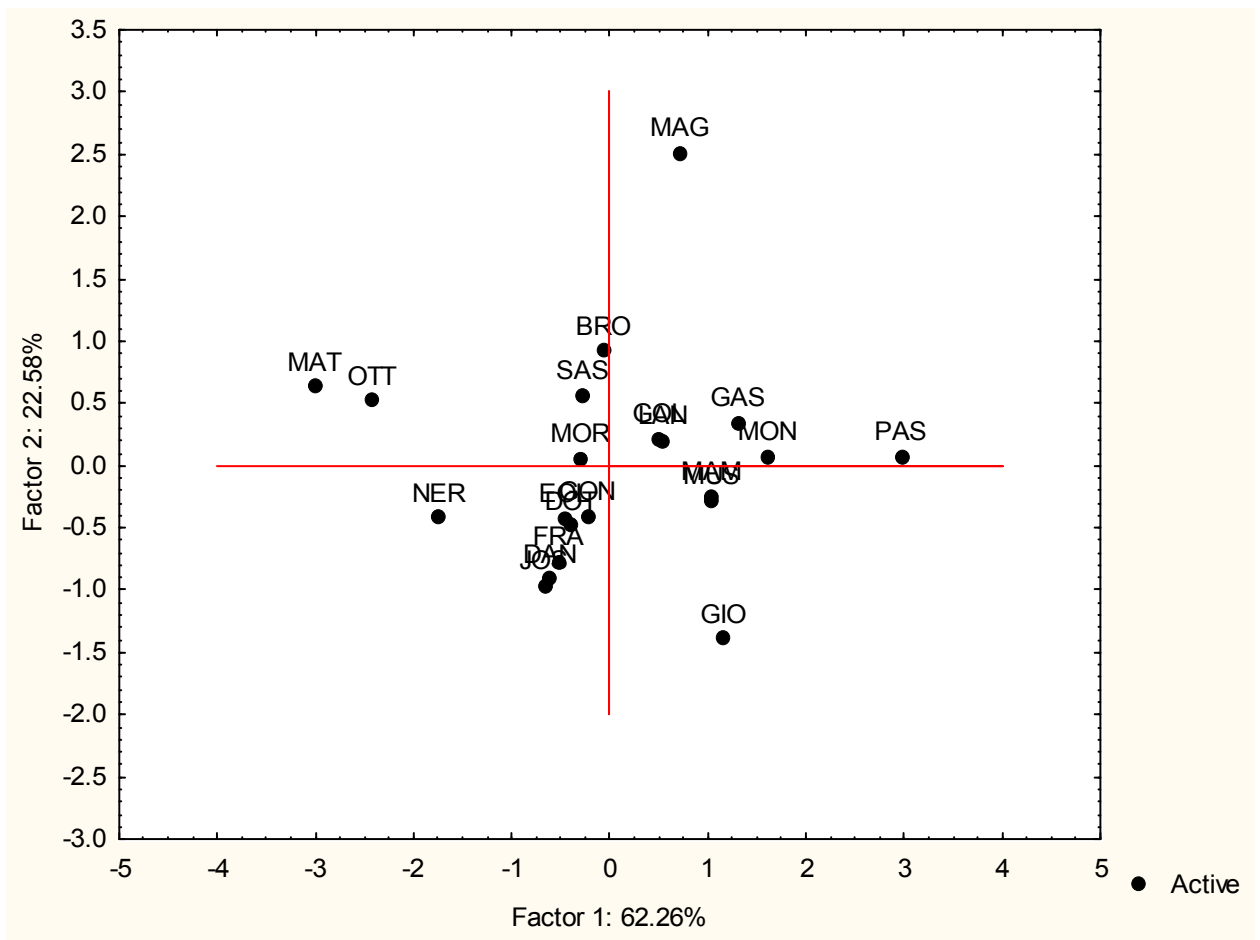


Figure 6. Predicted values for Factor 1 PCA in relation to “affiliative score”. High negative values on Factor 1 indicate higher levels of cooperation.

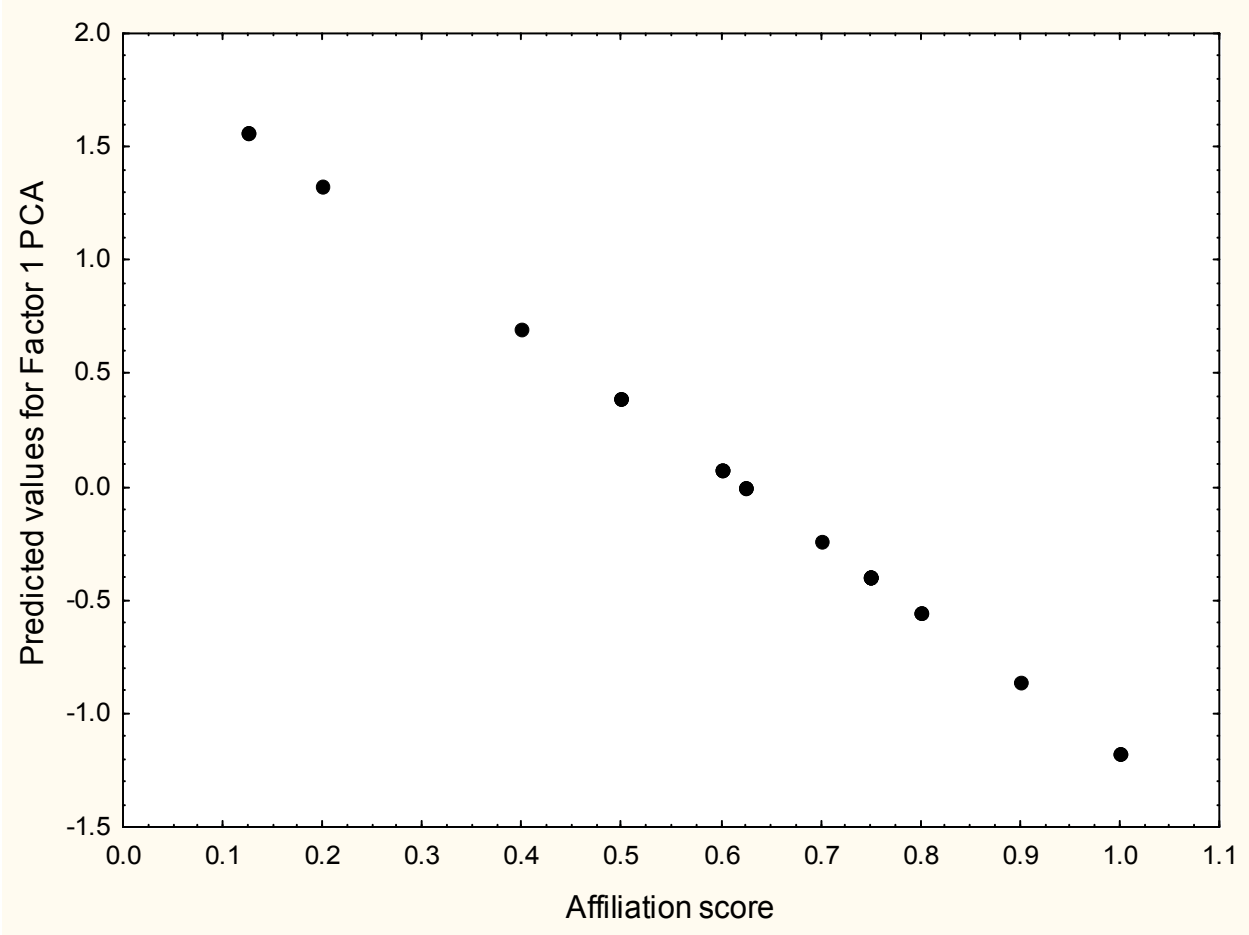
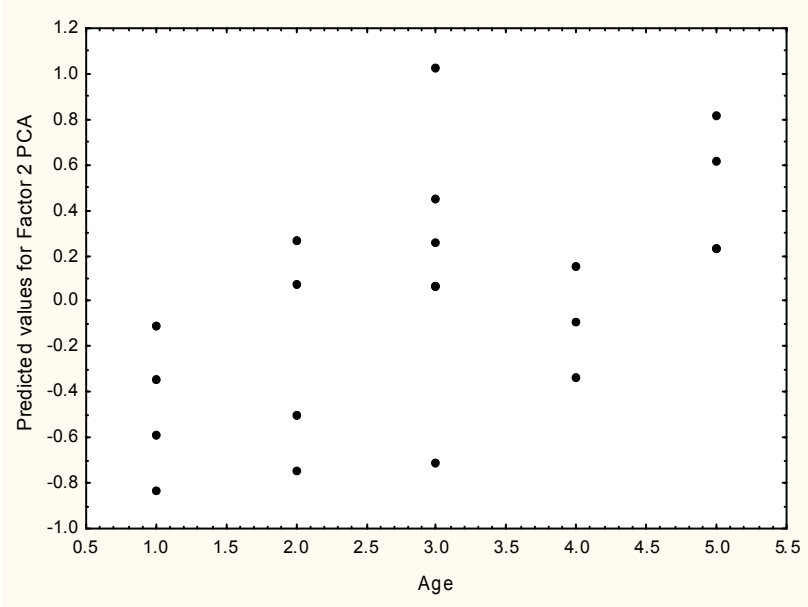
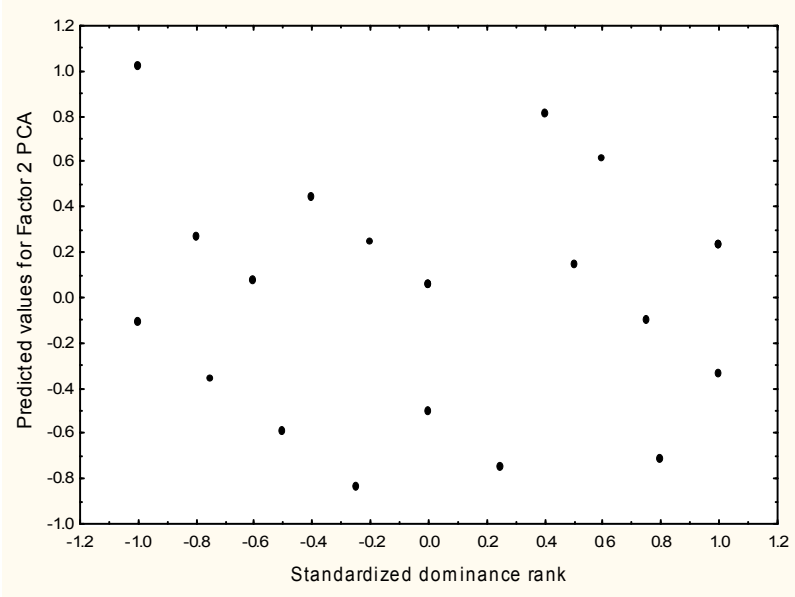


Figure 7. Predicted values for Factor 2 PCA in relation to (a) age and (b) standardized dominance rank. High negative values on Factor 2 indicate an higher level of cooperation with unfavourable odds, whereas high positive values indicate a higher frequency of being at the front of the group during conflicts.

(a)



(b)



SUMMARY

This thesis attempted to assess the adaptive value of the behaviour of feral dogs (*Canis lupus familiaris*) by using such species as a model for testing predictions based on evolutionary theories. In particular, the following topics concerning dogs' behaviour were examined: intergroup agonistic behaviour in relation to numerical assessment of opponents, cooperative behaviour during intergroup conflicts and decision making processes during collective activity changes.

The research focused mainly on three dogs packs living in a suburban environment whose members were not socialized to human beings although subsisted mostly on food provided by "volunteer dog caretakers".

Game theoretical arguments predict that in conflicts between social groups competitors should adjust their agonistic behaviour according to the relative size of the interacting groups. In the feral dogs studied, the overall probability of at least one pack member approaching aggressively opponents increased significantly with decreasing the ratio of the number of opponents to that of the present pack members. Moreover, a retreat response by more than half pack members was more likely to be elicited the higher the ratio of the number of opponents to that of the present pack members. However, such a ratio had no significant effect on the aggressive/retreat response of dogs when both the interacting packs comprised more than 4 individuals. A higher asymmetry in size between the interacting packs was actually required to make optimal decisions about the aggressive/retreat response when numbers larger than 4 were involved, but not with smaller numbers. This results suggest that feral dogs are able to assess relative group size and to adjust their agonistic behaviour

accordingly. Moreover, two different cognitive mechanisms, one of these based on noisy mental magnitudes, may be involved in such numerical assessment.

Social animals need to reach consensus decisions about the nature and timing of group activities in order to maintain group cohesion. Group members which contribute more to the decision outcome are termed leaders. Patterns of distribution of leadership within social groups are expected to be influenced by group size, age, gender and social relationships. In all feral dog packs studied, but the smallest, a limited number of habitual leaders made group decisions about activity changes. In one large pack the number of habitual leaders decreased after such pack underwent a drastic reduction in size. Individuals which behaved more frequently as leaders were those which received active submissions during greeting ceremonies from a higher number of partners. The results are consistent with the view that animal collective movements may result from the need by low-ranking individuals to maintain close proximity with specific valuable social partners.

Unravelling factors which promote individual participation in costly cooperative activities may help to explain how cooperation may evolve in animal societies despite the consistent defection of specific individuals. In the feral dogs studied, the individual level of cooperation during intergroup conflicts seemed to decrease with decreasing the difficulty of winning: the proportion of cooperating animals decreased when there were more companions present; the individual probability of cooperating decreased significantly, in one pack, when such pack outnumbered opponents; dogs belonging to the smallest pack tended to be more cooperative than those belonging to larger groups. Such pattern may be consistent with the view that individuals cooperate to maximize individual mutualistic benefits. Contrary to the predictions of the handicap hypothesis, social prestige (measured as the amount of active submissions

received) did not correlate with cooperation. The individual level of cooperation was, instead, positively affected by the number of affiliative partners.

In conclusion, the overall results of this thesis suggest that, despite a very long history as domesticated animals, feral dogs may still match some of the predictions based on evolutionary theories.

RIASSUNTO

L'obiettivo di questa tesi è stato quello di esaminare il possibile valore adattivo del comportamento dei cani vaganti (*Canis lupus familiaris*), utilizzando tale specie come modello di verifica di previsioni basate su teorie evolutive. In particolare, sono stati indagati i seguenti aspetti: comportamento agonistico intergruppo in relazione alla capacità di valutare la quantità di oppositori, cooperazione nei conflitti intergruppo, e decisioni collettive concernenti i cambi di attività.

La ricerca è stata incentrata soprattutto su tre branchi di cani vaganti viventi in ambiente suburbano e i cui membri non erano socializzati con gli esseri umani, sebbene dipendessero dal cibo reso disponibile da persone volontarie.

Argomenti teorici basati sulla teoria dei giochi predicono che, nei conflitti tra gruppi sociali, i competitori dovrebbero modificare il loro comportamento agonistico in relazione alla dimensione relativa dei gruppi interagenti. Nei cani studiati, la probabilità complessiva di

approccio aggressivo da parte di almeno un membro del gruppo cresceva significativamente al diminuire del rapporto tra il numero degli oppositori e il numero di cani presenti nel proprio gruppo. Inoltre, la probabilità di ritirata da parte di più della metà dei membri di un gruppo cresceva all'aumentare del rapporto tra il numero degli oppositori e il numero dei cani presenti in tale gruppo. Comunque, tale rapporto non aveva effetto significativo sul comportamento di attacco e ritirata qualora entrambi i gruppi interagenti comprendessero più di 4 individui. Un maggiore divario dimensionale tra i due gruppi interagenti era necessario per permettere ai cani di prendere decisioni ottimali circa il comportamento di attacco/ritirata, nel caso almeno uno dei due gruppi comprendesse più di 4 individui, ma ciò non era vero se entrambi i gruppi comprendevano meno di 4 individui. Tali risultati suggeriscono che i cani vaganti possiedono la capacità di valutare la dimensione relativa dei gruppi interagenti nei conflitti e modificano il loro comportamento agonistico in relazione a tale dimensione relativa. Inoltre è ipotizzabile che due diversi meccanismi cognitivi, uno dei quali basato su grandezze mentali continue soggette a variabilità scalare, siano coinvolti nella valutazione delle quantità.

Gli animali sociali hanno spesso bisogno di prendere decisioni collettive circa quali attività svolgere, e quando svolgerle, allo scopo di mantenere la coesione del gruppo. I membri del gruppo che contribuiscono in misura maggiore a tali decisioni sono i leaders. Sulla base di argomenti teorici ci si aspetta che la distribuzione di tale comportamento all'interno di un gruppo sia influenzata da variabili come la dimensione del gruppo stesso, l'età, il sesso e le relazioni sociali. In tutti i branchi di cani vaganti studiati, con l'eccezione del più piccolo, si è riscontrata la presenza di un numero limitato di leaders abituali in corrispondenza dei cambi di attività. In un grande branco il numero di leaders abituali è diminuito a seguito di una

drastica riduzione della dimensione del gruppo stesso. Gli individui che più spesso agivano come leaders si distinguevano come quelli che ricevevano atti di sottomissione attiva da un numero maggiore di partners sociali. Tali risultati supportano l'ipotesi che i movimenti collettivi nelle società animali derivino dalla necessità da parte di individui socialmente subordinati di mantenere rapporti di prossimità con specifici partners di alto valore.

Capire quali fattori promuovano la partecipazione individuale ad attività cooperative costose può facilitare la comprensione di come la cooperazione possa evolvere nelle società animali nonostante la sistematica defezione di specifici individui. Nei branchi di cani vaganti studiati, il livello individuale di cooperazione nei conflitti intergruppo sembrava diminuire al decrescere della difficoltà di vincere il conflitto stesso: la proporzione di animali cooperanti diminuiva all'aumentare del numero di compagni di gruppo presenti; in uno dei gruppi, la probabilità individuale di cooperazione diminuiva in modo significativo quando tale gruppo aveva un vantaggio numerico rispetto agli oppositori; cani appartenenti al branco più piccolo tendevano ad essere più cooperativi di quelli appartenenti ai gruppi più grandi. Tali risultati potrebbero essere compatibili con una strategia di cooperazione mutualistica, mirata a massimizzare i benefici individuali. Contrariamente alle previsioni dell'ipotesi dell'handicap, il prestigio sociale (misurato come la quantità di sottomissioni attive ricevute) non sembrava essere una conseguenza della cooperazione. Il livello individuale di cooperazione era invece positivamente influenzato dal numero di partners affiliativi.

In conclusione, questi risultati suggeriscono nel loro insieme che, a dispetto di una lunghissima storia come animali domestici, i cani vaganti sono ancora in grado di produrre alcune risposte comportamentali adattative.

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