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Free-ranging dogs assess the quantity of opponents in intergroup conflicts

**Roberto Bonanni · Eugenia Natoli ·
Simona Cafazzo · Paola Valsecchi**

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Abstract In conflicts between social groups, the decision of competitors whether to attack/retreat should be based on the assessment of the quantity of individuals in their own and the opposing group. Experimental studies on numerical cognition in animals suggest that they may represent both large and small numbers as noisy mental magnitudes subject to scalar variability, and small numbers (≤ 4) also as discrete object-files. Consequently, discriminating between large quantities, but not between smaller ones, should become easier as the asymmetry between quantities increases. Here, we tested these hypotheses by recording naturally occurring conflicts in a population of free-ranging dogs, *Canis lupus familiaris*, living in a suburban environment. The overall probability of at least one pack member approaching opponents aggressively increased with a decreasing ratio of the number of rivals to that of companions. Moreover, the probability that more than half of the pack members withdrew from a conflict increased when this ratio increased. The skill of dogs in correctly assessing relative group size appeared to improve with increasing the asymmetry in size when at least one pack comprised more than four individuals, and appeared affected to a lesser extent by group size asymmetries when dogs had to compare only small numbers. These results provide the first indications that a representation of quantity based on noisy mental magnitudes may be involved in the assessment of opponents in intergroup conflicts and leave open the possibility that an additional, more precise mechanism may operate with small numbers.

Keywords Domestic dogs · Game theory · Natural intergroup conflicts · Non-verbal numerical systems

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) 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 and 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 their opponents as a means of assessing whether or not to escalate a fight or retreat (Maynard Smith and Parker 1976; Parker and Rubenstein 1981; Hammerstein and Parker 1982; Enquist and 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 these intergroup conflicts victory usually goes to the side with the higher number of group members, thus strongly indicating that group size might be an approximate measure of one group's RHP (several primates, Cheney 1987; Kitchen

R. Bonanni · S. Cafazzo · P. Valsecchi
Dipartimento di Biologia Evolutiva e Funzionale,
Università di Parma, Viale Usberti 11/A, 43100 Parma, Italy

E. Natoli
Azienda USL Roma D, Area Dipartimentale Sanità Pubblica
Veterinaria, Ospedale Veterinario, via della Magliana 856,
00148 Rome, Italy

R. Bonanni (✉)
via Giuseppe Donati 32, 00159 Rome, Italy
e-mail: rbonanni75@gmail.com

et al. 2004; barnacle geese, *Branta leucopsis*, Black and Owen 1989; territorial ants, Adams 1990; Tanner 2006; lions, *Panthera leo*, Packer et al. 1990; spotted hyenas, *Crocuta crocuta*, Hofer and East 1993; free-ranging dogs, Macdonald and Carr 1995; ethiopian wolves, *Canis simensis*, Sillero-Zubiri and Macdonald 1998; coyotes, *Canis latrans*, Gese 2001). As a consequence, it has been hypothesized that in conflicts between social groups, individuals should assess the number of conspecifics belonging to their own, relative to the opposing group and adjust their cooperative agonistic behaviour accordingly. Studies testing this hypothesis in vertebrate species have used playback experiments in which the presence of intruders has been simulated using species-specific recorded vocalizations 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 and Mech 1979) are more likely to approach aggressively simulated intruders when facing favourable odds, i.e. in situations in which their own group outnumbers the intruders' group. The advantage of avoiding the costs of fighting against larger groups may have provided one of the possible selective pressures leading to the evolution of numerical assessment skills in social species (McComb et al. 1994).

It has been suggested that non-human primates, and possibly other taxa, share with humans two distinct non-verbal systems for representing numerosities, one that precisely represents small numbers (up to 3–4) and the other that approximately represents larger numbers (Gallistel and Gelman 2000; Hauser and Spelke 2004; Feigenson et al. 2004). However, many studies indicate that the approximate number system can also be used to represent smaller quantities (Meck and Church 1983; Brannon and Terrace 1998; Beran 2001, 2004, 2007; Cantlon and Brannon 2006; Cordes and Brannon 2009). This system is thought to represent quantities as continuous mental magnitudes subject to scalar variability. This means that representations of numbers (magnitudes) are not precise and become more approximate for increasingly larger quantities to be estimated (Gallistel and Gelman 2000). Consequently, large magnitudes are more likely to be confused with similar quantities. Discriminability between different quantities follows the Weber's law (Gallistel and Gelman 2000): it becomes progressively easier as the ratio of the smaller quantity to the larger one decreases (e.g. it is easier to discriminate between 6 and 12 than between 6 and 9).

The small precise number system has been described by an object-file model (Hauser et al. 2000; Feigenson et al. 2002; Feigenson and Carey 2005) in which 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. Discriminability of numerosities in this case does not follow the Weber's law (e.g. discriminating between 1 and 2 is as much easy as between 2 and 3).

Studies conducted in monkeys and human infants (Hauser et al. 2000; Feigenson et al. 2002; Feigenson and Carey 2005) suggest that when subjects have to compare small (≤ 4) versus larger quantities (that cannot be represented with object-files), then the two systems may come into conflict, possibly due to incompatibility of the representational formats, resulting in failure to discriminate these quantities. However, a recent study (Cordes and Brannon 2009) has shown that discrimination in these cases may be successfully achieved by decreasing the ratio of the smaller to the larger quantity beyond a given threshold (1:4, or possibly 1:3), indicating that under such circumstances only the approximate number system is used to represent both small and large numbers.

Up to now, few studies have attempted to ascertain the cognitive mechanisms underlying assessment strategies in naturally occurring intergroup conflicts. Studies investigating numerical cognition in several taxa have instead focused on the ability to discriminate between the quantities of food items and other objects (e.g. rats, *Rattus norvegicus*, Meck and Church 1983; tamarin monkeys, *Saguinus oedipus,* Hauser et al. 2003; rhesus monkeys, *Macaca mulatta,* Flombaum et al. 2005; orangutans, *Pongo pygmaeus,* Call 2000; chimpanzee, Beran 2001, 2004; salamanders, *Plethodon cinereus,* Uller et al. 2003; grey parrots, *Psittacus erithacus*, Pepperberg 2006; Al Aïn et al. 2009, and mosquitofish, *Gambusia holbrooki*, Agrillo et al. 2008). In this study, we investigated assessment of relative group size in naturally occurring conflicts between groups of free-ranging dogs, i.e. those domestic dogs whose movements and activities are not limited by human owners, and tested predictions about intergroup agonistic behaviour based on both cognitive and game theoretical approaches.

In areas where they have access to abundant food resources directly or indirectly provided by human beings, free-ranging dogs live in packs which have been described as territorial and cooperative in conflicts against competing packs (Font 1987; Daniels and Bekoff 1989a, b; MacDonald and Carr 1995; Boitani et al. 1995; Boitani and Ciucci 1995; Pal et al. 1998; Cafazzo 2007; Bonanni et al. 2010a), thus constituting a good model for testing hypotheses on group size assessment in intergroup conflicts.

Here, we addressed the following questions. First, we asked whether free-ranging dogs were able to assess relative group size in intergroup conflicts and used this information adaptively. We predicted that if free-ranging dogs adopted an evolutionarily stable strategy, as proposed by game theoretical models (Maynard Smith and Parker 1976; Parker and Rubenstein 1981), then they should be more likely to behave aggressively towards opponents when they estimate their own group to be larger than the opposing group, and should retreat from a conflict when they estimate their group to be smaller than the opposing group. Secondly, we asked whether assessment of relative group size in dogs was accomplished using cognitive mechanisms similar to those described in primates. We predicted that if the dogs' behaviour conformed to the Weber law, they should be more likely to make optimal decisions about whether to attack or retreat from opponents when the ratio of the number of dogs in the smaller pack to the number of dogs in the larger one is small (i.e. when the difference in size between the interacting packs is large and easier to assess). This would provide indications that dogs are representing quantities as noisy mental magnitudes. We also predicted that if dogs represented both small (≤ 4) and larger quantities as approximate mental magnitudes, they should be able to successfully discriminate small (≤ 4) from larger group sizes provided the ratio between them is sufficiently small.

On the other hand, if the performance of dogs in making optimal decisions does not improve with an increasing asymmetry in size, when the size of both the interacting packs is smaller than four, this would provide indications that assessment of relative group size is based on a more precise mechanism (possibly, 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 and Leimar 1987). For instance, wolves are more likely to respond to human howling in the presence of a valuable resource such as a recent kill (Harrington and Mech 1979). Moreover, the owners of a territory may value the contested resources more highly than the intruders (Krebs 1982; Tobias 1997; Johnsson and Forser 2002) and, thus, should be expected to be more motivated to fight. In order to control for these important confounding effects, 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 by recording the locations of scent-marking activities.

Methods

Study area

The research was carried out in a suburban environment sited in the south-west periphery of Rome (Italy), an area usually known as "Muratella". The study area covered a total surface of about 300 ha and was delimited to the north, west and south sides by roads with heavy traffic, and to the east side by cultivated areas. The area was split by another road in two different sectors, one in the south-west part and another in the north-east. The south-west sector was urbanized although not densely populated, whereas the north-east one was mainly occupied by a natural reserve called "Tenuta dei Massimi". The habitat in the reserve consisted mainly of open grasslands with interspersed wooded areas (see Bonanni et al. 2010a for a more detailed description).

Free-ranging 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 (mainly meat from a slaughterhouse) brought by volunteer dog caretakers. Food was placed, together with water, at specific feeding sites in the close vicinity of the road.

Animals and packs' history

This study was part of a longer research project begun in April 2005. A census of the dog population revealed that about 90–100 adult animals inhabited the study area, leading to a very conservative estimate of density of about 30 animals/Km^2 (Cafazzo 2007). All dogs of the studied population were medium-large sized mongrels, and there was not a recognizable predominant breeding type. Those that travelled, rested and defended resources as a cohesive unit (Cafazzo 2007), thus fitting the definition of a canid pack (Mech 1970), were considered to belong to the same group.

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

The studied population 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.

This research focused mainly on three of the eleven packs living in the area during the period May 2007–September 2008. These three groups were selected because they lived in a sector of the study area characterized by many wide open spaces and good observation 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 raise their hind leg higher than females; Bekoff 1979).

For the purposes of this research, individuals were assigned to broad age classes: they were considered as juveniles until the age of 11 months, subadults from 1 to 2 years of age and adults afterwards (see Bonanni et al. 2010a, b for details of age estimation).

At the beginning of this study (May 2007), the "Corridoio pack" comprised 11 individuals: four intact males (one adult and three subadults), two neutered males (one adult and one subadult), two intact females (one adult and one subadult) and three neutered females (one adult and one subadult). In November 2007, another intact female rejoined the pack after a long period of separation.

The "Curva pack" consisted of 10 individuals: one intact adult female, four intact males (three adults and one subadult), one neutered subadult male and four juveniles (three females and one male). One month after the beginning of the study, one of the males dispersed.

The "Piazza pack" included four individuals: one intact adult male, one neutered subadult male and two neutered females (one adult and one 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 four intact adult males and two 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 generalized linear model (see more details in the following paragraphs).

Behavioural observations

Observations on dogs' behaviour were conducted daily usually between 6:00 o'clock am and 5:00 o'clock pm 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 which individuals belonging to that pack were present at that time (group members were not together all the time) and monitored any subsequent variation. Dogs were observed from distances ranging between 20 and 150 m using 10 × 50 binoculars. If two packs were located within a few hundreds of metres (or less) of each other, we considered that an intergroup conflict might be imminent and thus selected an observation point from which the behaviour and composition of both packs could be recorded. Observation points were more elevated than the location where the conflict was expected to occur unless the dogs were so close that the observer could follow the packs on foot. 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 m of each other at the time when an intergroup conflict began. When resting, most pack members were often within 1–10 m of the nearest companion, 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.

A pack was considered as behaving aggressively towards another group when (1) at least one pack member approached aggressively at least 10 m towards another pack that was between 20 and 100 m away at the beginning of conflict, and (2) if at least one pack member lunged towards opponents when the distance separating the two packs was less than 20 m. This criterion was used because most interactions between groups did not involve aggressive physical contact (with bites and/or scratches), but rather threatening displays that consisted of group members running together towards the opponents, while barking furiously and snarling, or of group members walking towards opponents with a tense body posture while staring at opponents and keeping the tail raised. Opposing packs reacted to a threat with one of the following responses: retreat (walking or fleeing away from opponents); counterattack (at least one group member approaching aggressively as defined earlier); bark defensively but without any approach; no response to the threat.

A pack was regarded as having lost an intergroup conflict when 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 case the contested resource was food. Conflicts over access to food occurred in the following contexts: (i) when two packs were waiting for the food brought by people, and once the food was dispensed, conflict occurred; (ii) a pack or single dog approached a feeding site where another pack was already 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 participating individuals stopped showing signs of aggression. Two consecutive agonistic interactions involving the same packs were regarded as two distinct events in one of the following cases: (i) when all individuals belonging to the interacting packs returned to the locations they held before the interaction took place and then another one ensued; (ii) the packs did not resume their original locations but at least 10 min elapsed between the end of the previous aggression and the beginning of the second one; (iii) less than 10 min had elapsed since the end of the previous encounter, but the group composition had changed in the meantime.

Altogether, we spent in field 1,147.2 h during the period May 2007–September 2008, in which we observed 392 intergroup conflicts. We succeeded in collecting exhaustive 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. Moreover, interactions were discarded when an oestrus female was present within 50 m of any member of an interacting pack, given that oestrus females may be amicable towards stranger males. Finally, the individual frequencies of active participation in conflicts were examined in another paper (Bonanni et al. 2010a).

Defended areas

We defined a territory as a defended area from which competitors are excluded. In order to control for the effects of owner–intruder asymmetries on the agonistic behaviour of dogs, we recorded the locations of scent-marking events (ad libitum sampling, Altmann 1974) on a 1:1,250 scaled map of the study area (to the nearest 20–30 m). 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 and Mech 1975; Bradshaw and Nott 1995; Sillero-Zubiri and 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 Curva 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 m beyond the boundary of its own area.

Statistical design

Since we observed repeated interactions among a limited number of packs, many of our data were not statistically independent. To control for this 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 "focal pack" and to the non-selected one as "opposing pack". Then, we applied generalized linear models with a logit link function (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. Generalized linear models allowed assessing the effect of each numerical variable on the agonistic behavioural response of dogs while controlling for the effect of all potentially confounding variables simultaneously (Dobson 1990).

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. Predictor variables were the same for both the models: ratio of the number of opposing pack members present to the number of focal pack members present, number of focal pack members present, food presence (scored as a binary variable "yes" and "no"), the sex ratio of the two interacting packs and the identity of the focal pack. The "number of focal pack member present" was included in the model to control for the possibility that, by simple probability, larger packs would be more likely to contain at least one dog that will attack or retreat, and this would hold irrespective of the asymmetry in size between the conflicting packs. Moreover, inclusion of focal pack identity allowed controlling for the possibility that members of specific packs would be inherently more aggressive than others (or more prone to retreat), irrespective of the asymmetry in size between the conflicting packs. Note that it was not necessary to include opposing pack identity because, given the limited number of packs studied, this would have been dependent on the identity of the focal pack. 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.

We also carried out a post hoc analysis using three different subsets of the recorded interactions: the first subset consisted of the interactions in which both packs included more than four individuals present; the second subset comprised those interactions in which one pack was larger than four and the other one smaller than or equal to four; the third subset included the interactions in which the size of both packs was smaller than or equal to four. We ran again generalized linear models with the following predictor variables: ratio of the number of opposing pack members present to the number of focal pack members present and "odds of winning" (scored as a categorical variable "favourable" and "unfavourable" depending on whether the focal pack outnumbered opponents or was outnumbered, respectively). All other predictor variables were not included in this post hoc analysis because their effect on the agonistic behaviour of dogs was not significant (see Results). The variable "odds of winning" was included to check whether dogs were able to assess which pack held the numerical advantage even when the asymmetry in size was small (or, in other words, when the discrimination of quantities was more difficult). Since these predictor variables were related to each other, we used a backward stepwise procedure (Darlington 1990) in order to select the best predictor of the dependent variables or, in other words, the numerical variable that was most related to the agonistic response of dogs.

The goodness of fit of our generalized models was evaluated using the "deviance" statistic (Agresti 1996) which compares the maximized loglikelihood for the models of interest with that of the saturated model. Thus, adequate fit of the models will correspond to a finding of non-significance for such a test.

Finally, we calculated accuracy in discriminating larger versus smaller group size across these three subsets. This was defined as the percentage of conflicts in which dogs displayed an "adaptive response": attacked opponents when outnumbering them, did not attack when they were outnumbered (with respect to attacking behaviour); retreated when outnumbered by opponents, did not retreat when holding the numerical advantage (with respect to retreating behaviour). We compared the values obtained across the three subsets using a chi-square test.

Table 1 shows a list of the ratios opposing pack members present/focal pack members present faced by each focal pack.

Table 1 Summary of the ratios opposing pack members present/focal pack members present faced by focal packs. Within each subset, ratios are ordered from the lowest (top) to the highest (bottom) expected difficulty in quantity discrimination. Numbers in parentheses indicate the frequency of occurrence of that ratio

	Packs			
Subsets	Corridoio	Curva	Piazza	Fused
Both packs >4 members	5:10	11:5		5:9
	5:9	10:5		7:11 (2)
	11:7 (4)	9:5		5:7
	10:7	6:5		8:11 (7)
	6:8			6:8
	11:8 (6)			9:11 (3)
	11:9 (2)			10:9
	10:9			9:10
One pack >4 members One pack ≤4 members	1:10	10:2	9:1	10:1
	9:1	1:5 (2)	8:1	1:10
	2:11	11:3	6:1	1:9
	5:1 (5)	10:4 (2)	11:2	1:8
	2:9 (3)	2:5	5:1	7:1
	8:2 (2)	7:3	9:2	2:11 (2)
	2:8	8:4 (2)	11:3	2:10
	3:10 (2)	3:5 (3)	7:2	2:9
	3:9 (2)	5:3	10:3 (4)	3:9
	4:11 (2)	5:4 (2)	9:3 (2)	4:12
	3:8	4:5	11:4	3:5 (2)
	5:2		7:3 (2)	
	10:4			
	6:3			
	3:5			
	5:3 (2)			
Both packs ≤4 members	1:4 (2)	1:4 (2)	4:1	1:4
	3:1 (2)	1:2	3:1	2:3
	2:1	2:3	1:2 (4)	
	1:2	3:2	2:1	
	2:4	3:4 (3)	4:2	
	4:2	4:4	2:3	
	3:2 (2)			
	2:3			
	2:2 (2)			
	3:3			

Results

Defended areas

The spatial analysis of marking events ($n = 819$) seemed to indicate that dogs were not defending exclusive areas. 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. Since all of the 146 observed conflicts between the studied packs occurred within 100 m of the overlapping areas, we did not further consider the effect of the owner–intruder asymmetry on aggressive behaviour in this study.

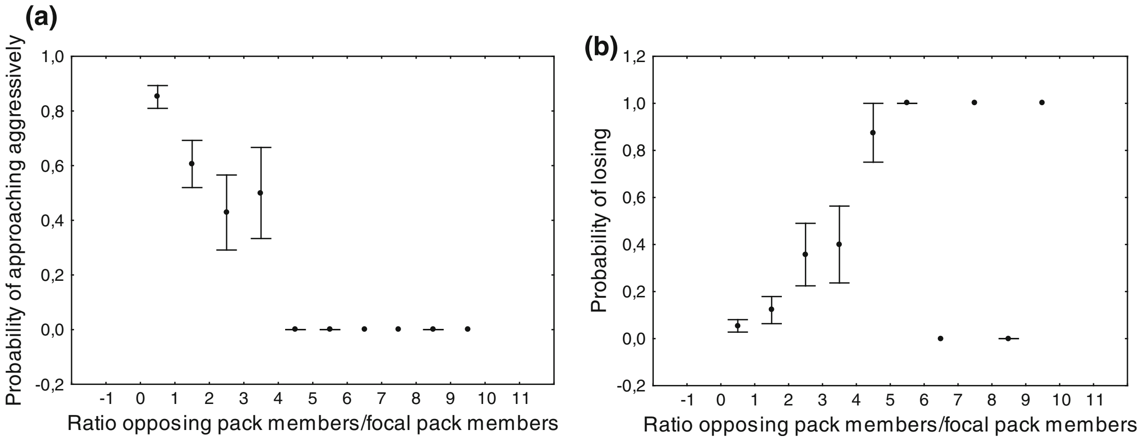

Fig. 1 Observed probability of approaching aggressively by at least one focal pack member (**a**) and of losing an intergroup conflict (**b**) versus the observed ratio of the number of opposing pack members present to that of focal pack members present (all interactions). *Points* indicate mean values; *whiskers* indicate standard errors

Intergroup conflicts

Out of 198 intergroup contests for which we had exhaustive information 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 three 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 eight interactions (8.7%). There were three 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 recorded in nine out of 198 interactions (4.5%).

The generalized linear model (GLZ) developed for the overall probability of approaching aggressively by at least one pack member showed that the ratio of the number of opposing pack members present to the number of focal pack members present was the only significant predictor variable (*coefficient* = −1.05 ± 0.32, *Wald Statistic* = 10.83, $P = 0.001$; *model deviance* = 126.74, $df = 124$, $P = 0.42$). Precisely, the probability of aggression increased with decreasing this ratio (Fig. 1a). Note that the effect of this ratio was significant when all other potentially confounding variables (including "focal pack identity" and "number of focal pack members present") were kept constant.

The GLZ of the binary variable "losing" or "non-losing" revealed a similar trend: the probability of losing an intergroup conflict was significantly affected only by the ratio of the number of opposing pack members present to the number of focal pack members present (*coefficient* = 0.50 ± 0.22, *Wald Statistic* = 5.19, $P = 0.023$; *model deviance* = 95.36, $df = 124$, $P = 0.97$) and increased with increasing this ratio (Fig. 1b). Again, the effect of the ratio was significant when all other predictor variables were kept constant. Moreover, note that this ratio was highly correlated to the ratio of the number of attacking opposing pack members to the number of focal pack members present (Pearson correlation: $r = 0.78$, $n = 146$, $P < 0.00001$).

When considering only the subset of interactions in which both the competing packs contained more than 4 dogs (mean ratio of the smaller to the larger pack ± SEM. was 0.71 ± 0.02; $n = 38$; range: 5:11–9:10), the backward stepwise procedure showed that none of the predictor variables had a significant effect on either the probability of approaching aggressively (ratio of the number of opposing pack members present to the number of focal pack members present: *Score Statistic* = 0.04, $P = 0.849$, Fig. 2a; odds of winning: *Score Statistic* = 0.49, $P = 0.485$) or that of losing the conflict (ratio of the number of opposing pack members present to the number of focal pack members present: *Score Statistic* = 0.87, $P = 0.352$, Fig. 2b; odds of winning: *Score Statistic* = 2.11, $P = 0.146$).

The generalized linear models developed for both the probability of aggression and that of losing on the subset of interactions when the size of one pack was larger than four and the size of the other was smaller than or equal to four (mean ratio of the smaller to the larger pack ± SEM was 0.33 ± 0.02; $n = 74$; range: 1:10–4:5) revealed that in both cases the ratio of the number of opposing pack members present to that of focal pack members present was the only significant predictor (*coefficient* = −1.06 ± 0.24, *Wald Statistic* = 20.27, $P < 0.0001$, *model deviance* = 56.2, $df = 72$, $P = 0.91$; *coefficient* = 0.53 ± 0.15, *Wald Statistic* = 13.17, $P < 0.0003$, *model deviance* = 65.35, $df = 72$, $P = 0.70$, respectively). The probability of aggressive

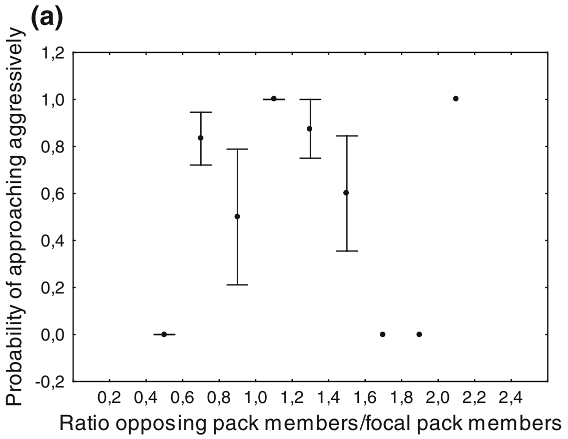

Fig. 2 Effect of the ratio of the number of opposing pack members present to that of focal pack members present on the probability of aggressive approach by at least one focal pack member (**a**) and of losing an intergroup conflict (**b**) in interactions where both the interacting packs comprised more than 4 individuals. *Points* indicate mean observed values; *whiskers* indicate standard errors

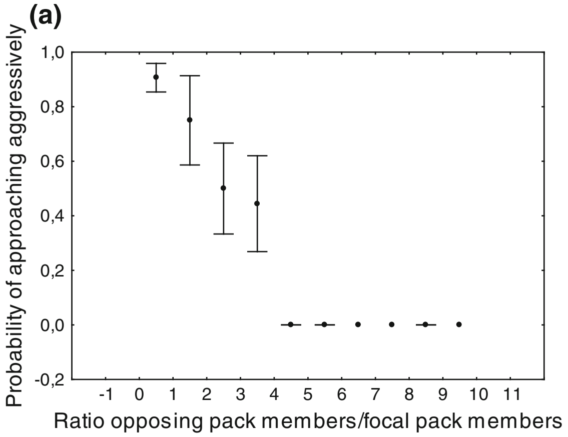

Fig. 3 Observed probability of approaching aggressively by at least one focal pack member (**a**) and of losing an intergroup conflict (**b**) versus the observed ratio of the number of opposing pack members present to that of focal pack members present in interactions when one pack comprised a number of individuals higher than 4 and the other one smaller than or equal to 4. *Points* indicate mean values; *whiskers* indicate standard errors

approach increased with decreasing the ratio and that of losing increased with increasing the ratio (Fig 3 a, b).

When considering the subset of interactions in which the size of both competing packs was smaller than or equal to four (mean ratio of the smaller pack to the larger one ± SEM was 0.50 ± 0.03; $n = 30$; range: 1:4–3:4; four interactions in which packs were equal in size were excluded from this analysis), we found that aggression was significantly affected only by the categorical variable "odds of winning" (*coefficient* = 2.20 ± 0.65, *Wald Statistic* = 11.59, $P < 0.0007$; *model deviance* = 18.27, $df = 28$, $P = 0.91$), that is the probability of attack was close to one with "favourable odds" and was close to zero with "unfavourable odds" (Fig 4a). The GLZ developed on the same subset of interactions for the probability of losing the conflict showed that the ratio of the number of opposing pack members present to that of focal pack members present was, this time, the only significant predictor of the dependent variable and the probability of losing increased with this ratio (*coefficient* = 1.67 ± 0.63, *Wald Statistic* = 7.16, $P = 0.0075$, *model deviance* = 20.9, $df = 28$, $P = 0.83$; Fig 4b).

Accuracy differed significantly across the three subset, being highest when both groups were small and lowest when both groups were large (aggressive response: $\chi^2 = 18.54$, $df = 2$, $P < 0.0001$; values: 45, 75.6, 90% for both groups > 4, one group > 4 and one group ≤ 4, both groups ≤ 4, respectively. Retreat response: $\chi^2 = 9.52$, $df = 2$, $P < 0.009$; values: 45, 66, 80% for both groups > 4, one group > 4 and one group ≤ 4, both groups ≤ 4, respectively.

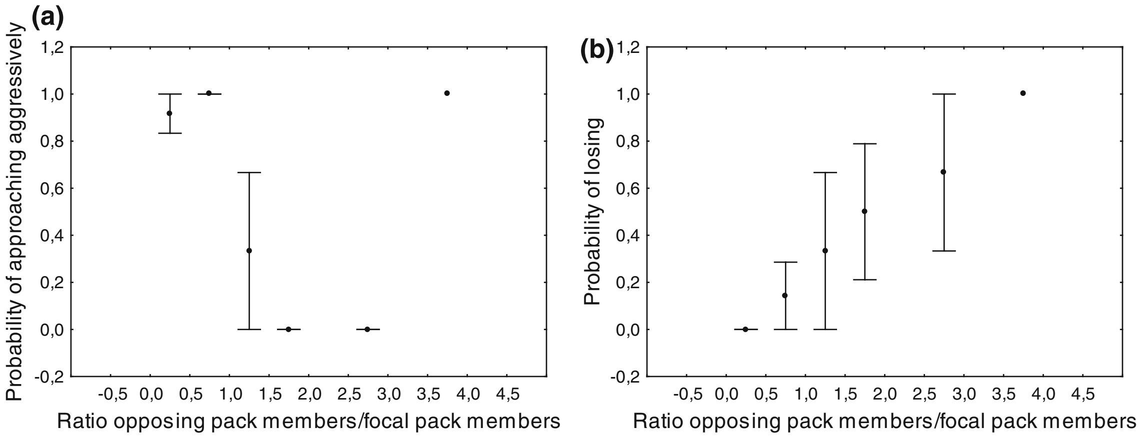

Fig. 4 Observed probability of approaching aggressively by at least one focal pack member (**a**) and of losing an intergroup conflict (**b**) versus the observed ratio of the number of opposing pack members present to that of focal pack members present in interactions when both interacting packs comprised a number of individuals smaller than or equal to 4. *Points* indicate mean values; *whiskers* indicate standard errors

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 and Schneider 1995). Consequently, 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 is evidence that they still retain important aspects of the social organization of their wild ancestors that evolved before domestication (Bonanni et al. 2010a, b; Cafazzo et al. 2010).

In this study, we have provided evidence that free-ranging dogs are able to assess relative group size in intergroup conflicts and to use this information adaptively: dogs of the packs studied were more likely to approach aggressively opposing packs when the ratio of the number of opposing pack members present to the number of focal pack members present was lower, and were more likely to withdraw from a conflict when the ratio of the number of opposing pack members present to that of the focal pack members present was higher. It is important to stress that the effect of the ratio on the intergroup agonistic behaviour of dogs was significant even when other potentially confounding variables, especially the total number of focal pack members present and the identity of focal packs, were kept constant. In fact, an apparent significant effect of the ratio opponents/companions on intergroup agonistic behaviour could simply result because larger packs are more likely to contain at least one individual that will attack or retreat, and also individuals that would be inherently more aggressive (or more prone to retreat) than others. However, since these effects were controlled and were not significant, our results suggest that the decision of dogs whether to attack/retreat was actually based on assessment of relative group size. Apparently, dogs were behaving in a manner resembling an evolutionarily stable strategy (Maynard Smith and Parker 1976) 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”.

However, there were also several cases in which smaller packs attacked larger ones and won the contest. Game theoretical models predict that aggression by competitors with the lower RHP should occur when the value of the contested resource is extraordinarily high so as to compensate for the costs of fighting a superior opponent (Parker and Rubenstein 1981; Austad 1983; Enquist and Leimar 1987; Bonanni et al. 2007). These arguments seem to apply to intergroup conflicts as well. For instance, male black howler monkeys respond 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). However, in our study we did not detect any significant effect of food resources on intergroup agonistic behaviour. Food resources were indeed abundant and of relatively low value when compared to the potential costs of an escalated fight. Under these 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 asymmetries in RHP between competitors are small. Consistent with this theory, in our study aggression by the smaller pack was more common in conflicts when both groups comprised more than four individuals, that is, when asymmetries in size between the two conflicting packs were smaller than average.

From a proximate perspective, aggression by smaller dog 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 conflicting groups comprised more than four individuals, the ratio of the number of opposing pack members present to the number of focal pack members present 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 an optimal decision about their intergroup agonistic behaviour when the size of both interacting packs was larger than four. However, it should be noted that in this subset of interactions dogs had to compare group sizes, in order to make the decision to attack/retreat, which 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 four individuals and the other one less than four, dogs had to estimate both large and small numerosities in order to make an optimal decision about their intergroup agonistic behaviour, but they also had 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 affected by the ratio of the number of rivals to that of companions (probability of aggression increased with a decreasing ratio, and that of losing increased with an increasing ratio), indicating that dogs were able to 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 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 this law and that dogs represent the quantity of conspecifics as noisy mental magnitudes subject to scalar variability. Moreover, this result supports the hypothesis that a single, general approximate number system can be used by dogs to represent both small (≤ 4) and large quantities. Actually, successful performance in discriminating small versus large quantities would not be easily predicted by postulating the existence of a system operating only with large numbers and of another one operating only with small numbers (see Introduction).

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 and Smuts 2007). Many other studies on a wide range of taxa support the view that animals represent numbers as approximate mental magnitudes (rats, Platt and Johnson 1971; monkeys, Flombaum et al. 2005; apes, Call 2000; Beran 2004; fishes, Agrillo et al. 2008), suggesting that this 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, a result consistent with the hypothesis that the need to reduce the costs of intergroup aggression might have contributed to the evolution of numerical cognitive abilities. Moreover, our results and those of Ward and 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.

Free-ranging dogs appeared to correctly assess relative group size also in situations when both the interacting packs comprised a number of individuals smaller than or equal to four, despite having to compare group sizes which differed by a greater mean ratio (0.50) than that recorded in interactions where one of the group sizes was larger than four. Assessment of relative group size appeared to be even more accurate in this case. The stepwise procedure indicated that the variable we termed "odds of winning" was, this time, a better predictor of the occurrence of intergroup aggression than the ratio of the number of opponents to that of companions. In particular, dogs approached aggressively with roughly the same probability when they outnumbered opponents by a ratio 1:2 as when the ratio was 2:3 or 3:4, indicating that, with small numbers, they discriminated the larger from the smaller group size equally well irrespective of the ratio (there were just three exceptions: one single dog approached aggressively a pack of four individuals, a pack of two dogs approached a group of three, and a pack of two dogs failed in attacking a single opponent; see Fig. 4a). Apparently, this may indicate that, in our study, free-ranging dogs might have been discriminating between 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; Feigenson and Carey 2005). This is in contrast with the results of the study by Ward and Smuts (2007) in which many dogs failed to discriminate the larger from the smaller quantity of food when these differed by one item. So, one could speculate that the object-file system may be activated in dogs in order to assess quantities of conspecifics, but not to assess quantities of food items. However, we have also found that the probability of losing the contest (retreating), with both group sizes smaller than four, was better predicted by the ratio of the number of opponents to that of companions (see Fig. 4b), thus suggesting that even the discrimination of small group sizes may become easier with more extreme numerical imbalances. Another explanation is 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 the evidence in support of the object-file model is equivocal, it remains possible that two different mechanisms are involved in the representation of small numbers, the first being more precise and the other being based on noisy mental magnitudes. Actually, it should be noted that, irrespective of which numerical variable was the best predictor of dogs' agonistic behaviour, the overall accuracy of dogs in assessing relative group size was higher when both groups were small (≤ 4), when compared to situations when one of the group sizes was larger than four, again despite the fact that, according to the Weber law, discrimination was expected to be easier in the latter subset of interactions (mean ratio of the smaller to the larger group for the two subsets was 0.50 and 0.33, respectively). However, an alternative explanation to that of the object-file is that dogs may assess small group sizes using perceptual variables relating to the spatial arrangement of individuals, and this may improve performance with small numbers (see Revkin et al. 2008 for a similar argument in adult humans).

It has been suggested that domestic dogs are able to remember mental representations of quantity (Ward and Smuts 2007) and also to operate over these representations by performing very simple additions (West and Young 2002). However, in this study, we have not implied the ability of the dogs to count. Moreover, it is possible that, in our study, free-ranging dogs were not actually representing numbers, but instead continuous variables which co-varied 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 seems to represent a common phenomenon in animals (e.g. bottlenose dolphins, *Tursiops truncatus*, Kilian et al. 2003; pigeons, *Columbia livia*, Emmerton and Renner 2009; grey parrots, Al Aïn et al. 2009; domestic cats, *Felis silvestris catus*, Pisa and Agrillo 2009). 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 and Gelman 2000).

In conclusion, we have provided the first evidence that free-ranging dogs spontaneously assess relative group size in natural intergroup conflicts and that they may do this using cognitive mechanisms that are similar to those operating in species tested under controlled conditions. Specifically, our results appear to be consistent with two interpretations: (1) dogs may assess large quantities as noisy magnitudes and small quantities using either object-files or noisy magnitudes depending on the context. For instance, the approximate number system may operate when they have to compare small versus large quantities, provided the ratio between these is small (see Cordes and Brannon 2009). (2) Dogs may rely on a single general system based on approximate magnitudes to assess both large and small quantities, although perceptual mechanisms (e.g. subitizing) may facilitate performance when dealing only with small numbers. Future research should also clarify whether dogs actually use number in order to assess opponents or rather continuous variables or both.

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