

Dominance in relation to age, sex, and competitive contexts in a group of free-ranging domestic dogs

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Current knowledge about social behavior of free-ranging domestic dogs is scarce, and the possibility that they could form stable social groups has been highly debated. We investigated the existence of a social-dominance hierarchy in a free-ranging group of domestic dogs. We quantified the pattern of dyadic exchange of a number of behaviors to examine to what extent each behavior fits a linear rank-order model. We distinguished among agonistic dominance, formal dominance, and competitive ability. The agonistic-dominance hierarchy in the study group shows significant and substantial linearity. As in random assortments of captive wolves, there is a prominent but nonexclusive male agonistic dominance in each age class. The agonistic rank-order correlates positively and significantly with age. Submissive–affiliative behavior fulfills the criteria of formal submission signals; nevertheless, it was not observed among all dogs, and thus, it is not useful to order the dogs in a consistent linear rank. Agonistic-dominance relationships in the dog group remain stable across different competitive contexts and to the behaviors considered. Some individuals gain access to food prevailing over other dogs during competitions. Access to food resources is predicted reasonably well by agonistic rank order: High-ranking individuals have the priority of access. The findings of this research contradict the notion that free-ranging dogs are “asocial” animals and agree with other studies suggesting that long-term social bonds exist within free-ranging dog groups. *Key words:* age–sex class relationships, *Canis lupus familiaris*, food competition, influence of competitive context, linear dominance hierarchy. [*Behav Ecol* 21:443–455 (2010)]

Social organization refers to the spatial relationships, group composition, and patterns of social interaction among individuals and the overall manner in which these variables interact to characterize a population (Bekoff and Wells 1986). Among Canids, we can observe an evident inter and intraspecific variation in social organization that is often a response to the quantity and distribution of local food resources and the strategy for acquiring those resources. The domestic dog (*Canis lupus familiaris*) is a member of Canids and descends from the wolf (*Canis lupus*) (Vilà et al. 1997; Clutton-Brock 1999), a highly social species; in spite of this, the possibility that free-ranging dogs form stable social groups has been intensely debated (Scott and Fuller 1965; Beck 1975; Fox et al. 1975; Kleiman and Brady 1978; Berman and Dunbar 1983; Daniels 1983a; Font 1987). Here, free-ranging dogs are defined as those domestic dogs that do not have an owner and whose movements and activities are not limited by human beings.

Only a small number of rural and urban field studies have been conducted on the behavior and ecology of free-ranging dog populations. Essentially, there are not many canine social groups suitable for behavioral studies because in westernized countries the presence of free-ranging dogs is forbidden by law. In addition, the available groups of free-ranging dogs are not likely to be stable over time because their activities come into conflict with those of human beings and they are

removed from the territory. Moreover, the study of intraspecific social relationships in domestic dogs has been largely ignored by scientists, because they consider domestic animals as “unnatural” species and therefore unworthy or unsuitable as subjects for serious scientific investigation (Serpell 1995). However, mounting evidence suggests that the social organization of free-ranging dogs is modulated by the same ecological constraints that influence wild canid social systems (Macdonald and Carr 1995). Available literature about the ecoethology of free-ranging dogs concerns groups of limited size (from 2 to 11 individuals) and reports contrasting results (Beck 1975; Fox et al. 1975; Kleiman and Brady 1978; Rubin and Beck 1982; Berman and Dunbar 1983; Daniels 1983a, 1983b; Font 1987; Daniels and Bekoff 1989a, 1989b; Boitani et al. 1995; Macdonald and Carr 1995; Pal et al. 1998a, 1998b; Pal 2003). According to a number of these studies, free-ranging dogs defend a common territory, exhibit a dominance hierarchy, and share food (Font 1987; Pal et al. 1998a); others however have questioned the existence of a dominance hierarchy among members of free-ranging dog packs (Scott and Fuller 1965; Kleiman and Brady 1978; Berman and Dunbar 1983; Daniels 1983a; Boitani and Ciucci 1995; Boitani et al. 2007; Bradshaw et al. 2009). We investigate to what extent the concept of dominance can be used to describe also dogs’ social relationships.

We distinguished among different types of dominance hierarchy: agonistic dominance, formal dominance, and competitive ability as de Waal (1989) made for primates (Table 1). Agonistic dominance is expressed in the outcome of agonistic encounters. When an aggression is ignored or not followed by submission of the target individual, the agonistic interaction may not express a mutually acknowledged dominance

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Table 1
Summary of predictions

| Hypotheses | Predictions |
|--------------------------------------|---|
| Agonistic dominance | Dogs interact agonistically. An aggression may be followed by a submission, by another aggression, or may be ignored. In the last 2 cases, the interaction may not express a mutually acknowledged dominance relationship. Submissive interactions are considered as better indicators of a dominance relationship, and they show a higher level of linearity aggressive behaviors. |
| Formal dominance | Aggressive conflicts are rare. A subordinate dog acknowledges the higher dominance status of the other by showing formalized submissive signals, thus by showing submissive–affiliative behavior. Therefore, formal and agonistic dominance relationships coincide. Submissive–affiliative behavior is shown by dogs in each context. Submissive–affiliative behavior is always direct from 1 dog toward another one; therefore, this behavior is unidirectional |
| Competitive ability | Agonistic dominance rank in one context does not necessarily correspond to the agonistic dominance rank in another context. The access to resources does not necessarily correspond to the agonistic dominance rank. |
| Age-graded dominance hierarchy model | The dominance relationships are influenced by age: Adult dogs dominate over subadult dogs, and subadult dogs dominate over juvenile dogs. Males dominate over females within each age classes. |

relationship. Rowell (1966) has already demonstrated that subordinate behaviors are remarkably consistent in direction as compared with most dominant or aggressive behaviors. Therefore, submissive interactions are usually considered as better indicators of a dominance relationship (Rowell 1974).

Formal dominance is characterized by ritualized communication signals and greeting rituals, the direction of which does not vary across social contexts. Sometimes, formal and agonistic dominance relationships coincide, and this happens when the agonistic-dominance relationship is accepted by the subordinate. In this case, aggressive conflicts are rare (de Waal 1989), and the subordinate acknowledges the higher dominance status of the other by showing formalized submissive signals. To fulfill the criteria of an expression of formal dominance/submission, the behavior should be multicontextual and unidirectional. It should be expressed by different individuals and covary with other selected measures of agonistic rank. For example, unidirectional submissive signals such as teeth baring in rhesus macaques (*Macaca mulatta*, de Waal and Luttrell 1985), bowing and pant-grunting in chimpanzees (*Pan troglodytes*, de Waal 1982), silent-bared teeth display in pigtailed macaques (*Macaca nemestrina*, Flack and de Waal 2007), and greetings in spotted hyenas (*Crocuta crocuta*, East et al. 1993) are reliable ritualized expressions of formal rank. In domestic dogs, we observe an asymmetry in displaying some behaviors during social play. Bauer and Smuts (2007) reported that play in adult dogs reflects the existing dominance structure outside of play. In fact, dogs may use play to establish stable social relationships and test their place in the existing social structure of a group (Bekoff 1972). Ward et al. (2008) reported an increased asymmetry over time among littermates during social play; this may simply reflect dominance relationships formed during the juvenile period, making puppy play more similar to that of adult dogs in this respect. Outside of play, other behavioral pattern could be used asymmetrically as formal rank signals. We hypothesize that in domestic dogs as in wolves, the formal rank could be displayed by submissive–affiliative signals, that is, muzzle-liking associated with tail wagging that occurs often during group ceremony (Schenkel 1967).

The competitive ability reflects the capacity of an individual to obtain access to limited resources (e.g., food). The motivation to compete may vary according to the value of the resource that causes competition (Syme 1974; Parker and Rubenstein

1981; Enquist and Leimar 1987). Because both the value of the resource and the cost of winning a conflict (in terms of energy and time investment as well as the risk to be injured) may change considerably depending on the competitive context, the dominance relationship in a given dyad of individuals may also vary according to it (Hand 1986). Therefore, the agonistic dominance rank in 1 context does not necessarily correspond to the agonistic dominance rank in another context. Temporal variation in competitiveness also implies that an individual not always shows the same tendency to use competitive abilities. As a result, the access to resources does not necessarily correspond to the agonistic dominance rank. This model may help to explain the cases of male food deference to females during periods when the food is of particularly high value for the latter (periods corresponding to egg laying or estrus, e.g., Western Gulls, *Larus* spp., Hand 1986; chimpanzees, Stopka et al. 2001) and also why adult individuals of both sexes allow juveniles' feeding priority in a variety of taxa (e.g., wild dogs, *Lycaon pictus*, Malcom and Marten 1982; spotted hyenas, Frank 1986; several primates, Hand 1986; and domestic cat, Bonanni et al. 2007).

Another issue about dominance hierarchy is its relationship to the age and sex of members of the group. To explain the dominance relationships in our dog group, we suggest the "age-graded dominance hierarchy" model (Table 1) that Zimen (1982) proposed to explain the dominance relationships in wolf packs. Practically, in interactions with adults, juveniles usually are more humble; therefore, older wolves effectively intimidate younger wolves. Littermates may squabble over food or during rough play, and pups are disciplined by older family members (Packard 2003). This model has been presented in 2 ways: first simply as separate linear hierarchies within each sex, influenced but not absolutely determined by age (Schenkel 1967; Zimen 1982) and second, as male dominance over females within each age classes (Rabb et al. 1967; Fox 1980; Zimen 1982; Van Hooff and Wensing 1987; Savage 1988). Packard (2003) hypothesized that the former is more likely in a young nuclear family (parents and their offspring) and the latter in disrupted or complex families (e.g., a family in which one or both of the original parents is missing and where the immigration of individuals not born into the pack has been accepted).

To our knowledge, nobody has yet attempted to systematically evaluate the dominance relationships among members

of a free-ranging group of dogs within the ethological construct of agonistic dominance, formal dominance, and competitive ability. Thus, the aim of our paper was to determine whether 1) a dominance hierarchy based on the outcome of agonistic encounters in the absence of any source of competition (food or receptive females) exists in a social group of free-ranging domestic dogs; 2) the dominance rank established in this context corresponds to that established in the presence of food and in the presence of receptive females; 3) submission is a possible sign of formal dominance in domestic dogs. Finally, to be a relevant concept, a dominance order should have a more general predictive value in the sense that the rank order should correlate with other social behaviors (Richards 1974; Syme 1974). Thus, we recorded the ability of the dogs to monopolize the food to establish if the high social rank is associated with the ability to gain access to food.

MATERIALS AND METHODS

Study area

The study was carried out in a suburban environment, in the city of Rome, Italy. The area extends for about 300 ha at the Southwest of the outskirts of the city.

This area is scarcely urbanized. The most important buildings are the Office district of "Alitalia" (the Italian airline company), which is surrounded by some wide parking areas; a new residence, made up of several buildings; a new hotel; and a few yards.

An asphalt road goes through the area from South to Northwest and divides it into 2 zones: the "Southeast zone" and the "Northwest zone." The Southeast zone is the built-up area, where all the buildings mentioned above are situated. In contrast, the Northwest zone, which belongs to Tenuta dei Massimi urban Natural Park, is an area rich in spontaneous vegetation. However, on the outskirts of the Natural Park, there is another area of human activity represented by a quarry.

Dogs had free access to the Natural Park, to the parking areas, to the quarry, and to the building yards. Nevertheless, the individuals of the group analyzed mainly frequented the area of the Natural Park where a lot of thick spontaneous vegetation, such as trees and several bushes, offered good shelter for the animals, especially for lactating females with puppies.

In the area, we identified 3 feeding sites frequented by dogs belonging to the group. In these sites, food and water were provided daily by human volunteers. One of these sites, which we named "the gate," was the most important and regular feeding source for the dogs. Sometimes, dogs moved southward, and during these periods, they fed at the site named "the meadow." Dogs rarely were seen feeding at the third sites named "the parking area."

Subjects

The group of animals chosen as subject of this research belonged to a population of about 100 free-ranging domestic dogs. All of them were free-ranging animals, and they were not socialized with humans; therefore, they could breed and move freely. Nevertheless, although they were not under immediate human supervision, they were dependent on humans for food.

All the animals studied were identified individually by their coat color and pattern, hair length, body size, and sex. There was a narrow phenotypic variation among individual dogs. The dominant phenotype was a mongrel-like, wolf-looking dog, but there were also some wirehaired pointing griffon individuals.

The sex of adult dogs could be determined on the basis of some morphological (presence of testes in males) and behavioral characteristics, especially urination postures (Bekoff 1979).

Observations of this group of dogs began in March 2005; thus, we had direct knowledge of the dogs' ages less than

2 years. The ages of the other dogs were mostly provided by a group of dog caretakers who had been regularly feeding the dogs for the past 10 years. The ages of the remaining dogs were assessed by estimating the dogs' body size and general appearance (e.g., white hair on the muzzle) as well as tooth wear (e.g., Gier 1968) and eruption (Kirk 1977) for 10 adult dogs captured and anesthetized for closer analyses. Dogs were thus reliably classified as pups (birth to 6 months), juveniles (6 months to 1 year), subadults (1–2 years), and adults (more than 2 years) (Table 2).

Throughout the period of study, the number of individuals ranged from 40 to 25 dogs (Table 2). At the start of the study, in April 2005, the dog group consisted of 27 individuals: 6 intact adult males, 1 vasectomized male, 8 intact adult females, 3 spayed adult females, 4 juveniles males, 2 juveniles females, 3 pups (2 males and 1 female); 2 of the adult females (STE, a spayed adult female and GIN, an intact adult female) were abandoned in the study area and joined the group (all this information was provided by the group of dog caretakers). All other dogs were born in the study area and, presumably, were closely related. Subsequently, several females became pregnant (7 adult, 1 subadult, and 2 juvenile females) and were observed raising litters. The study lasted for 15 months, and the mean of time adult and subadult dogs belonged to the study group was 11.13 ± 4.80 months with a range extending from 3 to 15 months. Practically, of the 27 dogs present at the start of the study, 3 died, 2 disappeared, 6 dispersed after 6 months, whereas 2 after 3 months (1 adult female joined another group; another adult female remained alone with her pups; all other dispersed dogs formed a separate group); the remaining 14 dogs stayed together until the end of the study. The most of newborn individuals remained into the group, whereas others disappeared. Because some dogs disappeared or died in the short time after the start of the study (Table 2), we did not totalize sufficient hours of observation for all individuals; therefore, the final statistical analysis was applied only to 27 dogs: 6 adult males, 5 adult females, 4 subadult males, 1 subadult female, 6 juveniles males, and 5 juveniles females (Table 2).

Behavioral observations

The study began in April 2005 and lasted until the end of May 2006. Between April and August 2005, we carried out preliminary observations in order to 1) identify all individuals belonging to the group; 2) become familiar with the study area and accustom all dogs to the presence of the observer; and 3) establish the data collection methods.

Dog behavior was observed in 3 different social contexts: in the presence of food, in the presence of receptive females, and in the absence of any source of competition. Data collection was carried out following Altmann's (1974) methods: Focal animal sampling method was used in the absence of sources of competition, whereas the subgroup animal sampling method was used in the presence of food and receptive females; we totalized 282.53 h of observation.

From June 2005 to May 2006, we also used the ad libitum sampling method (Altmann 1974) for recording all behavioral patterns occurring out of focal sampling sessions and which were considered important for the aim of the study; we totalized 630.40 h of observations distributed over 197 days.

Agonistic behavior (including aggressive, dominance, and submissive behavior) was recorded by "all occurrences" method (Altmann 1974). Aggressive behavior included the following: threats (assuming a threatening posture: pointing, staring at, curling of the lips, baring of the canines, raising the hackles, snarling, growling, and barking), chasing, physical

Table 2
Variation in group composition during the period of the study

| Name | Spring 2005 | Summer 2005 | Autumn 2005 | Winter 2006 | Spring 2006 |
|---|-------------|-------------|-------------|-------------|-------------|
| Merlino (MER)^a | Pr,a | Pr,a | Pr,a | Pr,a | Pr,a |
| Gastone (GAS)^a | Pr,a | Pr,a | Pr,a | Pr,a | Pr,a |
| Pippo (PIP)^a | Pr,a | Pr,a | Pr,a | Pr,a | Pr,a |
| Leon (LEO)^a | Pr,a | Pr,a | Pr,a | Dd | — |
| Golia (GOL)^a v | Pr,a | Pr,a | Pr,a | Pr,a | Pr,a |
| Lancillotto (LAN)^a | Pr,a | Pr,a | Pr,a | Pr,a | Pr,a |
| Balù (BAL) | Pr,a | Pr,a | Dp | — | — |
| Mamy (MAY) ^a | Pr,a | Pr,a | Pr,a | Pr,a | Pr,a |
| Nanà (NAN) ^a | Pr,a | Pr,a | Pr,a | Ds | — |
| Isotta (ISO) ^a | Pr,a | Pr,a | Pr,a | Pr,a | Pr,a |
| Stella (STE) ^a s | Pr,a | Pr,a | Pr,a | Pr,a | Pr,a |
| Diana (DIA) ^a | Pr,a | Pr,a | Pr,a | Pr,a | Dd |
| Ginevra (GIN) | Pr,a | Pr,a | Dp | — | — |
| Baghera (BAG) | Pr,a | Dp | — | — | — |
| Ricciola (RIC) | Pr,a | Dp | — | — | — |
| Luna (LUN) s | Pr,a | Pr,a | Dp | — | — |
| Nina (NIN) s | Pr,a | Pr,a | Dp | — | — |
| Molly (MOL) | Pr,a | Pr,a | Dp | — | — |
| Pongo (PON)^a | Pr,j | Pr,s | Pr,s | Pr,s | Pr,s |
| Simba (SIM)^a | Pr,j | Pr,s | Pr,s | Pr,s | Pr,s |
| Semola (SEM)^a | Pr,j | Pr,s | Pr,s | Pr,s | Pr,s |
| Kimba (KIM)^a | Pr,j | Pr,s | Pr,s | Pr,s | Pr,s |
| Agata (AGA) | Pr,j | Pr,s | Ds | — | — |
| Morgana (MOR) ^a | Pr,j | Pr,s | Pr,s | Pr,s | Pr,s |
| Moogly (MOO) | Pr,p | Pr,p | Dp | — | — |
| Hansel (HAN)^a | Pr,p | Pr,p | Pr,j | Pr,j | Pr,j |
| Gretel (GRE) ^a | Pr,p | Pr,p | Pr,j | Pr,j | Dd |
| Mammolo^b (MAM)^a | — | Nb | Pr,p | Pr,j | Ds |
| Dotto^b (DOT)^a | — | Nb | Pr,p | Pr,j | Pr,j |
| Gongolo ^b (GON) ^a | — | Nb | Pr,p | Pr,j | Pr,j |
| Brontolo^b (BRO)^a | — | Nb | Pr,p | Pr,j | Pr,j |
| Eolo^b (EOL)^a | — | Nb | Pr,p | Pr,j | Pr,j |
| Pisola ^b (PIS) ^a | — | Nb | Pr,p | Pr,j | Pr,j |
| Cucciola ^b (CUC) ^a | — | Nb | Pr,p | Pr,j | Pr,j |
| Emy ^c (EMY) ^a | — | Nb | Pr,p | Pr,p | Pr,j |
| Mag ^c (MAG) ^a | — | Nb | Pr,p | Pr,p | Pr,j |
| Lisa ^c (LIS) | — | Nb | Pr,p | Ds | — |
| Gioia ^c (GIO) | — | Nb | Pr,p | Ds | — |
| Beth ^c (BET) | — | Nb | Pr,p | Ds | — |
| Nuvole ^c (NUV) | — | Nb | Pr,p | Ds | — |
| Bob^c (BOB) | — | Nb | Pr,p | Ds | — |
| John^c (JOH) | — | Nb | Pr,p | Ds | — |
| Misha ^b (MIS) | — | — | — | Nb | Pr,p |
| Joshua^b (JOS) | — | — | — | Nb | Pr,p |
| Sasha ^b (SAS) | — | — | — | Nb | Pr,p |
| Raja ^b (RAJ) | — | — | — | Nb | Ds |
| Total | 27 | 40 | 33 | 29 | 25 |

Totals are referred to the number of dogs present at the end of each season. Individuals are listed in the age order from older to younger.

Pr = present; Dd = died; Ds = disappeared; Dp = dispersed; Nb = newborn; a = adult; s = subadult; j = juveniles; p = pups; v = vasectomized; and s = spayed. Bold type: males and standard type: females.

^a Dogs selected for the final statistical analysis.

^b Mamy's pups.

^c Isotta's pups.

fighting, and biting. Dominance behavior included upright and stiff body posture with the head and tail held high and the ears pricked, putting the muzzle or a paw on a conspecific's back, and wagging with the tail held high. Submissive behavioral patterns, which are usually displayed in response to a threat, included: avoiding eye contact, holding the head down, flattening ears, holding the tail down or tightly between the hindlegs and against the belly, cringing, laying down on

the back exposing the ventral side of the chest and sometimes the abdomen, avoiding, and retreating.

Submissive–affiliative behavior, called by Schenkel (1967) active submissions, includes both submissive and affiliative elements: The posture is slightly crouched, the ears are flattened, and the tail is down and wagging; the muzzle of the dog who receives a display of submissive–affiliative behavior is licked with fast movements. Only in the presence of food did we recorded a further 2 submissive behaviors, that is, “interruption of feeding” and “withdrawing from food,” both of them occurring after receiving an aggression or dominance display.

The individual measure of all behavior patterns was corrected for animal observation time because the latter varied between individuals.

Observation of feeding sessions

From June to August 2005, we collected data in the presence of food using only the ad libitum sampling method. From September 2005 to the end of April 2006, data were collected also using the focal subgroup sampling method. During this period, we observed a total of 50 experimental feeding sessions, corresponding to 34.23 h of watching.

Usually, food (butcher or restaurant leftovers) was delivered to dogs between 0730 and 0930 h in the morning. Each feeding session started just after the food was placed on the ground and continued until all individuals left the feeding area; the food was rarely completely consumed.

In order to determine the individual number of acts per hour for all behaviors recorded, it was necessary to estimate the time that each dog spent in the presence of food. Therefore, during preliminary observations, the “feeding area” was defined by means of landmarks such as trees, rocks, and bushes and measured approximately to be 450 m².

The focal subgroup sampling method was applied to record dog behavior while feeding: We observed all individuals present within the feeding area. Because subgroup composition changed during a session, we recorded the sequence in which dogs arrived at the “feeding area” and left it. Because the food was delivered in several places inside the “feeding area,” it was not possible to determine an overall feeding order. Nevertheless, an evaluation of priority of access to food was obtained recording 2 behavioral patterns: “stealing food” and “displace over food.” The former occurred when a dog approached by certain individuals left its food; the “displace over food” occurred always after the displaying of 2 submissive behaviors in sequence: “interruption of feeding” and “withdrawing from food.”

Estrous females' observation sessions

From November 2005 to April 2006, we collected data on 6 females in estrus (3 adults, 1 subadult, and 2 juveniles) using both focal subgroup sampling (for a total of 72.95 h of recording) and ad libitum methods during 3 seasons (autumn, winter, and spring). We recorded the position of all males present within 15 m from the estrous female.

An estrous female was characterized by a swollen vulva and by vaginal bleeding. Observation began when one or more males tentatively approached the female to sniff and try to mount. Observations continued through the period in which the female accepted the mount attempts and stopped when the female refused to allow the male(s) in her company to mount and copulate for 2 or more successive days.

Observational procedure in the absence of any source of competition

From June to the mid-September 2005, we collected data in the absence of any source of competition using only the ad libitum sampling method. From mid-September 2005 to May 2006, data were collected also using the focal animal sampling

method for a total of 175.35 h of observation (6.49 ± 1.56 h per dog). Each individual's observations were equally distributed over that time period, as well as across daytime between 0600 and 1800 h.

Dominance hierarchy and behavioral analysis

In order to determine the agonistic dominance hierarchy, the outcomes of aggressive, submissive, and dominance dyadic interactions were ranked in 3 different squared matrices with winners on 1 axis and losers on the other. This procedure was applied to each social context, resulting in a total of 9 matrices, 3 for each context. Obviously, in the presence of receptive females, we determined the dominance relationships only among males. In the same way, in order to analyze the formal dominance hierarchy, the submissive-affiliative interactions were ranked in a squared matrix.

For each matrix, "coverage" was examined in terms of the number and percentage of dyads in which events occurred; unknown relationships were dyads in which no act occurred; 1-way relationships were those in which only 1 dog in the dyad performed the action; 2-way relationships were those in which both dogs performed the action, irrespective of frequency of interaction; and tied relationships were those where both dogs performed the action the same number of times. The directional consistency index (DCI) of a matrix was calculated as the total number of times that a behavior was performed in the direction of higher frequency within each dyad (H) minus the total number of times the behavior occurred in the direction of the lower frequency within each dyad (L), divided by the total number of times the behavior was performed by all individuals: $DCI = (H - L)/(H + L)$. This score varies from 0 (completely equal exchange) to 1 (complete unidirectional) (Van Hooff and Wensing 1987).

We tested the transitivity of dominance relationships among members of the social group, based on submissive behaviors using de Vries' (1995) improved version of Landau's index of linearity (Appleby 1983), which corrects for unknown and tied relationships (h'); h' varies from 0 (absence of linearity) to 1 (complete linearity); a value of $h' \geq 0.80$ was taken to indicate a strongly linear hierarchy. The statistical significance of h' was tested by means of a 2-step randomization test with 10 000 randomizations (de Vries 1995) using MatMan 1.1 (Noldus Information Technology, Wageningen, The Netherlands). Subsequently, we reorganized the dominance matrices using a procedure proposed by de Vries (1998) for finding a dominance order most consistent with a linear hierarchy. We applied this procedure to the behavior pattern that showed a highly significant level of linearity in each contest considered. This method minimizes the number and strength of inconsistent dominance relationship following de Vries's (1998) inconsistencies and sum of inconsistencies (I&SI) method, where inconsistent dyads are defined as a lower-ranking individual that dominates a higher ranking individual, and the strength of an inconsistent dyad is its element's distance from the matrix diagonal. The solution of the I&SI method is achieved by switching the relative positions of individuals in the dominance order until the numbers of I&SI below the matrix diagonal are minimized (de Vries 1998). This ranking procedure was applied using MatMan 1.1 (Noldus Information Technology).

Dominance rank order obtained in the absence of any source of competition was correlated to the dominance rank order established in the other 2 contexts (in the presence of food and in the presence of receptive females) in order to determine if different contexts could influence dog dominance rank.

Relationship between rank, sex, age, and behavioral data were analyzed by nonparametric tests (2 tailed) using STATIS-

TICA 7.1 edition (StatSoft Italy s.r.l. 2005). Probability level for rejection of the null hypothesis was set at $P < 0.05$. Kruskal-Wallis test to analyze the influence of age class (adult, sub-adult, and juvenile) on some behavioral patterns; to adjust for multiple comparisons (7 comparisons) the significance level α was adjusted using the Bonferroni method (dividing α by the number of tests: $0.05/7 = 0.007$; Sokal and Rohlf 1995). Media and range of behavioral patterns analyzed are listed in Table 3.

RESULTS

Agonistic behavior in the absence of any source of competition

The matrix based on aggressive interactions ($N = 119$) recorded between dogs showed a lack of linearity (improved linearity test (ILT): $h' = 0.13$, $P = 0.28$), probably because in almost 79% of the dyads, the behavior did not occur (Table 4). However, a significantly linear dominance hierarchy based on direction of submissive behaviors ($N = 487$ interactions) and dominance behavior ($N = 528$ interactions) was found (submissive behavior: ILT: $h' = 0.41$, $P < 0.00001$; dominance behavior: ILT: $h' = 0.40$, $P < 0.00001$). Both submissive and dominance behavior showed a very high DCI (DCI = 0.96 and DCI = 0.94, respectively).

Agonistic behavior in the presence of food

Contrary to what we found in the absence of any source of competition, the matrix based on aggressive interactions ($N = 329$) recorded in the presence of food showed a significant level of linearity although it was very low (ILT: $h' = 0.25$, $P = 0.003$). This was probably due to low coverage (60% of unknown relationships). This matrix showed a low DCI due to the high percentage of bidirectional relationships (Table 4). Dominance interactions ($N = 299$) also showed a significant but low level of linearity (ILT: $h' = 0.23$, $P = 0.008$), probably due to the high level of noncoverage (59.26%). But in this case, the DCI was high because we recorded a few 2-way relationships (Table 4).

Submission behavior ($N = 531$ interactions) recorded between dogs in the presence of food occurred rarely bidirectionally (2-way relationships: 1.99%) resulting in the highest DCI (DCI = 0.97). The matrix also showed quite a good coverage and a significantly but moderate linearity (ILT: $h' = 0.41$, $P < 0.00001$).

Agonistic behavior in the presence of receptive females

Aggressive interactions ($N = 645$) recorded between males in the presence of receptive females showed a significant level of linearity (ILT: $h' = 0.46$, $P = 0.0023$) but a low DCI (Table 4). This was due to several dyads in which both dogs displayed aggressive behavior toward one another (2-way relationships: 10.00%).

Dominance interactions ($N = 302$) showed both a significant and moderate level of linearity (ILT: $h' = 0.41$, $P = 0.006$) and a high DCI (Table 4).

The matrix of submissive behaviors ($N = 797$ interactions) showed the best coverage, the highest level of linearity (ILT: $h' = 0.57$, $P < 0.00001$), and a very high directional consistency index (Table 4).

Agonistic dominance rank and its correlates

All agonistic behaviors fulfill the criteria of dominance markers although aggressive behavior showed a fairly low directional consistency.

Table 3
Media and range of hourly rates of behavioral patterns considered

| Behavioral pattern | <i>N</i> | Media | Minimum | Maximum |
|--|----------|-------|---------|---------|
| Aggressive behavior displayed in the absence of any sources of competition | 27 | × | × | × |
| Aggressive behavior displayed in the presence of food | 27 | 1.67 | 0.00 | 5.73 |
| Aggressive behavior displayed in the presence of receptive females | 16 | 1.13 | 0.00 | 3.48 |
| Aggressive behavior received in the absence of any sources of competition | 27 | × | × | × |
| Aggressive behavior received in the presence of food | 27 | 1.53 | 0.00 | 4.08 |
| Aggressive behavior received in the presence of receptive females | 16 | 1.15 | 0.00 | 3.27 |
| Dominance behavior displayed in the absence of any sources of competition | 27 | 1.62 | 0.00 | 6.36 |
| Dominance behavior displayed in the presence of food | 27 | 1.44 | 0.00 | 5.59 |
| Dominance behavior displayed in the presence of receptive females | 16 | 0.34 | 0.00 | 1.63 |
| Dominance behavior received in the absence of any sources of competition | 27 | 1.08 | 0.00 | 5.46 |
| Dominance behavior received in the presence of food | 27 | 1.32 | 0.00 | 4.75 |
| Dominance behavior received in the presence of receptive females | 16 | 0.55 | 0.00 | 1.57 |
| Submissive behavior displayed in the absence of any sources of competition | 27 | 1.12 | 0.00 | 4.19 |
| Submissive behavior displayed in the presence of food | 27 | 0.15 | 0.00 | 0.70 |
| Submissive behavior displayed in the presence of receptive females | 16 | 1.40 | 0.00 | 3.28 |
| Submissive behavior received in the absence of any sources of competition | 27 | 1.53 | 0.00 | 6.78 |
| Submissive behavior received in the presence of food | 27 | 0.18 | 0.00 | 1.00 |
| Submissive behavior received in the presence of receptive females | 16 | 1.09 | 0.00 | 3.87 |
| Submissive–affiliative behavior displayed | 27 | 0.11 | 0.00 | 0.59 |
| Submissive–affiliative behavior received | 27 | 0.23 | 0.00 | 1.20 |
| Stealing food displayed | 27 | 0.30 | 0.00 | 2.12 |
| Displace over food displayed | 27 | 0.18 | 0.00 | 0.67 |
| Stealing food received | 27 | 0.29 | 0.00 | 1.70 |
| Displace over food received | 27 | 0.19 | 0.00 | 0.78 |

×: Aggressive interactions in the absence of any sources of competition have been too scarce to be analyzed.

In each context, the submissive behavior emerged as the best dominance measure because it had the highest and significant linearity and the highest DCI (Table 4). Therefore, we applied the procedure proposed by de Vries (1998) in order to reorganize the submissive behavior's matrices for finding a dominance order most consistent with a linear hierarchy. Then, we compared the rank found in the absence of any source of competition with that obtained in the presence of food (feeding rank) and in the presence of receptive females (estrous rank). The rank based on submissive behavior found in the absence of any source of competition was highly correlated

with the feeding rank ($r_s = 0.94$, $n = 27$, $P < 0.00001$) and with the estrous rank found among males ($r_s = 0.95$, $n = 16$, $P < 0.00001$). Considering submissive behavior, feeding rank was also correlated with estrous rank found among males ($r_s = 0.93$, $n = 16$, $P < 0.00001$). Consequently, we could assert that the slight differences in the rank order were probably due to the quite high percentage of unknown relationships recorded in each context, and thus, the dominance relationships in the dog group did not vary according to different competitive contexts. Then, in order to minimize the number of unknown relationships and to obtain the most

Table 4
Linearity, unidirectionality, and coverage of the different agonistic behaviors

| | h' ^a | DCI ^b | Unknown ^c | 1-Way ^d | 2-Way ^e | Tied ^f |
|--|-------------------|------------------|----------------------|--------------------|--------------------|-------------------|
| In the absence of any sources of competition | | | | | | |
| Aggressive behavior | 0.13 | 0.77 | 277 (78.92%) | 62 (17.66%) | 12 (3.42%) | 4 (1.14%) |
| Submissive behavior | 0.41 | 0.96 | 162 (46.15%) | 181 (51.57%) | 8 (2.28%) | 4 (1.14%) |
| Dominance behavior | 0.40 | 0.94 | 165 (47.01%) | 173 (49.29%) | 13 (3.70%) | 4 (1.14%) |
| In the presence of food | | | | | | |
| Aggressive behavior | 0.25 | 0.76 | 212 (60.40%) | 114 (32.48%) | 25 (7.12%) | 11 (3.13%) |
| Submissive behavior | 0.41 | 0.98 | 142 (40.46%) | 202 (57.55%) | 7 (1.99%) | 4 (1.14%) |
| Dominance behavior | 0.23 | 0.91 | 208 (59.26%) | 133 (37.89%) | 10 (2.85%) | 2 (0.57%) |
| In the presence of receptive females | | | | | | |
| Aggressive behavior | 0.46 | 0.84 | 48 (40.00%) | 60 (50.00%) | 12 (10.00%) | 1 (0.83%) |
| Submissive behavior | 0.57 | 0.97 | 39 (32.50%) | 77 (64.17%) | 4 (3.33%) | 0 (0.00%) |
| Dominance behavior | 0.41 | 0.90 | 69 (57.50%) | 48 (40.00%) | 3 (2.50%) | 1 (0.83%) |
| All submissive behavioral patterns | 0.63 | 0.96 | 80 (22.79%) | 253 (72.08%) | 18 (5.13%) | 3 (0.85%) |
| Submissive–affiliative behavior | 0.33 | 1 | 237 (67.52%) | 114 (32.48%) | 0 (0.00%) | 0 (0.00%) |

^a Improved linear hierarchy index (de Vries 1995).

^b DCI (Van Hooff and Wensing 1987).

^c Number and percentage of unknown relationships.

^d Number and percentage of 1-way relationships.

^e Number and percentage of 2-way relationships.

^f Number and percentage of tied relationships.

reliable dominance hierarchy, the outcomes of all submissive dyadic interactions ($N = 1815$) were ranked in a squared matrix (Table 5). When analyzing the direction of all submission events, we detected both a significant and quite high level of linearity among dogs (ILT: $h' = 0.63$, $P < 0.00001$) and a very high DCI (DCI = 0.96). The matrix of all submissions showed good coverage, a low percentage of unknown relationships, and relatively few 2-way and tied relationships (Table 4).

We found a significantly high correlation between the rank order based on all submission interactions (the agonistic rank) and the rank orders based on all other agonistic behaviors recorded in each context (Table 6).

The hierarchy derived from all submissive behaviors showed that the top positions in the group were occupied by 6 adult males (Table 5).

The agonistic rank order based on all submissive interactions was positively correlated to age with adult dogs dominating subadult individuals and subadult dogs dominating juveniles individuals ($r_s = 0.90$, $n = 27$, $P < 0.00001$). Among adult and subadult individuals, males dominated over females; among juveniles dogs, 1 male dominated all other individuals; 1 of the 5 females dominated 3 males; another female dominated 2 males, and the other 3 females were at the bottom of the hierarchy. So, there was partial but not complete male dominance among juveniles dogs. Males and females did not differ in agonistic behavior (Mann–Whitney U test; dominance behavior $U = 54$, $n_1 = 16$, $n_2 = 11$, $P = 0.09$; submissive behavior: $U = 80$, $n_1 = 16$, $n_2 = 11$, $P = 0.71$). The agonistic rank was positively correlated with aggressive behavior displayed by dogs in each context (presence of food: $r_s = 0.55$, $n = 27$, $P < 0.003$; presence of females: $r_s = 0.80$, $n = 16$, $P < 0.0002$;

absence of sources of competition: aggressive interactions in this context have been too scarce for analyzing), as well as with dominance behavior (presence of food: $r_s = 0.72$, $n = 27$, $P < 0.00002$; presence of females: $r_s = 0.80$, $n = 16$, $P < 0.0002$; absence of sources of competition: $r_s = 0.77$, $n = 27$, $P < 0.000003$). In other words, the higher the dogs were in the group ranking, the more aggressive and dominant they were toward other dogs. Nevertheless, it is worth noting that the alpha male was not the most aggressive dog, except in the presence of receptive females.

The correlation between rank and hourly rate of aggressive (presence of food: $r_s = -0.65$, $n = 27$, $P < 0.002$; presence of females: $r_s = -0.20$, $n = 16$, n.s.) and dominance (presence of food: $r_s = -0.21$, $n = 27$, n.s.; presence of females: $r_s = -0.32$, $n = 16$, n.s.; and absence of sources of competition: $r_s = -0.70$, $n = 27$, $P < 0.00004$) behaviors received by each dog were, in some cases, quite low and some of them failed to reach a statistically significant level. In the presence of food, most aggressive and dominance behaviors were directed from adult individuals toward subadult middle-ranking dogs, rather than toward juvenile low-ranking dogs (Kruskal–Wallis test: Aggressive behavior received, $H_2 = 17.97$, $n = 27$, $P = 0.0001$; dominance behavior received, $H_2 = 12.05$, $n = 27$, $P = 0.003$). In the presence of receptive females, we did not find a relation between age and agonistic behaviors received by each dog.

In the absence of any source of competition, dominance behaviors were displayed more frequently than aggressive behaviors (Wilcoxon Signed-Ranks Test: $t = 6.00$, $z = 3.81$, $n = 27$, $P = 0.0001$). On the contrary, in the presence of receptive females, aggressive postures emerged significantly more frequently than dominance postures (Wilcoxon

Table 5
Dominance relationships based on all submissive behavioral patterns recorded among dogs

| | Receiver | | | | | | | | | | | | | | | | | | | | | | | | | | |
|------------|----------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Signaler | Mer | Gas | Pip | Leo | Gol | Lan | May | Nan | Iso | Dia | Sim | Pon | Sem | Kim | Mor | Ste | Han | Cuc | Mam | Dot | Gon | Gre | Bro | Eol | Mag | Emy | Pis |
| Mer | 94 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Gas | | 49 | | | | | | | | | | | | | | | | | | | | | | | | | |
| Pip | | | 3 | | | | | | | | | | | | | | | | | | | | | | | | |
| Leo | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | |
| Gol | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | |
| Lan | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | |
| May | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | |
| Nan | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | |
| Iso | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | |
| Dia | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | |
| Sim | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | |
| Pon | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | |
| Sem | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | |
| Kim | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | |
| Mor | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | |
| Ste | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | |
| Han | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | |
| Cuc | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | |
| Mam | | | | | | | | | | | | | | | | | | | 1 | | | | | | | | |
| Dot | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | |
| Gon | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | |
| Gre | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | |
| Bro | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| Eol | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | |
| Mag | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | |
| Emy | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | |
| Pis | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |

Bold type: males; standard type; females. The signalers are listed in rows, whereas the recipients in columns. The signalers are the performers of the submissions. For example Gas, the signaler in the second row, has performed 94 submissions toward Mer, the recipient in the first column, whereas Pip, the signaler in the third line, has performed 49 submissions toward Gas, the recipient in the second column.

Table 6

Spearman rank correlation between agonistic rank based on all submissive interactions and rank orders based on other agonistic behavior (aggressive and dominance behaviors) recorded in each competitive context

| | Agonistic rank r_s |
|--|----------------------|
| Rank based on aggressive behavior recorded in the absence of any sources of competition ($n = 27$) | — ^a |
| Rank based on dominance behavior recorded in the absence of any sources of competition ($n = 27$) | 0.96* |
| Rank based on aggressive behavior recorded in the presence of food ($n = 27$) | 0.84* |
| Rank based on dominance behavior recorded in the presence of food ($n = 27$) | 0.92* |
| Rank based on aggressive behavior recorded in the presence of receptive females ($n = 16$) | 0.97* |
| Rank based on dominance behavior recorded in the presence of receptive females ($n = 16$) | 0.87* |

* ≤ 0.00001 .

^a Aggressive interactions in the absence of any sources of competition have been too scarce for applying spearman rank correlation.

Signed-Ranks Test: $t = 0.00$, $z = 2.93$, $n = 16$, $P = 0.003$). In the presence of food, the difference between the 2 behavioral patterns failed to reach a statistically significant level (Wilcoxon Signed-Ranks Test: $t = 106.00$, $z = 0.97$, $n = 27$, $P = 0.33$) although the level of aggressiveness was slightly higher.

Differences in agonistic behaviors among the 3 competitive contexts

Hourly rate of agonistic behaviors varied across social contexts. In particular, in the presence of food dogs displayed and received more aggressive and submissive behaviors than in the absence of sources of competition; on the contrary, dominance behaviors did not differ between the 2 contexts (Table 7).

Aggressive and submissive interactions among males were more frequent in the presence of receptive females than in the absence of sources of competition and even more frequent in the presence of food (Table 7). Dominance behavior was more frequently displayed and received by males during struggles for food or in the absence of sources of competition, whereas they were rarely displayed in the presence of receptive females (Table 7).

Submissive–affiliative behavior as measures of formal dominance

Submissive–affiliative behaviors ($N = 374$ interactions; Table 8) showed a significant but very low linearity index (ILT: $h' = 0.33$, $P < 0.00001$). This was due to low coverage (Table 4): Actually this behavioral pattern was less frequently displayed than submissive behavior (Wilcoxon Signed-Ranks

Test: $t = 0.00$, $z = 4.54$, $n = 27$, $P = 0.000006$). Nevertheless, there were no bidirectional relationships, and this determined a complete unidirectionality (DCI = 1). Often, this behavior took place as an animal returned to the core area or, generally, when a dog joined the group again after a separation. Submissive–affiliative behavior was usually observed in the absence of sources of competition (60.96%), but it was also observed in the presence of food (30.48%) and in the presence of receptive females (8.56%). Because submissive–affiliative interactions did not occur between a lot of dyads, it was not possible to use this behavior to order dogs in a dominance rank most consistent with a linear hierarchy. Nevertheless, submissive–affiliative behavior was negatively correlated to agonistic rank ($r_s = -0.85$, $n = 27$, $P < 0.00001$). In other words, the higher the dogs were in rank, the fewer submissive–affiliative behaviors they displayed toward other dogs.

Submissive–affiliative behavior was positively correlated with submissive behaviors displayed in the absence of sources of competition ($r_s = 0.67$, $n = 27$, $P = 0.0001$), in the presence of food ($r_s = 0.46$, $n = 27$, $P = 0.017$), and in presence of receptive females ($r_s = 0.61$, $n = 16$, $P = 0.012$).

Age affected the display of submissive–affiliative behavior. In fact, juvenile dogs displayed this behavior more frequently than subadult and adult individuals (Kruskal–Wallis test: $H_2 = 21.58$, $n = 27$, $P = 0.0001$); besides, they usually showed submissive–affiliative behavior toward adult dogs (Kruskal–Wallis test: $H_2 = 14.97$, $n = 27$, $P = 0.0006$).

Considering all ages, males and female did not differ significantly in the hourly rate of submissive–affiliative behavior displayed and received (Mann–Whitney U Test; displayed = 64, $n_1 = 16$, $n_2 = 11$, $P = 0.25$; received: $U = 82$, $n_1 = 16$, $n_2 = 11$,

Table 7

Comparison of the hourly rates of agonistic behaviors among the 3 competitive contexts

| Wilcoxon signed-ranks test ($n = 27$) | Aggressive behavior | | Dominance behavior | | Submissive behavior | | Submissive–affiliative behavior | |
|---|---------------------|----------|--------------------|----------|---------------------|----------|---------------------------------|----------|
| | Displayed | Received | Displayed | Received | Displayed | Received | Displayed | Received |
| t | 0 | 3 | 130 | 116 | 17 | 12 | 43 | 41 |
| z | 4.20 | 4.29 | 0.87 | 1.51 | 4.03 | 3.83 | 1.29 | 1.94 |
| P | 0.00003 | 0.00002 | 0.381 | 0.131 | 0.00006 | 0.00012 | 0.20 | 0.053 |
| Friedman test ($n = 16$; $df = 2$) | | | | | | | | |
| χ^2 | 17.10 | 20.13 | 20.75 | 8.35 | 17.84 | 20.67 | 7.94 | 17.75 |
| P | 0.0002 | 0.00004 | 0.00003 | 0.015 | 0.0001 | 0.0003 | 0.019 | 0.00014 |

We used the Wilcoxon signed-ranks test to compare the hourly rates of agonistic behavior of all dogs ($n = 27$) among 2 competitive contexts: in the absence of any sources of competition and in the presence of food. We used the Friedman test to compare the hourly rates of agonistic behavior of male dogs ($n = 16$) among 3 competitive contexts: in the absence of any sources of competition, in the presence of food, and in the presence of receptive females.

Table 8
Dominance relationships based on submissive–affiliative behavior recorded among dogs

| | Receiver | | | | | | | | | | | | | | | | | | | | | | | | | | |
|------------|----------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Signaler | Mer | Gas | Pip | Leo | Gol | Lan | May | Nan | Iso | Dia | Sim | Pon | Sem | Kim | Mor | Ste | Han | Cuc | Mam | Dot | Gon | Gre | Bro | Eol | Mag | Emy | Pis |
| Mer | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Gas | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Pip | 2 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Leo | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Gol | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Lan | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| May | 2 | | 2 | | | | | | | | | | | | | | | | | | | | | | | | |
| Nan | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Iso | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | | | |
| Dia | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Sim | | | | 2 | | 2 | | | | 1 | | | | | | | | | | | | | | | | | |
| Pon | 1 | 3 | | 2 | | 1 | | | | | | | | | | | | | | | | | | | | | |
| Sem | | | | 2 | | 1 | 2 | 5 | | | | | | | | | | | | | | | | | | | |
| Kim | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Mor | 4 | 1 | 2 | | | | | | | | | | | | | | | | | | | | | | | | |
| Ste | 4 | | | | | | | | | | | | | | | | | | | | | | | | | | |
| Han | 4 | 1 | | 3 | | 1 | | | | | 2 | | | | | | 1 | 2 | | | | | | | | | 2 |
| Cuc | 2 | 1 | 1 | | 2 | 2 | 6 | | 5 | 1 | | 8 | 3 | 3 | 1 | | | | | | | | | | | | |
| Mam | 1 | 1 | | | 1 | 6 | | | 2 | | 3 | | | 2 | | | | | | | | | | | | | |
| Dot | 2 | 2 | | 5 | 17 | 4 | | | 7 | 1 | 9 | | | 2 | | | | | | | | | | | | | |
| Gon | 4 | | | | 9 | 3 | | | 3 | 6 | 3 | | | 5 | | | | | | | | | | | | | |
| Gre | 7 | | | | 2 | 1 | 5 | | | | | 1 | | | | | | | | | | | | | | | |
| Bro | 3 | | | | 1 | 1 | 3 | | 3 | 1 | | 4 | | 3 | | | | | | | | | | | | | |
| Eol | 3 | 3 | | 2 | 5 | 9 | 4 | | 9 | | 5 | | | 3 | | | | | | | | | | | | | |
| Mag | 2 | | | 4 | 4 | 3 | | | 5 | 2 | 4 | | | 1 | 1 | | | | | | | | | | | | |
| Emy | 3 | 1 | | | 8 | 6 | | | 11 | 2 | 22 | 1 | 1 | | | | | | | | | | | | | | |
| Pis | 4 | | | 2 | 3 | 2 | 4 | | 2 | | 1 | 3 | | 2 | | | | | | | | | | | | | |

Bold type: males; standard type: females.

The signalers are listed in rows whereas the recipients in columns. The signalers are the performers of the submissions. For example May, the signaler in the seventh line, has performed 2 submissions toward Mer, the recipient in the first column, whereas Pon, the signaler in the 12th line, has performed 3 submissions toward Gas, the recipient in the second column.

$P = 0.79$). Nevertheless, when considering only adult and sub-adult dogs, we found that females receive submissive–affiliative behavior more frequently than males (Mann–Whitney U Test: $U = 10$, $n_1 = 10$, $n_2 = 6$, $P = 0.03$).

Food competition

We observed 56 events of stealing food and 50 events of displace over food among dogs during feeding sessions. For both of these behaviors, a complete unidirectionality was found (DCI = 1). Agonistic rank affected the display of these behaviors. High-ranking dogs showed the stealing food more frequently than low-ranking individuals ($r_s = 0.79$, $n = 27$, $P = 0.000001$). Although the correlation between rank and displace over food is not high ($r_s = 0.38$, $n = 27$, $P = 0.05$), the complete unidirectionality of this behavior underlines its relations with dominance; in fact, the displace over food was always displayed by high-ranking dogs toward low-ranking individuals, and probably the correlation coefficient was low because this behavior was observed only in a few dyads.

Individual differences in age seemed to affect the competition for food. Adult dogs showed the highest total hourly rate of stealing food (Kruskal–Wallis test: $H_2 = 16.40$, $n = 27$, $P = 0.0003$), and they displayed this behavior especially toward subadult individuals, rarely toward other adult dogs, and only one time toward a juvenile individual (Kruskal–Wallis test: $H_2 = 15.10$, $n = 27$, $P = 0.0005$). On the contrary, the displace over food was not related to the age of dogs (Kruskal–Wallis test: $H_2 = 1.71$, $n = 27$, $P = 0.43$).

Males and females did not differ in displaying both stealing food ($U = 84$, $n_1 = 16$, $n_2 = 11$, $P = 0.82$) and displace over food ($U = 72$, $n_1 = 16$, $n_2 = 11$, $P = 0.40$).

DISCUSSION

To our knowledge, this is the first study on behavioral dominance in a group of free-ranging dogs carried out using matrix-ranking procedures (MatMan; de Vries 1995) that combines all the different principles developed in recent research on social hierarchies.

Agonistic dominance

The main result is that the dominance relationships among dogs were not distributed randomly in our group: Conversely to what asserted from other authors (Boitani et al. 2007; Bradshaw et al. 2009), we found a significant linear dominance hierarchy, although the level of linearity was not elevated. In order to quantify the dominance relationships in our study group, we first evaluated which behavioral measures were most suitable. All agonistic behaviors showed a fairly high level of unidirectionality resulting in a quite good measure of dominance relationships among dogs. Because we found a good level of unidirectionality of agonistic behaviors, the lack of a high level of linearity of the hierarchy is, undoubtedly, due to the high member of unknown relationships.

Submissive behaviors best fulfill the criteria of agonistic dominance marker; they are more consistent in direction than both dominant and aggressive behaviors as has also been

demonstrated in primates (Rowell 1974; de Wall and Luttrell 1985). Rowell (1974) highlighted the concept that subordinates play a central role in establishing dominance relationships because the outcome of a dyadic interaction is often determined by the subordinate individual's behavior. In our study group, we observed that subordinate dogs were usually responsible for the outcome of an agonistic interaction; in fact, they often approached the dominant dogs in submissive postures, with the tail and head down. A similar result was also found in a small group of dogs (8 individuals) in a shelter (Barillari 2004).

Aggressive behaviors were rarely displayed in the absence of sources of competition, and therefore, they showed the lowest directional consistence index and did not permit an ordering of dogs in a consistent linear hierarchy. These results confirm that in domestic dogs, as in wolves, when the group is stable, dominance postures (which do not necessarily include aggressive components) are sufficient to maintain social status. It is well known in nonhuman primates that hierarchical organization among members of a social group may limit the costs of aggression by limiting interactions to ritualized dominance displays as opposed to threats and physical contact (Rowell 1974; Bernstein 1981; Archer 1988). Conversely, in the presence of sources of competition, such as food and estrous females, we found that aggressive behavior was more frequent than dominance behavior. Although the hierarchical organization resulted in a priority order of access to resources (Wilson 1979; Hand 1986; Drews 1993), the direct competition for food or mate partners caused an increase of motivation to interact aggressively.

Formal dominance

Our results show that, following the definition by de Waal (1989), submissive–affiliative behavior fulfills the criteria of formal submissive signals. It is unidirectional and it occurred in all the social contexts analyzed. Nevertheless, it was not observed among all dogs: Juveniles displayed submissive–affiliative behavior especially toward adult dogs and among them preferentially toward females. Consequently, given that an individual preference in displaying submissive–affiliative behavior toward certain individuals was found, some dyads have never been observed to interact. This made submissive–affiliative behavior difficult to use to order the dogs in a consistent linear hierarchy.

Schenkel (1967) believed that submissive–affiliative behavior (called active submission by him) in wolves and dogs is derived from the food-begging behavior and Mech (1999), during a long research on a wolf pack in Ellesmere Island (Canada), found submissive–affiliative and food-begging behaviors indistinguishable. Moreover, he found that submissive–affiliative behavior was more common than submissions in wolves (Mech 1999). Conversely, in our dog group, we found that submissions are more common than submissive–affiliative behavior, and the latter was not directly associated with food-begging behavior because it was more frequently displayed in the absence of any source of competition than in the presence of food. Nevertheless, the tendency of juvenile dogs to display submissive–affiliative behavior preferentially toward females could be associated with the behavior “begging for food.” In fact, in domestic dogs, the role of females in parental care is predominant compared with the role of males.

Members of wolf packs usually interact displaying submissive–affiliative behavior and affiliative behaviors, whereas aggressive interactions are rare and of low intensity (Schenkel 1967; Zimen 1975; Harrington and Asa 2003; Packard 2003). In our dog group, we frequently observed affiliative interac-

tions (e.g., nonaggressive approaches, play, cooperative maintenance of the territory, mutual sniffing, passive contact, and wagging; Cafazzo S, Valsecchi P, Natoli E, in preparation) in each context analyzed. Although we rarely observed aggressive interactions in the absence of sources of competition, in the presence of food dogs became more aggressive; usually a dog responded to an attack or a threat from another dogs by displaying submissive behaviors. This suggests the existence (evolution) of a different pattern of submissive–affiliative behavior between wolves and our dogs (i.e., submissive behavior more common in dogs and not associated with food request).

Dominance relationships: influence of social context, age, and sex

In dogs, as in other mammal species, it is reasonable to predict the existence of asymmetries in resource value (e.g., because female dogs play the main role in rearing their pups, food should have a higher value for them than for males) and in the gain of winning a conflict; nevertheless, these asymmetries seem to play a marginal role in affecting dominance relationships among dogs.

In a captive wolf pack, individuals have been shown to be organized in a linear dominance hierarchy based on the direction of agonistic behaviors that are not influenced by the competitive contexts (Schenkel 1967; Van Hooff and Wensing 1987). In the natural environment, as well as in captivity, wolf packs have a dynamic composition: They can consist of several reproductive females or reproductive pairs and, occasionally, by some immigrant individuals (Van Ballenberghe 1983; Lehman et al. 1992; Mech 1998). The typical wolf pack is a nuclear or extended family (Murie 1944; Mech 1970), which consists of parents and their offspring (nuclear family) or parents plus one or more of their siblings, and their direct offspring (extended family) (Packard 2003). In these cases, a linear dominance hierarchy is a too simple way to describe the outcome of agonistic interactions among group members (Packard 2003).

The terms “alpha” (the individual who wins fights over all others), “beta” (the individual who loses fights with the alpha but wins over all others) and so on down the line up to “omega” (the individual who is least likely to win any fights) are generally used for describing interactions among orphaned siblings in a captive group (Rabb et al. 1967; Folk et al. 1970; Zimen 1975; Fox 1980, 1981) as well as in free-ranging wolves (Murie 1944; Mech 1993, 1970; Peterson 1977). The term may be appropriate in ambiguous situations in which the relatedness among pack members is unknown or complex (e.g., more than a single pair of breeders), but they are inappropriate for typical packs (Packard 1980; Mech 1999). The “age-graded dominance hierarchy” is a correct model to explain dominance relationships in typical wolf packs (nuclear family and extended family), as well as in complex families (Zimen 1982; Packard 2003).

In our dog group, all females, during their estrous period, were courted by and copulated with several males belonging to the group; the domestic dog is a promiscuous species, and therefore, in a group, there is no single pair of breeders. Besides, an abandoned adult female (STE) joined the group becoming well integrated. In other words, the composition of this dog group was similar to that observed in families of wolves that consist of more than a single pair of breeders and of some immigrant individuals. As in wolf packs with a complex composition, in our dog group, we found a sex-age graded hierarchy, in accordance with the model proposed by Zimen (1982).

In the sex age-graded hierarchy model, males dominate over females in each age class; adults dominate over subadults

and, subadults dominate over juveniles. This is the pattern found in the dog group, although we observed some exceptions: Among juveniles, some females dominated over some males, and the abandoned adult female mentioned (STE) was subordinate to all subadult dogs, although she joined the group when the subadult dogs were already born.

Adult dogs were more aggressive than juveniles in all competitive contexts. Conversely, although males dominated over females, they were not more aggressive than females. Therefore, the dominance of males over females in each age class was not related to aggressive interactions. It could be the outcome of higher competitive abilities of males than females (Archer 1988). In many species, body size (and/or weight) is a good indicator of a competitive ability (Archer 1988). In fact, in yellow baboons (*Papio cynocephalus*), males are larger than females and dominate over them (Post et al. 1980). In other species as *C. crocuta* or *Mesocricetus auratus*, females are larger than males and dominate over them (Ralls 1976). In Canids, we did not observe an evident sexual dimorphism (Bekoff et al. 1981; Bekoff et al. 1984; Gittleman and Van Valkenburgh 1997). Unfortunately, during this research, we could not capture animals and collect data concerning body weight and size. Although we can assert that adult males were larger than adult females, among subadult and juveniles dogs we did not observe a relevant difference in body size. Therefore, it is not possible to ascertain the influence of body size on hierarchical relationships in our dog group.

The level of competition among male dogs was higher in the presence of food than in the presence of receptive females and in the absence of sources of competition; we also observe a higher level of competition among females in the presence of food than in the absence of sources of competition. Besides, in the presence of food, most aggressive behaviors were directed from adults toward subadult individuals. Usually, in many mammal species, subadult individuals disperse from their place of birth. Inbreeding avoidance, mate competition, and resource competition may influence dispersal patterns (Kleiman 1977; Greenwood 1980; Dobson 1982; Moore and Ali 1984; Waser 1985). Generally, dogs were seen moving along the area in subgroups containing more than 1 animal (in 71.68% of sightings); usually, these subgroups contained about 6 dogs (5.99 ± 5.58) with a range extending from 1 to 29 animals. We observed a dog moving alone only in 14.29% of sightings, but in almost all these cases (85.71%), they were subadult dogs. Practically, subadult individuals showed a propensity to move away from the other group members during movements, and this might be indicate an attempt to dispersion. Probably, the high density of dogs in the study area made the dispersal of subadult individuals very difficult; therefore, the unavoidable resource competition between adults and subadults could explain the high level of aggressiveness displayed by adult dogs toward subadult individuals.

In conclusion, we can assert that the results of this study show that in domestic dogs, as well as in wolves, sex and age affect the dominance relationship, irrespective of the competitive contexts.

Influence of agonistic dominance on food competition

Food availability and intraspecific competition for its exploitation plays a central role in affecting social organization of many species. It is believed that dominance relationships influence the priority of access to resources, such as food. Besides, food is considered a major determinant of the reproductive success of individuals; consequently, several authors have tested the influence of dominance rank on access to food and have verified that higher ranking members of a social group gain priority of access to food over subordinates in an array of animal species

(e.g., red deer, *Cervus elaphus*, Appleby 1980; rhesus monkeys, *M. mulatta*, Deutsch and Lee 1991; olive baboons, *Papio anubis*, Barton and Whiten 1993; chimpanzees, *P. troglodytes*, Wittig and Boesch 2003; and brown bears, *Ursus arctos*, Gende and Quinn 2004).

Although, in this study we did not find a feeding order among dogs, we observed some individual gaining access to food prevailing over other dogs during competitions. High-ranking individuals stole food from other group members who often did not react.

In wolf packs, although a carcass potentially provides enough food for all, the breeding pair intimidates their offspring and limit their access to the meat until they have gorged enough to feed their pups and have torn off enough chunks to cache and eat at a distance in relative peace (Mech 1998). In a nuclear family, feeding order is correlated with submissive-affiliative behaviors rather than with conflict interactions (Packard 1980). Conversely, in a complex family, the order of access to food is correlated with agonistic interactions (Packard 1980), as we found in domestic dogs. In fact, in the dog group, dominance relationships, based on the directions of agonistic interactions, were correlated to “stealing food.”

Social dominance could be defined as the “power to control the access to resources” rather than the priority of access to them (Noë et al. 1980). Actually, high-ranking dogs usually stole food from subadult middle-ranking dogs, while they displayed a certain degree of feeding tolerance toward juvenile low-ranking individuals. In a wolf pack, especially when food is scarce, parents both dominate older offspring and restrict their food intake, in favor of pups. Thus, the most practical effect of social dominance is to give the dominant individual the choice of whom to allot food to (Mech 1999). We found a similar pattern in our dog group although both stealing food and displace over food were not observed frequently, probably due to the abundance of food.

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