Original Article

Age-graded dominance hierarchies and social tolerance in packs of free-ranging dogs

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It is believed that domestic dogs rarely form packs with age-graded hierarchical structures similar to those found in wolves. Dog-wolf comparisons in captivity suggest that human control has reduced dog dependency on cooperation with conspecifics, resulting in a more despotic dominance order. However, free-ranging dogs are under stronger natural selection than purebred dogs. They are dependent on companions' social support but usually exhibit lower reproductive skew than wolves, possibly because access to easily available human-derived food may have relaxed within-group competition. We investigated social dominance in 5 packs of mongrel dogs living in a free-ranging or semifree-ranging state. We aimed at replicating the findings of the few studies that detected a dominance hierarchy in dogs using a larger sample of packs. Additionally, we provided behavioral measures of social tolerance. We found that a linear hierarchy existed in all packs studied and that the rank order was positively related to age in all packs but one. In 2 packs in which testing was possible, age was a better predictor of dominance than body size. Potentially injurious aggression was very rare. Hierarchy steepness in dogs was similar to that found in wolves and in tolerant primates. Submissive reversals were more common in dogs than in wolves. These results suggest that age-graded hierarchies in dogs are more common than previously thought, that rank is not usually acquired through fighting because subordinates rely on the guidance of elders, and contradict the view that domestication has increased despotism in dogs.

Key words: **age, body size, domestic dogs, dominance, social tolerance, wolves.**

INTRODUCTION

Social dominance has been regarded as an attribute of a relationship in which 1 of 2 animals (the dominant) emerges as the consistent winner of repeated agonistic interactions and the other (the subordinate) defers without aggressive escalation (reviewed in Drews 1993). When dominance relationships exist among all or most members of a social group of animals, then it may be appropriate to describe the social structure of that group using a linear dominance hierarchy model, that is, by ranking group members from the one dominating all others to the one who is dominated by all others (Deag 1977; Martin and Bateson 1993; de Vries 1998).

It has been argued that dominance hierarchies are more likely to evolve in group-living species subsisting on limited resources (Wrangham 1980; Vehrencamp 1983; Sterck et al. 1997; Wheeler et al. 2013), as well as in species for which fighting would involve very high costs (Archie et al. 2006). From a functional perspective, dominance provides high-ranking animals with benefits through priority of access to contested resources (e.g., food, social partners) and allows subordinates to minimize costs by avoiding escalated fights (Deag 1977; Hand 1986). The acquisition of dominance is expected to depend on the recognition of several asymmetries among interacting animals, including asymmetries in resource holding potential (RHP) or fighting ability (Parker 1974; Parker and Rubenstein 1981; Packer and Pusey 1985; Arnott and Elwood 2009). Consistent with this view, it has been shown that in several species the dominance rank order is positively correlated to body

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weight and/or size that function as approximate measures of RHP (e.g., domestic horses, *Equus caballus*, Houpt et al. 1978; hens, *Gallus gallus domesticus*, Cloutier and Newberry 2000; red deer, *Cervus elaphus*, Veiberg et al. 2004; female reindeer, *Rangifer tarandus*, Holand et al. 2004; fallow deer, *Dama dama*, Jennings et al. 2006; free-ranging domestic cats, *Felis silvestris catus*, Bonanni et al. 2007).

However, dominance can be affected also by asymmetries that are not *necessarily* related to fighting ability, such as asymmetries in age (Grafen 1987; Šárová et al. 2013). In social groups formed through recruitment of newborns and comprising adults, subadults and juveniles, body size is likely to be positively correlated with age, and thus the dominance rank can be positively correlated to both variables (e.g., female meerkats, *Suricata suricatta*, Clutton-Brock et al. 2001; female African elephants, *Loxodonta africana*, Archie et al. 2006; male fallow deer, Jennings et al. 2006; male domestic cats, Bonanni et al. 2007). However, it has been shown that, at least in some species, age can be the best predictor of dominance rank even when the effect of body size is controlled (e.g., bighorn sheep, *Ovis canadensis*, Favre et al. 2008; female beef cattle, *Bos taurus*, Šárová et al. 2013). In these hierarchies, young individuals submit to older ones even if they are larger than them, and they are more likely to increase in rank when older individuals die or disperse than by challenging higher-ranking companions (Kokko and Johnstone 1999; Šárová et al. 2013). This pattern seems to occur in species in which old/experienced group members lead collective movements, and has led some authors to argue that age-graded hierarchies have evolved also in order to promote group coordination and not just to solve conflicts over resources (Šárová et al. 2013). Note that this hypothesis postulates that dominance will bring benefits also to subordinates because they can rely on the guidance of better-informed decision makers. The latter point is consistent with the observation that subordinates often develop affiliative relationships with individuals leading group movements (Byrne et al. 1990; King et al. 2008; Ramseyer et al. 2009; Bonanni, Cafazzo, et al. 2010).

So, although a portion of the existing literature emphasizes the role of dominance in competitive interactions, it is now clear that dominance can be expressed also in the context of social bonding (de Waal 1986). For instance, it has been argued that some highly social primates and carnivores have evolved so-called "formal submissive gestures" that communicate unambiguously the acceptance of subordinate status, thus facilitating the development of an affiliative relationship between dominant and subordinate individuals and reducing damaging aggression during conflicts (de Waal 1986; van Hooff and Wensing 1987; East and Hofer 2010; Cafazzo et al. 2010; Trisko and Smuts 2015). To be regarded as a formal indicator of social status, a submissive behavior should be nearly unidirectional within a given dyad (being expressed almost always by the same dyad member) and expressed also in affiliative contexts such as greeting; moreover, its directionality should be both independent of the social context and correlated with that of submissive gestures expressed in agonistic contexts (de Waal and Luttrell 1985; de Waal 1986; Preuschoft 1999). Species exhibiting formalized dominance relationships can still differ with respect to their "dominance style", which is related to the degree of social tolerance displayed by dominant animals towards subordinates, that is, the degree to which dominant animals withhold punishment when subordinates exert a dominant attitude (Flack and de Waal 2004; Cooper and Bernstein 2008). For example, in primates with a "despotic dominance style" hierarchies are enforced through severe aggression and dominance reversals (e.g., aggression directed by subordinates to dominants) are very rare, whereas in primates with a "tolerant dominance style"

aggression is mild, dominance reversals are more frequent, relationships are more often unresolved (i.e., in some dyads no clear dominant individual emerges), and levels of affiliation and cooperation are higher. In primates with a "relaxed" and "egalitarian style" social tolerance is even higher and most social relationships are unresolved (Sterck et al. 1997; Flack and de Waal 2004; Thierry 2008; Thierry et al. 2008; Balasubramaniam et al. 2012). More generally, in behavioral ecology, a despotic dominance style has been also associated with a stronger fitness bias in favor of the dominant members of a social group (Vehrencamp 1983). However, up to now few studies have tested the correlation between behavioral measures of despotism/tolerance and degree of reproductive skew, despite the fact that measures of hierarchy steepness have been designed for this specific purpose (e.g., de Vries et al. 2006).

Moreover, relatively few studies have investigated the above topics in free-ranging domestic dogs (*Canis lupus familiaris*), carnivores whose degree of intraspecific social complexity has been questioned. Genetic studies indicate that dogs evolved from gray wolves, *Canis lupus*, (Vilà et al. 1997; Sacks et al. 2013; Shannon et al. 2015; Fan et al. 2016; Wang et al. 2016) through a domestication process that has changed their morphology, physiology, and behavior by making them adapted to anthropogenic and anthropic environments (Coppinger and Coppinger 2001; Axelsson et al. 2013; Bonanni and Cafazzo 2014; Coppinger and Coppinger 2016; Wang et al. 2016). There is actually evidence that dogs who are free to range and breed out of human control are genetically distinct from purebred dogs artificially selected by humans (Boyko and Boyko 2014; Shannon et al. 2015; Pilot et al. 2015, 2016), making adaptive interpretations of their behavior more reasonable. However, despite the fact that nowadays most dogs in the world are free-ranging (Hughes and Macdonald 2013; Lord et al. 2013; Bonanni and Cafazzo 2014; Smuts 2014; Udell et al. 2014), there are relatively few investigations of how their social relationships compare to those of wolves. Social dominance has always been regarded as an important component of wolf society (Schenkel 1967; Zimen 1975; van Hooff and Wensing 1987; Mech 1999; Peterson et al. 2002; Bloch 2002; Packard 2003; Sands and Creel 2004; Mech and Cluff 2010). Wolves exhibit a flexible social system ranging from living in simple families, comprising a monogamous breeding pair and their offspring, to more complex social groups comprising multiple sexually mature individuals as well as unrelated members (Mech 1999; Packard 2003; vonHoldt et al. 2008). In family packs, there is an age-graded dominance order in which offspring submit to parents and puppies submit to older siblings (Mech 1999; Bloch 2002; Packard 2003); moreover, males tend to be dominant over females within a given age class (Haber 1977; van Hooff and Wensing 1987; Mech 1999; Sands and Creel 2004), although this is not always the case (e.g., Bloch 2002). Members of the dominant breeding pair usually lead pack movements (Mech 2000; Peterson et al. 2002; Bloch 2002) and dominance also plays a role in regulating reproductive activities in packs comprising several mature individuals, in which often only a dominant pair breeds (Peterson et al. 2002; vonHoldt et al. 2008). Conversely, some studies on free-ranging dogs report that they either are semisolitary animals (e.g., Beck 1973; Berman and Dunbar 1983; Daniels 1983; Ortolani et al. 2009) or live in social groups of mainly unrelated members that do not have a hierarchical social structure affecting group activities (e.g., Boitani and Ciucci 1995; van Kerkhove 2004; Boitani et al. 2007; Bradshaw et al. 2009; Boitani et al. 2016). The latter was partly inferred by the presence of multiple breeding individuals in dog groups, taken to indicate an apparent lack of social control over reproduction but the authors did not publish any test

of hierarchy linearity or any behavioral data that could be used to implement such a test. However, other studies (e.g., Font 1987; Majumder et al. 2014; Bonanni and Cafazzo 2014) have questioned these claims, suggesting that long-term social bonds in free-ranging dogs went undetected because some former studies were not based on continuous observations of animals, and/or included a considerable portion of free-ranging pets that are less likely to form stable packs. Moreover, a recent study, based on a detailed analysis of social interactions recorded over an extended period, found a linear dominance hierarchy in a large pack of unowned free-ranging dogs in Italy (Cafazzo et al. 2010). The social structure of this pack was relatively similar to that of wolves in some respects: The dominance rank order was positively related to both the individual frequency of leading pack movements (Bonanni, Cafazzo, et al. 2010) and the individual reproductive/copulatory success (Cafazzo et al. 2014); older dogs dominated younger ones and males tended to dominate females of similar age, although the potentially confounding effect of body size on these variables was not controlled. Subsequently, linear hierarchies were also found in Indian free-ranging dogs (Pal et al. 1998, data reanalyzed in Bonanni and Cafazzo 2014), and in captive groups of purebred and mixed breed dogs (Trisko and Smuts 2015; van der Borg et al. 2015), showing that dominance is not restricted to free-ranging animals. Studies by Cafazzo et al. (2010) as well as Trisko and Smuts (2015) suggested that "muzzle-licking" displayed by dogs during affiliative interactions, a component of the behavior described as "active submission" by Schenkel (1967), fulfills the criteria for a formal display of submission, whereas van der Borg et al. (2015) proposed several additional behaviors as potential formal indicators of social status. Despite all these evidences, there is still a considerable debate concerning the appropriateness of the dominance paradigm to describe the social relationships of dogs (e.g., McGreevy et al. 2012; Bräuer et al. 2013; Schilder et al. 2014; Bradshaw and Rooney 2016). For example, Bradshaw et al. (2016) suggested that the social structure found by Cafazzo et al. (2010) may be unusual because free-ranging dogs usually forage in small groups with a fluid membership. So, given the contrasting positions held by different researchers, it seems useful to further investigate dominance in additional dog packs.

Another important debate concerns the effect of domestication on the degree of social tolerance exhibited by dogs. This topic has been mainly investigated by comparing the social behavior of captive dogs (mainly purebred) and wolves raised by humans in similar conditions in order to detect differences due to genetic influences. These studies report a much higher rate of potentially injurious aggression in some dog breeds than in wolves (Frank and Frank 1982; Feddersen-Peterson 1991; Feddersen-Petersen 2007; Viryáni and Range 2014) and that dogs seem to be less likely to share food with subordinates than wolves, thus suggesting that dogs may have steeper hierarchies than wolves (Range et al. 2015). The latter may be surprising, because in the wild wolf packs usually show a higher level of reproductive skew than free-ranging dog packs (Cafazzo et al. 2014). An alternative approach to the study of this topic would consist in comparing social tolerance in dogs and wolves living in their respective natural ecological settings, that is, in the environments where their behavioral differences have probably evolved. However, currently, there are no published data on either hierarchy steepness or frequency of aggressive escalation in free-living dogs or wolves.

In this study, we investigated social dominance in 5 additional packs of mongrel dogs (4 free-ranging and 1 living in seminatural conditions) with stable membership. First, we aimed to replicate the findings by Cafazzo et al. (2010) and see how common dominance

hierarchies are in dogs. We predicted that if dogs have retained wolves' ability to form structured social groups, then their social structure should fit a linear hierarchy model (prediction 1a), the dominance order should be positively related to age (prediction 1b), and males should dominate females of similar age (prediction 1c). Second, we extended previous knowledge by exploring the function of age-graded hierarchies. We predicted that if dominance in dogs has evolved only to solve conflicts for resources, then any correlation between age and dominance should disappear once the effect of body size has been removed (prediction 2); conversely, if dominance has evolved to also promote pack coordination, then any correlation between age and dominance should remain significant even after controlling for body size (prediction 3). Then we provided the first data on hierarchy steepness in free-ranging dogs and wolves, by analyzing dominance matrices published for both subspecies. If the despotic–egalitarian axis proposed for primates is relevant to canids, then the following predictions should be verified: dogs should display signals qualifying as formal indicators of social status (prediction 4a); because free-ranging dogs are cooperative carnivores (Daniels and Bekoff 1989; Macdonald and Carr 1995; Pal 2005; Bonanni and Cafazzo 2014; Paul et al. 2014; Pal 2015), the steepness of their hierarchies should compare to that of primate species described as "tolerant" (e.g., chimpanzee, *Pan troglodytes*, steepness = 0.3–0.7, Kaburu and Newton-Fisher 2015; prediction 4b); because free-ranging dogs are likely to be more dependent on the cooperative support of conspecifics than purebred dogs controlled by humans, they should exhibit a lower rate of potentially injurious aggression than that reported for pure breeds (prediction 4c); because free-ranging dogs are supposed to be less cooperative than wolves in activities such as hunting and breeding ("canine cooperation hypothesis", Range et al. 2015), they should have steeper hierarchies than wolves (prediction 4d). Finally, we examined the effect of domestication on dog behavior by developing an alternative "ecological hypothesis." We start with 2 premises: 1) a causal relationship between hierarchy steepness and reproductive skew is supposed to exist; 2) in the cooperatively breeding wolves, lack of reproduction in subordinates is partly due to inbreeding avoidance (vonHoldt et al. 2008) and partly to the high costs of reproduction which force dominants to interfere with the reproductive activities of subordinates in order to increase the amount of food available to their own puppies (Creel and Creel 1991; Derix et al. 1993; Asa 1997; Derix and van Hoof 1995). We hypothesize that since free-ranging dogs subsist mainly on human derived food sources that are energetically less costly to acquire than wolf prey (Coppinger and Coppinger 2016), they can bear the costs of reproduction and allow subordinates to breed to a higher extent than wolves. This is supported by the observation that subordinate breeding in cooperative breeders is usually more common when food resources are more abundant (e.g., Clutton-Brock et al. 2001; Mech and Boitani 2003; Clutton-Brock et al. 2010). If so, dogs should have less despotic hierarchies than wolves (prediction 5).

MATERIALS AND METHODS
Study locations

This research was carried out at 3 different locations, 2 sited in Rome and 1 in Southern Italy. In particular, free-ranging dogs were studied in 2 suburban districts located at the east and south–west periphery of Rome, called "La Rustica" and "Muratella" respectively. The "La Rustica" study area covered more than 40 hectares. It was characterized by many, partly cultivated, open fields although it also comprised isolated houses, shopping centres, buildings with

offices, a railway station, and a railway yard. The latter was the core area of the dog pack studied here. The "Muratella study area" has been described in detail in several papers (e.g., Bonanni, Cafazzo, et al. 2010; Bonanni, Valsecchi, et al. 2010; Cafazzo et al. 2010; Bonanni et al. 2011). It covered about 300 hectares, comprising a southwest urbanized sector (not densely populated) and a northeast sector occupied by a natural reserve called "Tenuta dei Massimi". The habitat in the reserve consisted mainly of open grasslands with interspersed wooded areas. In both areas, dogs subsisted mainly on human-derived food sources (e.g., meat provided regularly by human volunteers, garbage bins) and occasionally on natural prey.

The third study location was a private dog shelter located in a village called "Caraffa" in Southern Italy. The studied dog pack was housed in a 600 m² fenced area containing spontaneous vegetation and trees (*Eucalyptus* spp.). Dogs were provided daily with food and water by the personnel of the shelter.

Packs' membership and history

All free-ranging and shelter dogs studied here were medium to large sized mongrels and were not owned at the time when we conducted this study. With very few exceptions, free-ranging animals displayed strong avoidance responses to humans. Dogs were individually recognized based on their morphology, body size, and coat color and sexed based on genital morphology. Table 1 reports details about age, gender, pack membership, attitude to humans, and known relatedness of all individuals included in the data analysis.

The "La Rustica" pack comprised 2 intact males and 4 females who were sterilized about 6 months before the initiation of the study, and its membership remained unchanged throughout the study period (August 2003 to August 2004).

In the "Muratella" site, we studied 3 free-ranging packs during the May 2007 to September 2008 period, as a part of a research project initiated in 2005. The "Corridoio pack" descended from the group studied by Cafazzo et al. (2010) during the 2005–2006 period. When we conducted this study it comprised 11 members (Table 1), 6 of which were sterilized at least 6 months before the study started, who remained together throughout the duration of the study. Direct observation of mother–offspring relationships and the recruitment of puppies into the pack indicate that this pack was primarily composed of relatives.

The "Curva pack" comprised initially 10 members (Table 1). One month after the beginning of the study 1 male dispersed (not included in the data analysis) and, subsequently, a juvenile male died. Importantly, in November 2007, these dogs were joined by another pack coming from the wooded sector of the area, consisting of 4 intact males and 2 intact females, to form what we called the "Fused pack". Subsequently, one of the new arriving males disappeared (not included in the analysis) and one of the females gave birth to 2 puppies. Moreover, after the fusion event 2 males and 7 females of this pack were sterilized by the Rome Municipality. Because this pack underwent some important changes, we ran 2 different analysis for it, one including only the members who were present before the fusion event (i.e., the Curva pack) and another including the initial members plus the new immigrants (i.e., the Fused pack). Despite the change in membership, we stress that 7 members of the initial Curva pack stayed together throughout the duration of the study and they stayed with the immigrants for at least 10 months. So, overall, even the membership of this pack was relatively stable.

The "Piazza pack" comprised initially 4 members. However, because one female died a few months after the initiation of data collection, only 3 members of this pack were included in the data analysis (Table 1). We stress that they stayed together for the entire duration of the study.

Nine dogs who were members of the Corridoio pack during this study, plus 3 dogs of the Curva/Fused pack, and one of the Piazza pack, had been members of the Corridoio pack at the time when it was studied by Cafazzo et al. (2010). So, the results we present here for the Muratella population are not completely independent from those previously published in that study. On the other hand, we stress that 17 out of 30 dogs (57%) of the Muratella population for whom we present data in this paper were not included in the study by Cafazzo et al. (2010).

The "Caraffa" pack comprised 4 sterilized males, 1 cryptorchid male, and 3 intact females, its membership had been stable for 2 years before the initiation of our study (September 2003) and remained unchanged until the end of it (April 2004). These animals were either brought to the shelter as puppies found in the streets, or were born by females housed in it, who also probably descended from the local free-ranging dog population. Five individuals were siblings belonging to the same litter, whereas relatedness among the other group members was not known with certainty (Table 1).

All female dogs of this study who were sterilized underwent surgical ovariohysterectomy (they were "spayed") and all sterilized males underwent orchiectomy (they were "castrated") with the exception of a male of the Corridoio pack who was vasectomized (see Table 1). The latter individual was the only sterilized dog who displayed a normal reproductive behavior, which is consistent with the observation that vasectomy does not seem to affect male reproductive hormones (Tunsaringkarn et al. 1999).

Behavioral observations

Dogs were observed daily, usually between 0600 and 2000 h, to cover the entire daylight period when possible. In "La Rustica" the observer stayed inside a vehicle to avoid any interactions with the animals; in "Muratella" dogs were followed on foot and observed from distances of 20–150 m using 10 × 50 binoculars, whereas in "Caraffa" the observer stayed on a wooden platform (2 m high) placed in a favorable point inside the fence. The social behavior of the dogs was studied using the *focal animal sampling* method (Altmann 1974) when sources of competition such as food and mates were absent (hours of observation were: 157.8 in La Rustica, 221.4 in Muratella, 184 in Caraffa). Moreover, we studied dogs during feeding using a *focal subgroup sampling* technique (Altmann 1974), although there were some differences between sites reflecting different ways to deliver food to the dogs. Specifically, in La Rustica, we recorded the behavior of the group members who were present within 2.5 m of a single food bowl (8.1 h of observation); in Muratella, where the food was usually spread over a large area on the ground, we recorded the behavior of dogs present within a feeding area (about 500 m²) that was delimited by specific topographic landmarks, when feasible (7.58 h); in Caraffa, we recorded the behavior of the group members who were within 1.5 m of 4 food bowls placed near each other (10.45 h of observation). Furthermore, in Muratella, where there were intact dogs of both sexes, we also used the *focal subgroup sampling* method to study the behavior of dogs during estrus periods, by recording social interactions among individuals who were present within 15 m of the estrus female (8.87 h of observation). Notably, in Muratella, a considerable amount of data concerning social interactions in all the 3 above cited contexts was also collected ad libitum during 1147.2 h spent in the field. This was necessary due to the rarity of social interactions.

Table 1

Information about individuals studied

Dog identity	Pack	Gender	Birth year	Age class at the beginning of the study[b]	Dominance rank	Attitude to humans	Notes
RY	La Rustica	Male	Before 2001	Old adult	1.00	Sociable	
LA	La Rustica	Spayed female	Before 2001	Adult	0.60	Sociable	
RO	La Rustica	Male	2002	Subadult	0.20	Avoidant	
BA	La Rustica	Spayed female	2002	Subadult	−0.20	Avoidant	
MA	La Rustica	Spayed female	2002	Subadult	−0.60	Avoidant	
SU	La Rustica	Spayed female	2002	Subadult	−1.00	Avoidant	
GOL	Corridoio	Male	Before 2004	Adult	1.00	Avoidant	Vasectomized male; displayed a normal reproductive behavior
DOT	Corridoio	Male	2005	Adult	0.80	Avoidant	Son of MAM; littermate of GON, EOL, BRO
LAN	Corridoio	Castrated male	Before 2004	Adult	0.60	Avoidant	
MAM	Corridoio	Female	Before 2004	Adult	0.40	Avoidant	Mother of DOT, GON, EOL, BRO, SAS, MON, JOS
ISO	Corridoio	Spayed female	Before 2004	Adult	0.20	Avoidant	Mother of MAG
GON	Corridoio	Male	2005	Adult	0.00	Avoidant	Son of MAM; littermate of DOT, EOL, BRO
EOL	Corridoio	Castrated male	2005	Adult	−0.20	Avoidant	Son of MAM; littermate of DOT, GON, BRO
BRO	Corridoio	Male	2005	Adult	−0.40	Avoidant	Son of MAM; littermate of DOT, GON, EOL
SAS	Corridoio	Female	2006	Subadult	−0.60	Avoidant	Daughter of MAM; littermate of MON, JOS
MON	Corridoio	Spayed female	2006	Subadult	−0.80	Avoidant	Daughter of MAM; littermate of SAS, JOS
MAG	Corridoio	Spayed female	2005	Adult	−1.00	Avoidant	Daughter of ISO
POM	Fused	Male		Looked adult	1.00	Avoidant	
CES	Fused	Male		Looked adult	0.86	Avoidant	
GAS	Curva/Fused	Male	Before 2004	Adult	0.71	Avoidant	Previous member of the Corridoio pack
CLEO	Fused	Female	Before 2004	Old adult	0.57	Avoidant	Mother of LOR, FAB; spayed during the study
MOR	Curva/Fused	Female	2004	Adult	0.43	Avoidant	Previous member of the Corridoio pack; mother of GIO, PAS; spayed during the study
BRU	Fused	Male		Looked adult	0.29	Avoidant	Castrated during the study
NER	Curva/Fused	Castrated male	2006	Subadult	0.14	Sociable	Previously affiliated to a human family that he left spontaneoulsy to live in the Curva pack
MUS	Curva/Fused	Male	2004	Adult	0.00	Avoidant	
JOS	Curva/Fused	Male	2006	Subadult	−0.14	Avoidant	Previous member of the Corridoio pack; son of MAM; castrated during the study
AGR	Fused	Female		Possibly subadult	−0.29	Avoidant	Spayed during the study
DAN	Curva/Fused	Female	2007	Juvenile	−0.43	Avoidant	Spayed during the study
LOR	Fused	Female	2007	Juvenile	−0.57	Avoidant	Daughter of CLEO
FAB	Fused	Female	2007	Juvenile	−0.71	Avoidant	Daughter of CLEO; spayed during the study
FRA	Curva/Fused	Female	2007	Juvenile	−0.86	Avoidant	Spayed during the study
GIO	Curva/Fused	Female	2007	Juvenile	−1.00	Avoidant	Daughter of MOR; littermate of PAS; spayed during the study
PAS[a]	Curva	Male	2007	Juvenile		Avoidant	Son of MOR; littermate of GIO
MAT	Piazza	Male	2004	Adult	1.00	Sociable	Previously affiliated to a human family that he left spontaneoulsy to live in the Piazza pack
OTT	Piazza	Castrated male	2005	Adult	0.00	Avoidant	
STE	Piazza	Spayed female	Before 2004	Adult	−1.00	Avoidant	Previous member of the Corridoio pack
VAO	Caraffa	Castrated male	1997	Adult	1.00	Sociable	

Table   1
Continued

Dog identity	Pack	Gender	Birth year	Age class at the beginning of the study[b]	Dominance rank	Attitude to humans	Notes
TEA	Caraffa	Female	1997	Adult	0.71	Sociable	
PIO	Caraffa	Castrated male	2000	Adult	0.43	Sociable	Littermate of MAO, BIO, STA, PIA
MAO	Caraffa	Castrated male	2000	Adult	0.14	Sociable	Littermate of PIO, BIO, STA, PIA
BIO	Caraffa	Male	2000	Adult	−0.14	Sociable	Littermate of MAO, PIO, STA, PIA; cryptorchid male
STA	Caraffa	Female	2000	Adult	−0.43	Avoidant	Littermate of MAO, PIO, BIO, PIA
PAO	Caraffa	Castrated male	2000	Adult	−0.71	Sociable	
PIA	Caraffa	Female	2000	Adult	−1.00	Sociable	Littermate of MAO, PIO, BIO, STA

[a]He died before the formation of the Fused pack, and this is the reason why he has no score for dominance rank in this table. However, as a member of the Curva pack he was the last in dominance rank but GIO. [b]Adult dogs were individuals older than 2 years; subadults were dogs between 1 and 2 years old; juveniles were dogs younger than 1 year.

We recorded *all occurrences* (Altmann 1974) of the behavioral patterns used in the assessment of social dominance and social tolerance. These were the same in all 3 sites and included submissive, aggressive, and dominance displays. Behavioral patterns displayed by dogs during play could not be recorded in detail and so they were not used to assess social status. Table 2 reports a complete list and definition of each behavioral pattern. Submissive behavior included both affiliative and agonistic submissions. The former were defined by the behavior of the submissive animal who took the initiative to approach the recipient before displaying his/her signal and were associated with a minimum display of fear and tension; the latter were displayed in response to aggressive and/or dominance signals and were associated with higher levels of fear and distress. This distinction seems to be justified by empirical data: 1) affiliative submissions were associated with an overall increase of proximity among interacting dogs, whereas this was not necessarily true for agonistic submissions (Bonanni, Cafazzo, et al. 2010); 2) affiliative submissions were mainly recorded when contested resources were absent (61–91.4%), whereas agonistic submissions were mainly recorded when dogs were competing for food and/or mates (73.2–80.4%).

Statistical assessment of hierarchy linearity

To test whether the social structure of dog packs fits a linear hierarchy model, we used submissive behavior, because it is generally accepted that a dominance relationship is determined mainly by the behavior of subordinates (Deag 1977; de Waal and Luttrell 1985), and since even in domestic dogs submissions proved to be more useful than both aggressive and dominance displays in order to detect linear hierarchies (Cafazzo et al. 2010; Bonanni and Cafazzo 2014; Trisko and Smuts 2015; van der Borg et al. 2015). However, we report the results of statistical analyses based on aggressive and dominance displays in a Supplementary File for descriptive purposes. We entered the outcomes of all submissive dyadic interactions into squared matrices with performers on the vertical axis and recipients on the horizontal axis, showing both the direction and the frequency of interactions within each dyad. The dominant animal of a given dyad was the one who received more submissive acts than he/she performed. We initially developed a squared matrix for each social context (no sources of competition, feeding, estrus periods when applicable) for each pack.

Subsequently, we combined the data collected in different contexts to produce a matrix reporting the total number of interactions recorded for each pack, because the dominance orders obtained in different contexts were strongly correlated with each other (not shown here for the sake of brevity).

For each matrix, we tested whether the distribution of social interaction outcomes fitted a linear hierarchy model using the method proposed by de Vries (1995). The latter is based on a modified version of the Landau's linearity index (h; Landau 1951), which corrects for tied and unknown relationships (i.e., those in which dyad members exchange an equal number of behavioral gestures, and those in which they do not interact at all, respectively). The modified linearity index (h') ranges from 0 (indicating total lack of linearity) to 1 (perfect linearity), and its value is lowered by the presence of circular triads (relationships in which individual A dominates B, B dominates C, and C dominates A), as well as by the percentage of unknown relationships into the social group (de Vries 1995; Klass and Cords 2011). The latter was calculated for each matrix as a measure of "coverage" (van Hooff and Wensing 1987). The statistical significance of h' was tested using a 2-step randomization test, with 10 000 randomizations (de Vries 1995). Note that, with this method, a statistically significant level of linearity can be found only in matrices comprising a minimum of 6 individuals (Appleby 1983; de Vries 1995).

We arranged the members of each pack in the dominance order that was most consistent with a linear hierarchy by applying the procedure proposed by de Vries (1998), which minimizes both the number of inconsistencies (i.e., cases in which an individual is dominated by a companion who is ranked below him/her) and the strength of inconsistencies (i.e., the absolute difference between the ranks of 2 individuals involved in an inconsistency). The dominance rank order obtained for each matrix was standardized by distributing ranks evenly between the highest (+1) and the lowest (−1), with the median rank being scored as 0 (East and Hofer 2001).

Estimates of age, body size, and related statistics

For the purposes of statistical analysis, dogs of each pack were assigned to age classes that were ranked from the youngest to the oldest one, based on their actual or estimated time of birth (see Table 1). The latter was known with good approximation (year and, in some

Table 2

Definition of all behavioral patterns used in the assessment of dog social status

Behavior	Description	Notes
Aggressive signals		
Staring at	Actor fixes his/her own eyes on recipient with tense body and head projected forwards.	
Pointing	Actor approaches recipient with a tense body while staring at him/her.	
Curling of the lips	Actor raises his/her upper lip laterally without necessarily showing recipient his/her canines.	
Baring of the canines	Actor raises his/her lips and this results in showing the recipient his/her canines.	
Raising the hackles	Actor erects the hair of the neck, shoulders, and anterior part of the back.	
Snarling	Actor emits a rumbling, harsh, low-pitched vocalization towards recipient.	
Barking	Actor emits an abrut, loud, noisy, and often repetitive vocalization, toward recipient while staring at him/her	
Lunging at	Actor moves abruptly and rapidly towards recipient, for a distance of 1 or a few meters, while staring at him/her but without making physical contact.	
Chasing	Actor runs after recipient covering a minimum distance of 10 meters, while staring at him/her and barking.	
Biting	Actor takes a part of the recipient's body between jaws and press it.	
Dominance displays		
High posture	Actor assumes an upright body posture with head and tail held high, legs straight and stiff, ears hold forwards, while staying close to recipient.	
Head over	Actor approaches recipient and place his/her head over recipients's back or neck.	Actor can either place his/her head over recipient without making body contact, or can push recipient's head downwards.
Paw over	Actor approaches recipient from the side and puts one forepaw or both over recipient's back	It refers to social interactions occurring outside both sexual and playful contexts.
Mounting	Actor places his forepaws around recipient's torso and he/she may or may not thrust his/her pelvis.	It refers to social interactions occurring outside both sexual and playful contexts.
Pinning	Actor stands over recipient body with 4 feet on the ground, so as to prevent recipient from raising up.	While standing over recipient actor can assume a high posture or not, or can push recipient down if the latter tries to raise up.
Wagging the tail held high	Actor assumes a high posture and moves the tail sidewards while the tail is held high.	
Affiliative submission	Actor approaches recipient and licks his/her muzzle or pushes recipient's muzzle with the nose. Actor may assume a relaxed or slightly lowered posture.	It is frequently observed during greeting ceremonies, i.e., when pack members reunite after a temporary separation.
Muzzle-licking	Actor licks recipient's muzzle after receiving an aggressive or dominance display.	Observed in a very few cases. Included in the matrix of total submissive behavior but not included in the test of the correlation between affiliative and agonistic submissions.
Agonistic submissions		
Avoiding eye contact	Actor turns his head away from recipient following an aggressive or dominant display	
Lowering head	Actor lowers his/her head following an aggressive or dominance display.	During the displaying of this behavioral pattern, the actor's muzzle may point downwards or forwards but the head and neck are leaning downwards.
Tail between hind legs	Actor lowers his/her tail after receiving an aggressive or dominance display. The tail can be held against the hind legs, or tucked between them.	
Flattening ears	Actor retracts the ears into the neck or holds them backwards after receiving an aggressive or dominance displays.	
Low posture	Actor assumes a crouched posture with lowered head, legs bent and a rounded back after receiving an aggressive or dominance display, or simply when approached by recipient.	
Lying down on back	Actor lies down on his/her side or back exposing the belly to the recipient after receiving an aggressive or dominance display.	Equivalent to "passive submission" by Schenkel 1967.
Yelping	Actor emits a high-pitched, plaintive vocalization in response to an aggressive or dominance signal.	
Withdrawing	Actor moves away from the recipient, covering a minimum distance of 1 meter, after receiving an aggressive or dominance display.	
Fleeing	Actor runs away from the recipient after an aggressive or dominance display.	
Interruption of feeding	Actor stops feeding and relinquishes the food to the recipient after receiving an aggressive or dominance display.	Observed only in the context of feeding.
Interruption of mounting	A male dog stop mounting an estrus female and alights after receiving an aggressive or dominance signal by another male.	Observed only in the context of mating for male dogs.

cases, month) for free-ranging individuals who were born during our studies and for the Caraffa dogs (who were brought as puppies to the shelter). Dogs who were born in the same year were assigned to the same age class. Free-ranging dogs who were born before the initiation of our studies, and whose dates of birth were unknown, were assigned to different age classes depending on whether they appeared to be fully-grown or juvenile (based on allometry and body size) when we observed them for the first time. Free-ranging dogs who showed obvious signs of old age, such as presence of grey muzzle hair and worn teeth, were assigned to the oldest age class. For each pack, we assessed the relationship between age and the dominance rank order derived from the matrix of total submissive behavior using Spearman correlation. However, note that we could not include in this test most adult dogs that joined the Fused pack in November 2007 because there was no way to estimate their ages relative to those of the other adult members of that group. An exception was a female who showed obvious signs of old age.

In the Muratella study site, we were able to collect data on body size from dogs who were either captured or found dead during our studies. Dogs were captured by the Rome Municipality, in collaboration with the local Department of Public Veterinary Health, within a management project of the dog population aimed at sterilizing the animals and at releasing them back in the area. Animals were immobilized using dart guns (Daninject JM Special, Denmark) filled with anaesthetic (Zoletil 100, 6 mg/kg, Virbac Srl) and several body measurements were taken: chest girth, length of the vertebral column, height at the withers, head size (obtained by summing the following distances: nose-occipital bone, temporal-temporal, mandible-forehead), and average length of canines. We used Spearman correlation to assess the relationship between dominance rank and all the linear measurements cited above. Note that we did not apply Bonferroni correction due to our small sample size (see Nakagawa 2004). Also, note that multiple significant results for these tests are likely to be due to interdependence between multiple body measurements (which are constrained by dog body shape) and not to chance effects. We were able to collect morphometric data for members of the Fused pack during the period 2007–2008, and for members of the Corridoio pack in 2006 (those previously studied by Cafazzo et al. 2010), and so we could carry out the test only for these groups. One member of the Fused pack was measured in 2008, although she had been a member of the Corridoio pack in 2006. Since at that time she was already 2 years old, and since dogs reach full body size well before that age (Hawthorne et al. 2004), we used her measurements in tests referring to both packs. To test whether the effect of age on dominance rank depended on body size we used partial rank correlation (Conover 1999), when possible.

Furthermore, we tested the effect of gender on dominance rank, age, and body size using Mann–Whitney U-test.

Directional consistency of behavior, hierarchy steepness, and aggression intensity

For each matrix, we also calculated a directional consistency index (*DCI*) as the total number of times that a behavior was performed in the direction of its higher frequency within dyads minus the total number of times that a behavior was performed in the direction of its lower frequency within dyads, divided by the total number of times that behavior was performed by all individuals (van Hooff and Wensing 1987). This index also varies from 0 (indicating equal exchange or complete bidirectionality) to 1 (complete unidirectionality). This index has been regarded as an accurate measure of the "power asymmetry" of a dominance relationship (i.e., the

degree to which individuals differ in their probability of winning a dominance interaction) and, unlike linearity and steepness (de Vries et al. 2006), it is not sensitive to the presence of unknown relationships into the dominance matrix (Koenig et al. 2013).

We tested whether affiliative submissions could fulfil the requirements for a formal signal of subordination in dogs by assessing their *DCI* and how their directionality was related to that of agonistic submissions. The latter was accomplished by calculating row wise correlations between the matrices reporting affiliative and agonistic submissions, using row totals to control for individual differences in behavior (de Vries 1993). However, note that this analysis could be applied only to the packs living in the Muratella area, due to loss of raw data concerning the other study sites.

We also calculated the steepness of dog hierarchies using the method proposed by de Vries et al. (2006). We included this additional measure of power asymmetry of social relationships for the following reasons: 1) it facilitates comparison with studies on dominance style in primates; 2) unlike DCI, it is affected by the presence of unknown relationships within social groups, and it cannot be ruled out that the latter represents a component of the dominance style of a species (see Flack and de Waal 2004). Operationally, steepness is the absolute slope of the straight line fitted to the normalized David's score plotted against subjects'ranks (de Vries et al. 2006). David's score (Gammell et al. 2003) provides a cardinal rank measure, and it measures individuals' success in winning dominance interactions while taking into account the relative strength of interacting animals. Here, we calculated normalized David's scores on the basis of a dyadic dominance index (Dij) corrected by chance which allows comparison of matrices that differ with respect to number of interactions (de Vries et al. 2006). Steepness can vary between 0 and 1; the maximum value is obtained when the hierarchy is perfectly linear and when dominants win all interactions with subordinates. To test whether the observed values of steepness differed significantly from those to be expected under the null hypothesis of random win chances for all pairs of individuals we applied a randomization procedure (10 000 randomizations). The significance of a right-tailed *P*-value was obtained by calculating the proportion of times that a randomly generated steepness under the null hypothesis was greater than or equal to the observed steepness (de Vries et al. 2006). In order to provide a comprehensive picture of dog social tolerance, hierarchy steepness was calculated not just for the submission matrices developed in this study but also for those published in the previous literature (Pal et al. 1998; Bonanni and Cafazzo 2014; Trisko and Smuts 2015).

As a further measure of social tolerance, we calculated the intensity of aggression as the total number of interactions involving biting (i.e., potentially injurious aggression) divided by the total number of agonistic interactions (total number of interactions in which aggressive and dominance signals were recorded). We could do this for each dog pack presented in this study and also for that studied by Cafazzo et al. (2010), for which data on aggression intensity were not previously published.

Furthermore, we ran a post hoc analysis aimed at checking whether social tolerance was affected by the presence of sterilized dog within packs by calculating Spearman correlation between all measures of social tolerance and the proportion of pack members who were either spayed or castrated.

Comparison with the social system of wolves

We conducted a preliminary test aimed at comparing domestic dogs and wolves with respect to 2 measures of power asymmetry.

Specifically, we used Mann–Whitney U-test to compare *DCI* and hierarchy steepness calculated for published dominance matrices of dogs and wolves. For dogs, we used the matrices of total submissive behavior published in the current study (except that developed for the shelter pack; Supplementary Tables S1–S4), as well as Table 3 published in Pal et al. (1998) and Table 3-1 published in Bonanni and Cafazzo (2014). We limited our analysis to submissive behavior because most data available for wolves concerned this behavioral category, comprising both submissions displayed in the context of greeting and those in response to dominance postures (Tables 2–5 in Mech 1999; Tables 1–4 in Bloch 2002; Tables c1–c4 in Bloch and Marriot 2016). Moreover, we limited our analysis to free-living packs of both subspecies because few dominance matrices on captive dogs have been published.

All statistics concerning dominance matrices were implemented in MatMan 1.1 (Noldus Information Technology, Wageningen, The Netherlands), except for steepness which was analyzed using the "Steepness" package (Leiva and de Vries 2015) in R v3.2.5 (R Development Core Team 2011). All other statistical analyses were carried out using Statistica release 8 (StatSoft Inc., Tulsa, OK). Significance level was set at α = 0.05.

RESULTS

Hierarchy linearity in the studied dog packs (prediction 1a)

Table 3 reports in detail the results of the statistical analyses concerning linearity and coverage for all submission matrices considered in this study. We found that, in the "La Rustica" pack, the matrix based on total submissive behavior recorded showed perfect and statistically significant linearity (Table 3; Supplementary Table S1). As regards the Muratella study site, during 2007–2008, in the Corridoio pack, the matrix based on total submissive behavior showed a good and statistically significant level of linearity (Table 3; Supplementary Table S2). In the Curva pack, the outcomes of total submissive interactions resulted in a hierarchy whose degree of linearity was good, although just marginally significant (Table 3). However, this lack of significant linearity appeared to be due partly to low coverage and partly to the relatively low number of pack members, because the matrix of total submissive behavior of the Fused pack, obtained by summing up all interactions recorded before and after the "fusion" event, was significantly linear (Table 3; Supplementary Table S3). As regards the Piazza pack, note that it was too small to allow us to detect any statistically significant result. However, the matrix of total submissive interactions of this pack exhibited complete coverage and perfect linearity (Table 3; Supplementary Table S4). Moreover, the matrix of total submissive behavior developed for the "Caraffa" pack also fitted significantly a linear hierarchy model (Table 3; Supplementary Table S5). Conversely, the matrices based on total aggressive and dominance behaviors for the above packs did not always fit a linear hierarchy model (Supplementary Table S6).

Effect of age, gender, and body size on dominance rank (predictions: 1b, 1c, 2, and 3)

In all groups for which we present data here, except for the Piazza pack, there was a positive and statistically significant correlation between dominance rank and age (La Rustica: $rs = 0.85$, $n = 6$, $P = 0.034$; Corridoio 2007–2008: $rs = 0.73$, $n = 11$, $P = 0.011$;

Table 3

Results of statistical analyses for all dog matrices based on submissive behavior considered in this study: number of pack members; corrected Landau's linearity index (h') and its statistical significance ($P < 0.05$ are marked in bold); directional consistency index (*DCI*); number and percentage of all types of dyadic relationships, i.e., unknown (no behavior exchanged), 1-way (only one individual expressed the behavior), 2-way (both dyad members displayed the behavior but at different rates), and tied (equal number of behaviors exchanged); Steepness and its statistical significance ($P < 0.05$ are marked in bold)

Pack	Living conditions	N members	h'	P	DCI	Unknown relationships	1-way relationships	2-way relationships	Tied relationships	Steepness (Dij)	P	Data source
La Rustica	Free-ranging	6	**1**	**0.021**	0.90	0 (0%)	11 (73.33%)	4 (26.67%)	0 (0%)	**0.77**	**0.0001**	This study
Corridoio 2007/08	Free-ranging	11	**0.74**	**0.0013**	0.96	15 (27.27%)	37 (67.27%)	3 (5.45%)	0 (0%)	**0.40**	**0.0001**	This study
Curva	Free-ranging	9	0.58	0.09	1	13 (36.11%)	23 (63.89%)	0 (0%)	0 (0%)	**0.34**	**0.0001**	This study
Fused	Free-ranging	15	**0.44**	**0.013**	1	47 (44.76%)	58 (55.24%)	0 (0%)	0 (0%)	**0.25**	**0.0001**	This study
Piazza	Free-ranging	3	1	0.75	1	0 (0%)	3 (100%)	0 (0%)	0 (0%)	**0.76**	**0.0146**	This study
Caraffa	Captive	8	**0.8**	**0.013**	0.98	3 (10.71%)	21 (75%)	4 (14.29%)	3 (10.71%)	**0.69**	**0.0001**	This study
Corridoio 2005/06	Free-ranging	27	**0.65**	**0.0001**	0.96	78 (22.22%)	254 (72.36%)	19 (5.41%)	2 (0.57%)	**0.52**	**0.0001**	Bonanni and Cafazzo 2014
HIG	Free-ranging	5	0.95	0.11	0.73	0 (0%)	7 (70%)	3 (30%)	1 (10%)	**0.72**	**0.0005**	Pal et al. 1998
LIG	Free-ranging	8	**0.9**	**0.0009**	0.82	3 (10.71%)	17 (60.71%)	8 (28.57%)	2 (7.14%)	**0.56**	**0.0001**	Pal et al. 1998
Daycare facility	Captive	24	**0.26**	**0.014**	0.97	191 (69.2%)	81 (29.35%)	4 (1.45%)	1 (0.36%)	**0.11**	**0.0001**	Trisko and Smuts 2015
Dutch kennel	Captive	10	**0.94**	**0.0001**	0.97	4 (8.9%)	34 (75.6%)	7 (15.6%)	3 (6.7%)	**0.67**	**0.0001**	van der Borg et al. 2015

Statistics concerning intensity of aggression for the dog packs for which the data was available

Pack	Number of bites	Number of agonistic interactions	% Bites
La Rustica	0	314	0
Corridoio 2007/08	10	188	5.32
Fuso	3	106	2.83
Piazza	0	10	0
Caraffa	0	467	0
Corridoio 2005/06	20	2272	0.88

Agonistic interactions refer to the sum of aggressive and dominance interactions. Percentage of bites is calculated in relation to the total number of agonistic interactions.

Curva before the fusion: $rs = 0.95$, $n = 9$, $P < 0.0001$; Fused: $rs = 0.92$, $n = 11$, $P < 0.0001$; Piazza: $rs = -0.5$, $n = 3$, $P = 0.667$; Caraffa: $rs = 0.76$, $n = 8$, $P = 0.03$; Figure 1).

Moreover, in our studied packs, gender had a significant effect on dominance rank ($U_{21,22} = 85$, $Zadj = 3.55$, $P < 0.0004$) with males being, on average, higher in rank than females (mean standardized dominance rank ± SE: males $0.34 ± 0.11$; females $-0.36 ± 0.13$). Overall, males and females did not differ significantly with respect to age (Mann–Whitney test: $U_{19,20} = 149$, $Zadj = 1.23$, $P = 0.22$); so, it is unlikely that the correlations between dominance rank and age emerged as a consequence of males being older than females.

In the Corridoio pack, studied during the period 2005–2006, the dominance rank order was positively correlated to all the measurements we took to assess body size (chest girth: $rs = 0.72$, $n = 9$, $P < 0.03$; length of the vertebral column: $rs = 0.81$, $n = 10$, $P = 0.004$; height: $rs = 0.91$, $n = 10$, $P = 0.0002$; head size: $rs = 0.75$, $n = 10$, $P = 0.013$; mean canine length: $rs = 0.61$, $n = 10$, $P = 0.06$). However, in this pack the dominance rank order was also affected by age (Cafazzo et al. 2010) and we found that none of the above correlations with body size remained statistically significant after controlling for age (chest girth: $rs = 0.34$, *NS*; length of the vertebral column: $rs = 0.037$, *NS*; height: $rs = 0.47$, $P < 0.10$; head size: $rs = 0.05$, *NS*; mean canine length: $rs = 0.48$, $P < 0.10$). Conversely, the partial correlations between dominance rank and age always remained statistically significant after controlling for the effect of measurements (chest girth: $rs = 0.86$, $P < 0.005$; length of vertebral column: $rs = 0.80$, $P < 0.005$; height: $rs = 0.67$, $P < 0.025$; head size: $rs = 0.86$, $P < 0.0025$; mean canine length: $rs = 0.92$, $P < 0.0005$). Moreover, we found that in the Fused pack, studied during the period 2007–2008, dominance rank was significantly correlated with mean canine length but not with any other measure (chest girth: $rs = 0.47$, $n = 8$, $P = 0.24$; length of vertebral column: $rs = 0.57$, $n = 8$, $P = 0.14$; height: $rs = 0.56$, $n = 7$, $P = 0.19$; head size: $rs = 0.50$, $n = 8$, $P = 0.21$; mean canine length: $rs = 0.79$, $n = 7$, $P = 0.036$). For this pack we did not calculate partial rank correlations because data on both age and body size were available for a very low number of individuals ($n = 5$).

Taking all dogs we measured together, we found that males tended to be larger than females, although the difference was significant only for some measurements (Mann–Whitney test: chest girth, $U_{7,9} = 16$, $Zadj = -1.64$, $P = 0.10$; length of the vertebral column, $U_{8,9} = 10$, $Zadj = -2.51$, $P = 0.011$; height, $U_{7,9} = 10.5$, $Zadj = -2.23$, $P = 0.023$; head size, $U_{8,9} = 11$, $Zadj = -2.41$, $P = 0.016$; mean canine length, $U_{7,9} = 17$, $Zadj = -1.53$, $P = 0.12$).

Formal dominance (prediction 4a)

Affiliative submissions showed complete unidirectionality (DCI = 1) in all packs studied in the Muratella area during 2007–2008. Agonistic submissions also showed complete unidirectionality in all packs but the Corridoio one, in which directional consistency of this behavior was slightly lower (DCI = 0.97). In both the Curva and the Fused packs the matrices of affiliative and agonistic submissions were significantly correlated to each other (Curva: taurw, av = 0.36, $P = 0.024$; Fused: taurw, av = 0.22, $P = 0.019$), whereas the same did not hold for the Corridoio pack (taurw, av = 0.02, $P = 0.38$). The latter result contrasts with that found for the Corridoio pack during 2005–2006, when the correlation between the 2 matrices was highly significant (taurw, av = 0.50, $P = 0.0005$). A post hoc examination of the matrices revealed that there were 2 main differences between the 2 phases of the study: first, during 2007–2008, in the Corridoio pack, there was one dyad in which the dog receiving the higher frequency of affiliative submissions was also the one displaying the higher frequency of agonistic submissions, whereas in the Corridoio pack studied during 2005–2006, as well as in all other packs studied, there were no dyads of this kind; moreover, during 2007–2008, agonistic submissions were expressed in only 47.6% of all dyads of the Corridoio pack in which affiliative submissions were also recorded, whereas this percentage was 98.2% during 2005–2006. As regards the Piazza pack, it was too small to carry out matrix correlation, although we noted that the only instance of agonistic submission was recorded between 2 dogs that were never observed exchanging affiliative submissions.

Measures of social tolerance in dog packs (predictions: 4b, 4c)

We found that submissive behavior had high directional consistency in all dog packs considered in this study (Table 3). We also found that all submission matrices exhibited a degree of steepness that differed significantly from that expected under the null hypothesis of random win chances for all groups members, although the recorded values varied considerably across different packs (Table 3). Variation in hierarchy steepness was unrelated to DCI across all packs included in Table 3 (except Curva which was excluded since it was not independent of Fused; $rs = -0.231$, $n = 10$, $P = 0.52$), and indeed steepness was inversely correlated to "percentage of unknown relationships" ($rs = -0.966$, $n = 10$, $P < 0.00001$), which, in turn, increased with the number of pack members ($rs = 0.877$, $n = 10$, $P < 0.001$).

We found that the proportion of biting in relation to the total number of agonistic interactions was very low in all packs for which this measure could be calculated (Table 4). Overall, there were 33 bites in 3357 dyadic agonistic interactions recorded in 6 packs (i.e., the total percentage of potentially injurious aggression approached 1%) and none resulted in any serious injury.

The proportion of spayed/castrated pack members tended to be positively correlated to DCI across packs ($rs = 0.617$, $n = 10$, $P = 0.057$), and it was not significantly correlated either to hierarchy steepness ($rs = -0.168$, $n = 10$, $P = 0.64$) or to the "proportion of biting in relation to the total number of agonistic interactions" ($rs = -0.419$, $n = 6$, $P = 0.41$). We repeated these tests after removing the Fused pack (whose members were spayed/castrated during the study) and found no statistically significant results (DCI: $rs = 0.58$, $n = 9$, $P = 0.10$; hierarchy steepness: $rs = 0.026$, $n = 9$, $P = 0.95$; proportion of biting in relation to the total number of agonistic interactions: $rs = -0.80$, $n = 5$, $P = 0.10$).
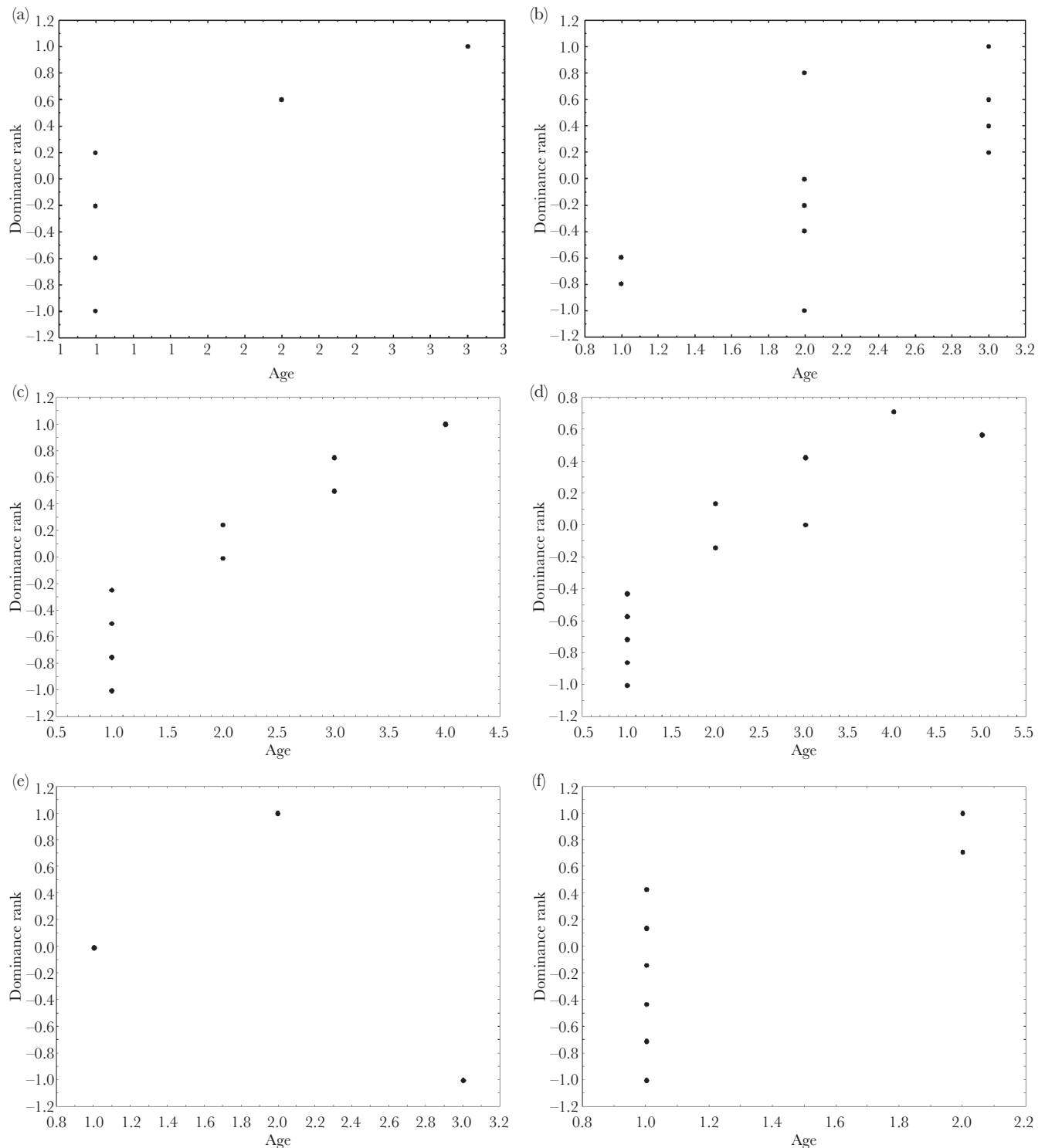
Figure 1

The relation between standardized dominance rank (based on total submissive behavior) and age in the packs studied here: a) La Rustica; b) Corridoio 2007/08; c) Curva; d) Fused; e) Piazza; f) Caraffa.

"Dominance style" in free-ranging dogs and wolves (predictions: 4d, 5)

We found that free-ranging dog submission matrices had significantly lower *DCI* than free-ranging wolf submission matrices ($U_{7,12} = 19$, $Zadj = -2.06$, $P < 0.04$; mean ± SE: dogs 0.910 ± 0.039,

$n = 7$; wolves 0.992 ± 0.004, $n = 12$; Figure 2), whereas the difference between the 2 subspecies was not statistically significant in relation to hierarchy steepness ($U_{7,12} = 30$, $Zadj = -1.01$, $P = 0.31$; mean ± SE: dogs 0.569 ± 0.075, $n = 7$; wolves 0.651 ± 0.076, $n = 12$).
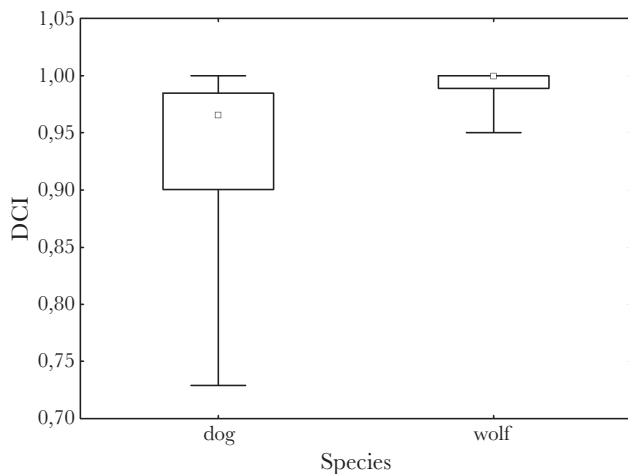
Figure 2
Comparison of the directional consistency indexes (*DCI*) calculated for published matrices reporting displays of submission in free-ranging dogs and wolves. Boxes show the median and the 25–75% interquartile range respectively; whiskers indicate minimum and maximum values.

DISCUSSION

The effect of domestication on the social structure of dog packs (predictions: 1a, 1b, 1c)

In this paper, we have provided statistically significant evidence of linear dominance hierarchies in 4 packs of unowned domestic dogs living in 3 different areas of Italy. Three of these packs were living in a free-ranging state and one was housed in a shelter, although its members also originated from the local free-ranging dog population. Moreover, the finding of linear hierarchies in multiple groups of dogs suggests that the perfect linearity (*h* = 1) found in the Piazza pack, which was too small (*n* = 3 members) to allow us to demonstrate its statistical significance (see Appleby 1983), probably did not emerge by chance. Our results confirm those previously published by Cafazzo et al. (2010) and Pal et al. (1998; reanalyzed by Bonanni and Cafazzo 2014) for free-ranging dogs, and are in accordance with those published by Trisko and Smuts (2015) as well as by van der Borg et al. (2015) on captive (mainly purebred) dogs. Taken together, all these studies support the view that dominance hierarchies are common in domestic dogs. Furthermore, they strongly contradict the previously held notion of lack of social structure in this species (e.g., Boitani and Ciucci 1995; Boitani et al. 2007; Bradshaw et al. 2009; McGreevy et al. 2012; Boitani et al. 2016; Bradshaw et al. 2016; Bradshaw and Rooney 2016), which was never supported by detailed analysis of social interactions.

We have also shown that the dominance rank order was positively correlated to age in all dog packs considered in our study, with the exception of the small Piazza pack. One interpretation to explain this pattern is that an age-graded dominance hierarchy will be likely to develop in family dog packs that naturally form through recruitment of newborns, because the latter will spontaneously submit to the adult pack members, as has been observed in wolf family packs (Mech 1999). Although we lack genetic data to confirm relatedness among group members, based on our observations (see Table 1), we believe that most groups studied were at least to some extent formed by relatives, although this probably did not hold for the Piazza pack, that is, the only group lacking an age-based hierarchy. However, it should be noted that even in a large group of mainly unrelated dogs of various breeds (Trisko and Smuts 2015)

the correlation between age and dominance rank was fairly high. So, another hypothesis is that dogs could simply rely on olfactory cues to assess the relative age of companions (Trisko 2011), and this would lead to the development of an age-graded dominance hierarchy even in groups formed primarily by unrelated members. With regards to the Piazza pack, we note that the oldest dog of this group was a female in poor physical condition and this may have affected her social status, leading to a hierarchy that was not affected by age.

Anyway, the fact that an age based dominance order can be found both in wolves (Mech 1999; Bloch 2002; Packard 2003) and in dogs (Cafazzo et al. 2010; Trisko and Smuts 2015; this study) suggests that dogs have inherited some relevant social rules from their wild ancestors (support for predictions 1a, 1b). This seems to be also supported by the fact that, in our studied dogs and in those studied by Cafazzo et al. (2010), males tended to dominate females of comparable age (prediction 1c verified), a result which parallels those found in several studies on wolves (e.g., van Hooff and Wensing 1987; Mech 1999; Packard 2003).

The acquisition and function of dominance in dog packs (predictions: 2, 3)

We found that in the 2 free-ranging dog packs in which testing was possible the effect of age on social status was independent of body size, and overall age showed a closer correlation with dominance rank than body size (support for prediction 3 but not for prediction 2). So, dogs may be an example of a species in which social conflicts are settled mainly using conventional cues which are not necessarily related to RHP (see Maynard Smith and Parker 1976; Hammerstein and Parker 1982; Grafen 1987). Social status in dogs may be mainly acquired by following queuing conventions (e.g., when elders die or emigrate), and/or through dispersal to other packs comprising young animals, rather than by challenging and physical fighting. Moreover, this result is consistent with the hypothesis that age-graded hierarchies in dogs have evolved to promote group coordination and not just to solve social conflicts for resources. An age-based dominance order seems to be typical for species in which old/experienced individuals take responsibility in leading collective activities (e.g., wolves, Peterson et al. 2002; beef cows, Šárová et al. 2010; female African elephants, McComb et al. 2011; feral horses, Krueger et al. 2014), which also include domestic dogs (free-ranging animals, Bonanni, Cafazzo, et al. 2010; pets, Ákos et al. 2014). In these species, subordinates may get benefits by accepting the decisions of older dominants, who have better knowledge about resource locations and so may even incur a cost by challenging them for status (Šárová et al. 2013). However, when young subordinates have much higher RHP than elders, then the cost of challenging them would be lower and they can try to jump the queue (Šárová et al. 2013).

Actually, the fact that in our study age was a better predictor of dominance than body size does not imply that the latter does not play any role in the acquisition of social status, although a bigger sample of dogs than that considered in our study would be necessary to demonstrate that body size has a significant effect on dominance independent of that of age. Our field observations suggest that, as in beef cattle (Šárová et al. 2013), some young dogs with a bold temperament can initially submit to their older companions and then successfully challenge them when they grow much larger. Overall, in our study there were 7 out of 39 dogs (17.9%) of known age who outranked one or more older companions, and younger

dogs dominated older dogs in just 4.3% of dyads in which a dominance relationships existed, indicating that successful rank challenges are not frequent (see also Trisko et al. 2016 for examples of successful rank challenges in pet dogs). Moreover, it remains to be clarified whether a young dog who gets a high-ranking status would also lead pack movements (see Bonanni, Cafazzo, et al. 2010).

Our result that age is a better predictor of social status than body size is consistent with the results found by Trisko and Smuts (2015) in a large group of pet dogs. Conversely, in the group mainly formed by young female dogs of various breeds studied by van der Borg et al. (2015), the dominance rank order was not significantly related either to age or to body weight. However, we note that in that group age was inversely related to weight (see Table 1 in van der Borg et al. 2015). In such a situation, asymmetries in age and size may perhaps offset each other, resulting in a lack of detectable effect of both variables on dominance rank.

The result that in our studied packs males tended to be dominant over females of similar age may be explained by asymmetries in size between sexes indeed. Actually, in the "Muratella" population, male dogs tended to be slightly larger than females, so one speculation is that dogs could rely on asymmetries in body size to settle contests when there are no marked asymmetries in age among interacting animals. It should be noted that in the group studied by Trisko and Smuts (2015), in which 62.5% of members were purebred, dominance was not significantly affected by gender. Nevertheless, genetic studies suggest that sexual selection has been relaxed in purebred animals (Boyko and Boyko 2014; Pilot et al. 2016) and so it is possible that free-ranging dogs, or more generally mongrels, exhibit a higher degree of sexual dimorphism in body size than purebred dogs. More generally, we suggest that rank acquisition in dogs may be affected primarily by age, especially in family packs formed through recruitment of newborns, and that both asymmetries in body size and differences in individual temperament may contribute to explain why dominance relationships can also be found among dogs of similar age (including siblings, see Table 1, Supplementary Tables S2 and S5).

Formal dominance in dogs (prediction 4a)

In comparison to previous studies (e.g., Cafazzo et al. 2010; Trisko and Smuts 2015), we found less clear, although still substantial, evidence that affiliative submission (see Table 2) fulfills the criterions for a formal signal of subordination in dogs (i.e., partial support for prediction 4a). This behavioral pattern was completely unidirectional in all packs studied in the "Muratella" area during 2007–2008 and, unlike agonistic submissions, occurred primarily when pack members were not competing for resources. However, the correlation between the matrices of affiliative and agonistic submissions was statistically significant only in the Curva/Fused pack, and not in the Corridoio pack. Nevertheless, in our view, this should not be taken to signify that the 2 behavioral patterns did not have the same main directionality within dyads, because even in the Corridoio pack there was only one single dyad in which affiliative and agonistic submissions covaried in opposite directions (which probably reflected a challenge for social status). Aside from directionality, it is noteworthy that in our studied packs there was a considerable percentage of dyads in which affiliative submissions were expressed, whereas agonistic submissions were not. One hypothesis to explain this result is that once a dominance relationship has been formally recognized, this could lead to a decrease of conflicts in that dyad (see Trisko et al. 2016 for a similar argument in pet dogs).

A recent study (van der Borg et al. 2015) proposed that, besides muzzle-licking, several other body postures and behaviors can function as formal signals of social status in dogs. Some of these signals (e.g., muzzle-bite, body tail wag, pass under head) were not included in our ethogram, whereas "high-posture" was. However, at least in our study, the latter pattern was not recorded in peaceful contexts such as greeting and so it does not fit our definition of formal indicator of social status (see Introduction and Table 2).

Social tolerance and "dominance style" in dogs (predictions: 4b, 4c)

We have found that submissive behavior (as well as dominance and aggressive behavior) showed high directional consistency in all dog packs studied up to now (Table 3, Supplementary Table S6). This indicates that when a dominance relationship exists in a given dyad it is rarely contested by subordinates, which, in turn, seems to be consistent with the hypothesis that dominance in dogs is more likely to be achieved through queuing than by challenging. Unlike DCI, hierarchy steepness varied greatly across different dog packs (Table 3), ranging from values comparable to those reported for despotic to egalitarian primate species (see Stevens et al. 2007; Balasubramaniam et al. 2012; Duboscq et al. 2013; Kaburu and Newton-Fisher 2015). The mean steepness calculated for free-ranging dog packs (see Results for details) fell in the range reported for primate species with a tolerant or relaxed dominance style (support for prediction 4b). However, the degree of steepness of dog hierarchies was largely influenced by unknown relationships and it was lower in packs characterized by a higher percentage of unknown relationships (usually in packs comprising a higher number of members; Table 3). The meaning of unknown relationships should be interpreted cautiously, because they may reflect either the difficulty of collecting data on social interactions in free-ranging dogs, or the actual lack of dominance in some dyads. Because all dogs in our studied packs had clearly many chances of interacting with companions during a long period of observation, we cannot rule out the actual presence of some egalitarian or unresolved relationships, especially in light of the recent findings by Trisko et al. (2016) who proved the existence of egalitarian relationships (those in which dogs exchange affiliative signals but not submissive ones) in pet dogs.

Overall, we suggest that the dominance style of free-ranging dogs should be regarded as tolerant also on the basis of the following considerations: the currently available data suggest that the degree of reproductive skew in dog packs (Cafazzo et al. 2014) seems to be lie in between that of despotic species (in which a single female breed) and that of egalitarian species (in which reproduction is equally shared among all females; Vehrencamp 1983; Clutton-Brock 1998); leadership in group decision making is partially shared among group companions and there are close affiliative relationships between leading dogs and their subordinates (Bonanni, Cafazzo, et al. 2010); the percentage of potentially injurious aggression in our studied packs was very low (Table 4), similar to that of primates with a tolerant/egalitarian style (Thierry 1986; Duboscq et al. 2013), and it never resulted in any serious injury. The fact that some dogs in our studied packs were spayed/castrated undoubtedly could have contributed to reduce opportunities for competition and aggression (e.g., over estrus females). However, among our measures of social tolerance, DCI was the only one showing a marginally significant, and positive, correlation with the proportion of pack members who were spayed/castrated. One interpretation of this result is

that neutering may have further decreased incentives to challenge higher-ranking dogs and, consequently, also the overall number of dominance reversals. If so, it seems unlikely that we would have found a less tolerant dominance style had our sample been entirely formed by intact dogs. Actually, even the large pack of intact dogs studied by Cafazzo et al. (2010) was characterized by rare biting, as well as by total lack of aggression in a high percentage of dyads (see Table 4, Supplementary Table S6). Because free-ranging dogs are known to engage in a variety of cooperative behaviors (Daniels and Bekoff 1989; Macdonald and Carr 1995; Bonanni, Valsecchi, et al. 2010; Paul et al. 2014; Pal 2005; Pal 2015), the finding of a tolerant dominance style is not surprising, and suggests that the despotic-tolerant axis described for primates (Flack and de Waal 2004; Balasubramaniam et al. 2012) may be, to some extent, applied to canids as well.

On the other hand, the highly ritualized agonistic behavior observed in our free-ranging dogs seems to contrast with the frequent escalated aggression observed in some captive purebred dogs. For example, in poodles, agonistic interactions escalated to bite-shaking in 70% of cases (Fedderson-Peterson 1991). This seems to be consistent with our hypothesis that dogs under strong artificial selection may exhibit a more despotic dominance style than free-ranging dogs (prediction 4c verified). However, the few data available on hierarchy steepness in captive groups of various purebred and mixed breed dogs (Table 3) are suggestive of a tolerant (van der Borg et al. 2015) or even egalitarian dominance style (Trisko and Smuts 2015). Taken together, these studies indicate that either breeds vary greatly in their genetic predisposition to aggression, or that variation in aggression is explained by additional factors. For example, when managing dogs in captivity, humans may put together in a restricted space dogs who are not strongly affiliated to each other. Moreover, in studies in which dogs (purebred, Fedderson-Peterson 1991; Feddersen-Petersen 2007; mongrels, Range et al. 2015) were depicted as highly aggressive, subjects were raised by humans after early separation from mothers, an event that has been related to the development of increased aggression and resource possession in dogs (Pierantoni et al. 2011). Furthermore, "early separation from mothers" may interact with "breed" to produce a more aggressive phenotype.

The effect of domestication on social tolerance in dogs (predictions: 4d, 5)

The dog–wolf comparison we have conducted using published matrices reporting outcomes of submissive interactions in free-ranging packs, showed that subordinate dogs were significantly more likely to elicit a submissive response in dominants than subordinate wolves (lower DCI in dogs than in wolves). Note that this result is unlikely due to the presence of some sterilized individuals into dog packs, because we found that DCI tended, indeed, to increase with an increasing proportion of spayed/castrated pack members (see above). However, we also found that dogs and wolves did not differ significantly with respect to hierarchy steepness. The latter measure was mainly affected by the percentage of unknown relationships which was considerable in both subspecies and slightly higher in wolves. The general similarity in both measures of power asymmetry is probably due to evolutionary inertia, because dogs and wolves have evolved in different ecological settings for a relatively short time (Fan et al. 2016; Wang et al. 2016). We note that high DCI in wolves are consistent with the observation that challenges for dominance are relatively rare in the wild, because the dominant breeding status is often acquired through inheritance and/

or dispersal into groups in which a dominant breeder position is vacant (Mech 1999; vonHoldt et al. 2008). However, the lower DCI recorded for dogs may partially support our "ecological hypothesis" (prediction 5), suggesting that the lower reproductive skew usually found in dogs packs relative to wolf packs (Cafazzo et al. 2014) may depend on reduced power asymmetries, or higher tolerance of subordinates' reproduction in the former, which, in turn, may depend on easy access to human-derived food. Nevertheless, we stress that lower reproductive skew may also depend on other variables, including, for example, higher availability of unrelated mating partners in dogs due to higher population density (which also probably results from access to abundant human-derived food; Bonanni and Cafazzo 2014).

Conversely, our dog–wolf comparison seems to contradict the "canine cooperation hypothesis" (prediction 4d; Range and Virányi 2014) and also the general trend found in primates that suggests an inverse relationship between cooperation and power asymmetry. One possible explanation is that such inverse relationship may not hold when comparison involves closely related taxa (see Balasubramaniam et al. 2012 and Koenig et al. 2013 for a similar explanation in primates). Alternatively, dogs may be more cooperative than it is usually supposed. Unlike wolves, who are mainly monogamous (Mech 1999), free-ranging dogs exhibit a flexible and more promiscuous mating system (Macdonald and Carr 1995; Pal 2005; Lord et al. 2013; Bonanni and Cafazzo 2014) which is usually associated with a reduction (although not absence) of paternal care. The latter point has been the focus of the "canine cooperation hypothesis." However, communal nursing of puppies has been recorded in several female free-ranging dogs (Daniels and Bekoff 1989; Pal 2005; Paul and Bhadra 2017) and it may be more common in dogs, because wolf packs usually comprise a single breeding female (vonHoldt et al. 2008). Consequently, assessing which subspecies is more cooperative may depend on gender, type of cooperation, and measure considered.

The "canine cooperation hypothesis" has been recently supported by a food-sharing test carried out using dogs and wolves raised in similar conditions in captivity (Range et al. 2015). However, the validity of this experiment is questionable, because the authors have compared the behavior of animals who were probably undergoing different developmental stages: based on the ages reported in Table 1, it is likely that all dogs who took part in the test were sexually mature, whereas no wolf was sexually mature.

However, we also stress that our dog–wolf comparison must be regarded as preliminary because it has some limitations: 1) it was based on a small sample of matrices; 2) although each matrix included in our test was unique with respect to membership, and we have treated it as an independent statistical data point, some individual wolf/dog appeared in more than one matrix, so matrices were not "completely independent"; 3) wolf matrices did not include submissions recorded during feeding and mating situations, whereas some dog matrices did. However, a recent study on a family pack of captive arctic wolves (Cafazzo et al. 2016) found that the feeding dominance rank was strongly correlated to the rank found in absence of food and the DCI was very high in both contexts.

CONCLUSIONS

With this work, we believe to have provided convincing evidence that free-ranging dogs possess the ability to form well-structured social groups and that such structure can be described reasonably

well as an age-graded dominance hierarchy similar to that of wolves. Intragroup agonistic interactions in free-ranging dogs are usually characterized by low-intensity aggression, which is consistent with the fact that they are cooperative carnivores. Moreover, our preliminary dog–wolf comparison contradicts the view that domestication has reduced social tolerance in dogs relative to wolves. Future studies should explore the meaning of "unknown relationships" in free-ranging dogs. If egalitarian/unresolved relationships actually exist in free-ranging dog packs, then we should conclude that a linear hierarchy model is just an approximate one (although effective) to describe the social structure of these animals.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Bonanni et al. (2017).

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