

The Social Organisation of a Population of Free-Ranging Dogs in a Suburban Area of Rome: A Reassessment of the Effects of Domestication on Dogs' Behaviour

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3.1 INTRODUCTION

Analysis of several genetic markers, together with assessment of archaeological remains, has shown that dogs were domesticated from Eurasian wolves (*Canis lupus*) some 15,000–35,000 years BP, although there is still considerable debate about the exact timing and location of the domestication event, how many wolf populations were involved, and the selective mechanism by which wolves were turned into dogs (Vilà et al., 1997; Bokyo et al., 2009; Pang et al., 2009; vonHoldt et al., 2010; Ding et al., 2012; Larson et al., 2012; Wang et al., 2013; Druzhkova et al., 2013). Traditionally, it was thought that dogs had been domesticated only through artificial selection, i.e., by capturing wild wolves and by selectively breeding those bearing desirable traits such as tameness (reviewed in Price, 1984; Clutton-Brock, 1995; Coppinger & Schneider, 1995). Partial support for this view is provided by artificial selection experiments on captive foxes (*Vulpes vulpes*). In this species, selection for a single behavioural trait, i.e., ‘tameness towards humans’, led to the appearance, through pleiotropic effects, of several morphological and physiological characters that are typically observed in dogs, such as piebald coat, floppy ears, earlier sexual maturation, and dioestrus breeding cycle (Trut, 1999). So, it seems conceivable that similar processes also might have operated during the evolution of dogs. However, more recently, researchers have suggested that natural selective forces also probably

contributed to the evolution of wolves into domestic dogs (e.g., [Morey, 1994](#); [Clutton-Brock, 1995](#); [Coppinger & Coppinger, 2001](#); [Zeder, 2012](#); [Wang et al., 2013](#)). Actually, one problem with the hypotheses of dog domestication based entirely on artificial selection is that, although genetic studies indicate that several hundred wolves were probably involved in the domestication process ([Savolainen, 2007](#); [Vilà & Leonard, 2007](#); [Pang et al., 2009](#); [Ding et al., 2012](#)), there is currently no archaeological evidence that Mesolithic humans artificially bred such a large number of wolves ([Coppinger & Coppinger, 2001](#)). For these and other reasons, [Coppinger and Coppinger \(2001\)](#) hypothesised that domestication of dogs was initiated through natural selection when some wolves started scavenging on food leftovers around the first permanent human settlements. According to this hypothesis, wolves that had a shorter flight distance from humans (or higher tameness) had a natural selective advantage over shyer individuals because they were more efficient in exploiting the new available food source provided by humans. At a later stage, once wolves had already evolved into tamer primitive dogs, humans began selecting dog breeding types to meet their requirements and to make dogs suitable for performing specific tasks. The hypothesis of dog self-domestication by natural selection ([Coppinger & Coppinger, 2001](#)) seems to be partially supported by two recent genetic studies: one showing that domestication of dogs was accompanied by a positive selection on genes involved in starch metabolism ([Axelsson et al., 2013](#)), which suggests an adaptation of dogs to a different ecological niche, and a parallel switch from a strictly carnivorous diet to a more generalised, omnivorous diet; the other one suggesting that during domestication dogs underwent a much milder genetic bottleneck if compared to other domesticated animals ([Wang et al., 2013](#)), indicating that domestication was most probably a continuous and dynamic process.

Whichever the mechanisms that led to dog domestication, it is clear that dogs have evolved in association with humans for a very long time ([Axelsson et al., 2013](#); [Wang et al., 2013](#)), and that in this new ‘domestic environment’ they were subjected to selective pressures (both natural and artificial) that were quite different from those experienced by wolves in their original environment of adaptation. Consequently, it is expected that important behavioural differences between dogs and wolves also evolved in the meantime, some of these probably reflecting adaptations to different ecological niches, and others resulting from artificial selection on dogs. Moreover, during their long association with humans, dogs have very often formed heterospecific social groups with them, and the complexity of the human social system may have provided further selective pressures leading to the evolution of new social skills in these animals ([Miklósi et al., 2004](#); [Miklósi & Topál, 2013](#)). Most studies aimed at investigating the effect of domestication on the behaviour of dogs have focussed on the dog–human relationship, and results suggest that dogs may have evolved a higher ability to understand human communicative gestures in comparison to wolves, possibly due to their reduced emotional reactivity and higher capacity for attention towards human beings ([Miklósi et al., 2003](#); [Hare & Tomasello,](#)

2005; Gacsi et al., 2009; Topál et al., 2009; Hare et al., 2010). However, other researchers have stressed that at least some of the wolf–dog differences with respect to interspecific communication can be greatly diminished when wolves are provided with intense socialisation with humans (Udell & Wynne, 2010; Udell et al., 2010a; Udell et al., 2012). But what about the effects of domestication on dogs' intraspecific social relationships? Although there are far fewer studies on this topic, it is usually believed that artificial selection for retention of juvenile traits (morphological and behavioural) into adulthood caused a reduction in the capacity of dogs to communicate visually with conspecifics and to perform ritualised agonistic behaviour, at least in some breeds (Frank & Frank, 1982; Bradshaw & Nott, 1995; Goodwin et al., 1997; Feddersen-Petersen, 2007). Moreover, there are frequent statements that intraspecific relationships would be less relevant to dogs than relationships with humans, given that many dogs actually spend more of their lifetime in association with humans than with other dogs (e.g., Frank & Frank, 1982; Tuber et al., 1996; Gacsi et al., 2005; Miklósi, 2007a,b; Nitzschner et al., 2012; Brauer et al., 2013). However, the fact that dogs evolved in a 'domestic environment' does not necessarily imply that they can live *only* integrated into a human family. Dogs vary greatly in their degree of association/dependence on human beings (Udell et al., 2010b; Miklósi & Topál, 2013): at one extreme, some dogs develop life-long attachments to their owners (Topál et al., 1998, 2005), whereas, at the opposite extreme, other dogs can even attack and kill humans as prey (Borchelt et al., 1983; Avis, 1999). Moreover, many dogs live in a free-ranging state (Coppinger & Coppinger, 2001); i.e., they do not have any constraints placed by humans on their activities, either because they are unowned or because they are unsupervised by their owners. Free-ranging dogs typically live around human dwellings, scavenging on human refuse (Coppinger & Coppinger, 2001), and have higher opportunities for social interactions with conspecifics than restrained dogs. In spite of the common belief that intraspecific relationships are not so relevant for dogs (see previous references), current estimates suggest that free-ranging dogs represent about 76%–83% of the global dog population (Hughes & Macdonald, 2013; Lord et al., 2013). Furthermore, even reproductive events involving pet dogs are often not planned by human beings (New et al., 2004; Lord et al., 2013), indicating that activities of these animals are probably influenced by conspecifics to a higher degree than expected. Consequently, in order to obtain a comprehensive picture of dogs' evolution and biology, we need to increase our knowledge of dogs' intraspecific relationships and of the social behaviour of free-ranging dogs. This leads directly to the question of whether free-ranging dogs are really social animals and, if so, to what extent they retain features of the wolves' social organisation after their prolonged evolution in a domestic environment. Several studies on free-ranging dogs concluded that those living in urban areas are often solitary or form only small temporary associations with conspecifics (usually 2–3 individuals) indeed (Beck, 1973, 1975; Rubin & Beck, 1982; Berman & Dunbar, 1983; Daniels, 1983a; Daniels &

Bekoff, 1989a; Ortolani et al., 2009). According to Coppinger & Coppinger (2001), since dogs have evolved to scavenge on human refuse, they do not need to form large packs to cooperate in hunting and in raising pups as wolves do, and so they are semi-solitary carnivores. However, note that this view assumes that pack living in wolves has evolved to allow for cooperative hunting and breeding, which is difficult to demonstrate and may not necessarily be true (Harrington et al., 1983; Packard, 2003; MacNulty et al., 2013). Moreover, cooperation in food and territorial defence is another important functional consequence of pack living in wolves (Harrington & Mech, 1979; Mech & Boitani, 2003; Stahler et al., 2013), and it may be potentially functional also for animals scavenging at dumps, at least under certain ecological conditions. In fact, many other studies on free-ranging dogs, carried out in various environments, found that these animals do form stable social groups (2–12 individuals), and some of these also exhibit cooperation in territorial defence (Scott & Causey, 1973; Nesbitt, 1975; Fox et al., 1975; Causey & Cude, 1980; Borchelt et al., 1983; Gipson, 1983; Font, 1987; Daniels & Bekoff, 1989a,b; Macdonald & Carr, 1995; Boitani et al., 1995; Pal et al., 1998). So, it appears that free-ranging dogs exhibit considerable variation with respect to their social organisation, possibly reflecting differences in ecological conditions, in the degree of human influence on their activities, and also in the methodologies applied by different researchers. Indeed, it must be stressed that free-ranging dogs are a very heterogeneous category of animals. For example, Boitani et al. (2007) made a distinction between ‘village dogs’, i.e., those free-ranging dogs living in proximity to human dwellings, and ‘feral dogs’, i.e., those that actively avoid human proximity by living in more natural environments. However, note that both kinds of dogs actually subsist mainly on food provided by humans and, according to this definition, they can comprise animals that differ with respect to the degree of human influence on their behaviour, i.e., both dogs that are socialised to humans and animals that are not (Boitani et al., 2007). So, for the purposes of this chapter, we prefer to classify free-ranging dogs based on their degree of dependency/socialisation to humans in the following categories: (1) free-ranging pets, i.e., dogs that are owned, although they are allowed to roam free for varied amounts of time; (2) abandoned/escaped dogs, i.e., dogs that are socialised to humans although, having lost their owner, they are completely free to roam; and (3) non-socialised free-ranging dogs, i.e., dogs that were born free and have formed social bonds only with conspecifics during the earlier stages of their development. The last two categories can be collectively referred to as ‘unowned free-ranging dogs’ when it is not possible to discriminate between abandoned and non-socialised animals. As we discuss later, these categories are likely to differ with respect to their intraspecific social skills (Daniels, 1983a; Daniels & Bekoff, 1989a,b).

Since there is evidence that at least some free-ranging dogs form stable social groups, we should ask how domestication has changed their organisation in comparison to wolf packs. Some authors (Boitani & Ciucci, 1995;

Boitani et al., 2007) suggest that groups of feral dogs seem to lack both the hierarchical social structure and the strong social bonds that are typical of wolf packs, and that this lack of a clear organisation places an upper limit to the number of individuals that can effectively cooperate as a social unit. Moreover, recently, there have been many claims that dogs' social relationships cannot be described in terms of a dominance–subordination paradigm (Coppinger & Coppinger, 2001; Semyonova, 2003; van Kerkhove, 2004; Bradshaw et al., 2009; Eaton, 2011; McGreevy et al., 2012). However, we stress that most previous studies on free-ranging dogs focussed mainly on ecological aspects (e.g., population censuses, demography, spacing pattern, diet), and only very few of the previously cited papers actually published quantitative data useful to describe the pattern of social interactions among group members, and how these social interactions may potentially affect cooperation. Consequently, we believe that the refusal of a hierarchical model to describe the social relationships of dogs is not fully justified on the available data, and that much more information is needed to assess how domestication has changed dogs' intraspecific social behaviour.

In this chapter, we summarise the main results of our 6-year research on the social organisation of a large population of free-ranging dogs living in a suburban area of Rome (Italy). We focus particularly on quantitative analyses of the social interactions among group companions and between dogs of different groups, given that these aspects have received little attention in the past. Moreover, we set our results in the general framework of the existing literature on dogs and compare the social organisation of dogs with that of wolves. Finally, in the last section of the chapter, we discuss the factors that are likely to explain variation in the social organisation of free-ranging dogs.

3.2 DOG POPULATION

Our study area was located at the southwestern periphery of Rome (a district traditionally called 'Muratella') and covered a surface of about 300 ha. It was delimited to the north, west, and south sides by roads with intense traffic and to the east side by cultivated areas. The area was crossed by a central road that split it into two clearly distinct sectors: the southwest sector was urbanised, although not densely populated, whereas the northeast sector was occupied by a nature reserve called 'Tenuta dei Massimi'. The habitat in the reserve consisted mainly of open grasslands with interspersed wooded areas (for a more detailed description of the environment, see Bonanni et al., 2010b; Cafazzo et al., 2010; Bonanni et al., 2011). Free-ranging dogs were free to move across the entire area, although they usually had their resting sites and dens within the reserve. However, in the early morning, they frequently approached the central road crossing the study area to feed on the food brought there by voluntary dog caretakers. These people drove along the central road every morning and placed food (mainly meat from a slaughterhouse) and water at specific feeding sites located alongside the road itself.

We regularly monitored the dogs of this population from April 2005 to October 2011. Detailed population censuses were carried out periodically in 2005–2006, 2007–2008, and again in 2010–2011, by enumerating all individually recognised dogs that approached the road to feed. Moreover, we conducted an intensive behavioural study of a 27-member pack from April 2005 to May 2006, and another similar study focussed on three packs (ranging in size from 3 to 15 individuals) from May 2007 to September 2008 (for a detailed description of packs, see [Bonanni et al., 2010b](#); [Cafazzo et al., 2010](#)). The studied packs were selected because they inhabited sectors of the study area characterised by good visibility. These behavioural studies were based mainly on direct observation and recording (*ad libitum* and *focal sampling*; [Altmann, 1974](#)) of affiliative, agonistic, and sexual interactions among dogs belonging to the same or to different packs. Additionally, we performed direct observation and recording of the location of animals (on a 1:1,250 scaled map of the area, to the nearest 20–30 m), of scent marking events (e.g., raised leg urinations; [Bekoff, 1979](#)), and of intergroup conflicts. Demographic data (number of individuals born, dead, dispersing, immigrating, etc.) were also collected, although those concerning infant survival were meaningful only with respect to the period 2005–2006. The reason is that in 2006 a management programme was started by the Rome Municipality, consisting in periodically trapping, neutering, and releasing back in the area adult dogs and in removing most puppies. All the behavioural results presented in the next sections of the chapter refer to dogs that were intact or sterilised at least 6 months before data collection, unless specified otherwise.

Population size was relatively stable across years. Censuses revealed that about 90–100 adult dogs were living in the area, leading to an estimate of density of about 30 animals/km². This density is much lower than that recorded for dog populations living in urban areas, although still much higher than that recorded in natural environments for both free-ranging dogs and wolves (see [Boitani et al., 1995](#), for review). Sex ratio in adult dogs was male biased, similar to other populations (reviewed in [Ortolani et al., 2009](#)), although by a small margin (about 1.3–1.4:1).

Almost all dogs of the population lived in packs. We defined a pack as a distinct and stable unit of individuals that travelled, fed, and defended resources together. Packs were identified by observing animals continuously and for several weeks. Mean pack size \pm SD was 12.6 ± 7.4 in 2006 (range: 6–27, $N = 7$), 9.0 ± 5.2 in 2008 (range: 2–16, $N = 10$), and 7.6 ± 6.6 in 2011 (range: 3–24, $N = 12$). Although the size of these groups is quite unusual if compared to that reported for other populations (see previous references), it should be noted that groups of 11–25 free-ranging dogs have already been observed both in North America and in Italy ([Beck, 1973](#); [Gipson, 1983](#); [Borchelt et al., 1983](#); [Boitani, 1983](#)). The percentage of solitary dogs in the overall population was in the range 0.011–0.043 across years.

We stress that the composition of our studied packs showed remarkable stability over time and thus was very different from the temporary associations

described by several authors (see previous references). Although undoubtedly several individuals could join or leave a given group on a daily or monthly basis, each pack usually contained a building block of animals that stayed together for several years. For example, in 2008, the 'Corridoio pack' comprised 9 dogs that had been together for at least 3 years, plus 2 members that had been born in this pack at the beginning of 2006. Although most members of this group eventually died in 2010, due to an epidemic, the 3 remaining dogs were still together in 2011, which means that they had shared pack membership for at least 6 years. Another example was the 'Fused pack': it comprised 13 individuals at the end of 2007, and 9 out of these were still group companions during the census we carried out 4 years later.

Several of the packs we closely monitored were undoubtedly composed of relatives at least to some extent, given that newborn puppies were usually recruited into their natal group. Survival of puppies was recorded for the 'Corridoio pack' in 2005–2006, and it was about 50% to 1 year of age. Notably, this figure is much higher than the 0%–5% reported by Beck (1975) and by Boitani *et al.* (1995), respectively, although comparable to the 15%–40% survival reported by many other authors (Scott & Causey, 1973; Nesbitt, 1975; Oppenheimer & Oppenheimer, 1975; Gipson, 1983; Daniels & Bekoff, 1989a,b; Macdonald & Carr, 1995; Butler & Bingham, 2000; Pal, 2001).

All free-ranging dogs of the studied population were medium- or large-sized mongrels (height at the withers 55–80 cm, weight 20–50 kg), and it was not possible to identify any predominant breeding type. Most animals had floppy ears and lacked a pronounced 'stop' between the muzzle and the forehead, whereas their coat colour was highly variable, ranging from uniform tawny/grey to black and tan, with some white/black piebald.

We are reasonably confident that almost all dogs of the population were 'non-socialised' to humans, although we could directly ascertain this only for those animals that were born during our study (e.g., 20 out of 39 dogs for which we have behavioural data were born free during the study). However, even dogs that were born before the initiation of our research never showed any sign of affiliation towards humans, and instead they usually displayed fear/aggressive responses to people. At the beginning of the study, they were very elusive, avoiding human presence at about 50 m of distance. Therefore, to be able to observe and follow them in different parts of the studied area, we spent 2–3 months to get them used to us by following them every day and by decreasing little by little the distance of observation. After this period, all dogs accepted our presence within about 20–50 m of distance, losing interest in us.

The few dogs that showed obvious signs of socialisation to humans, during our behavioural studies, were two 'free-ranging pets' that spent virtually all their time integrated into two different packs. That they had not been abandoned, but rather had spontaneously opted for a 'free-ranging life', was clearly indicated by the fact that, after losing their status as pack members, they went back to their respective human families and they were well received by them

(R. Bonanni, personal observation). Moreover, after the end of our behavioural studies, few other dogs socialised to humans appeared in the area, including some abandoned dogs and a pack affiliated to a gipsy family.

3.3 WITHIN GROUP RELATIONSHIPS

3.3.1 The 'Dominance Debate'

Before we discuss the applicability of the concept of dominance to domestic dogs, it is useful, first of all, to revise briefly its ethological meaning, as well as the methodological issues concerning its assessment, and the applicability of the concept itself to the dogs' wild ancestors, since this has also been questioned in the past (e.g., [Lockwood, 1979](#)).

According to [Drews \(1993\)](#), dominance is an attribute of a social relationship between two individuals in which one of two (the dominant one) emerges as the consistent winner of repeated agonistic interactions, whereas the other (the subordinate) usually defers without escalation. From a functional perspective, social dominance can be interpreted as a 'convention' allowing animals to resolve social conflicts in a relatively peaceful manner; i.e., when two animals with a dominant/subordinate relationship compete for a given resource, usually the dominant one gets it and no physical conflict takes place ([Hand, 1986](#)). More in general, 'dominance' refers to the asymmetric distribution of a given behaviour between two individuals (e.g., submissive gestures directed from subordinate to dominant animals and aggressive/dominance gestures displayed by dominant animals towards subordinates; see [van Hoof & Wensing, 1987](#)). When dominance relationships characterise all or most dyads in a social group of animals, then it may be possible to describe the social structure of that group as a 'linear dominance hierarchy'. However, in a stringent sense, a linear hierarchy model can be applied only when dominance relationships within the group are 'transitive' ([Appleby, 1983](#)). This means that if individual A is dominant over B and B is dominant over C, then A has to be dominant over C as well. Conversely, relationships in which C dominates A are called 'circular triads', and their presence may indicate that the organisation of the group under consideration does not fit a 'linear hierarchy model' ([Appleby, 1983](#)). Quantitatively, a dominance hierarchy can be described using indexes of linearity (e.g., [Landau's \$h\$, 1951](#)), whose values usually range from 0, indicating complete absence of transitivity (or no hierarchy), to 1, indicating a perfect linear hierarchy. However, in natural animal societies, perfect linear hierarchies are rare, and lower scores for the linearity indexes will be obtained, the higher the proportion of circular triads and of unknown and tied relationships (i.e., dyads that never interact or that exchange equal rates of the behaviour used to assess dominance, respectively) within the group ([Appleby, 1983](#)). However, it is possible to obtain an improved estimate of the Landau's linearity index (h') that takes into account both unknown and tied relationships ([de Vries, 1995](#)). So, in summary, the best

way to demonstrate that the social structure of a group fits a 'linear hierarchy model' consists in applying appropriate statistical methods (de Vries, 1995) to test whether the number of circular triads is lower than that expected by chance. However, statistical significance of linearity can be demonstrated only with hierarchies comprising a minimum of six individuals (Appleby, 1983).

Sometimes, even when dominance is transitive, the structure of a group may be better described as a 'pyramidal hierarchy', rather than as a linear one (van Hoof & Wensing, 1987). This happens, for example, when dominance relationships are clearly manifested between top-ranking animals and subordinates, but not among animals ranking below the top.

Although definitions like that of Drews (1993) undoubtedly place emphasis on the role of dominance in competitive interactions, it must be stressed that dominance relationships can also be expressed in the context of affiliative bonding (de Waal, 1986). For example, some highly social primates have evolved 'formal submissive gestures', i.e., signals that unambiguously communicate the acceptance of a subordinate status, and that allow the subsequent development of affiliative relationships between dominant and subordinate animals, thus resulting in enhanced group cohesion (de Waal, 1986). It is conceivable that such a formalisation of dominance relationships also exists in canids, if we think that Schenkel (1967) defined submission in the wolf and dog as 'the effort of the inferior to attain friendly or harmonic social integration'. Actually, although the first studies on the social behaviour of captive wolves conveyed the impression that the life of these animals involved frequent fighting to achieve the top-rank (or alpha) position in a dominance hierarchy (e.g., Schenkel, 1947; Zimen, 1975, 1976), more recent works in the wild have actually emphasised the cohesive nature of wolf packs (Mech, 1999). In particular, it has been stressed that whereas many captive wolf groups consisted of assemblages of unrelated individuals, or of orphaned siblings, in the wild most wolf packs are families comprising a breeding pair and their offspring of various ages (Mech, 1999, 2000; Packard, 2003). Within these family groups, there is a natural age-based dominance order in which offspring submit to parents, and puppies submit to both parents and older siblings (Mech, 1999). Around the age at which they attain sexual maturity (2 years), offspring disperse from their natal pack to start a new family elsewhere, and so they usually do not need to fight in order to achieve a dominant-breeder status (Mech, 1999; Mech & Boitani, 2003). However, under some ecological conditions, like those found in Yellowstone National Park, individuals may delay dispersal, and packs will contain several sexually mature individuals (MacNulty et al., 2009, 2012; Stahler et al., 2013). In these cases, competition for dominance and reproduction may be stronger (Mech, 1999), and usually only the top-ranking male and female breed, although in a few cases subordinate females related to the highest-ranking female also succeed in breeding (Peterson et al., 2002; vonHoldt et al., 2008). In any case, using submissive/dominance postures, it is mostly possible to arrange the members of a wolf pack in a dominance hierarchy, whose function in family packs is probably that of

regulating access to food resources (Mech, 1999; Packard, 2003). Sometimes this hierarchy will be pyramidal, as when most submissions are directed by offspring to parents, and there are few submission/dominance displays between offspring of 1–2 years of age (e.g., Table 2 in Mech, 1999; Peterson et al., 2002; Packard, 2003). However, at other times the hierarchy will be linear because submissive/dominance signals are exchanged by most members of the group (e.g., van Hoof & Wensing, 1987; Tables 3 through 5 in Mech, 1999; Packard, 2003; Sands & Creel, 2004). Note that the difference between a pyramidal and a linear hierarchy could also be explained in terms of reduced coverage in the former (higher percentage of dyads in which submissive/dominance signals are not observed), which in turn may be due to insufficient sample size concerning social interactions. This point may be especially relevant with respect to wild packs for which prolonged observations of social interactions, and even individual recognition of group members, can be often difficult to achieve (Sands & Creel, 2004). Another point is that not every wolf behavioural pattern seems appropriate to rank group members. For example, van Hoof and Wensing (1987) found an almost perfect linear dominance hierarchy ($h = 0.99$) in a captive family pack based on the direction of the behaviour ‘low posture’, whereas aggressive behaviour was basically intransitive. On the other hand, Lockwood (1979) found quite low h when using either submissive or aggressive patterns in several small captive packs, although it is unclear if this was due to the presence of circular triads or rather to reduced coverage.

In our studies on free-ranging dogs, we assessed hierarchies using basically the same behavioural patterns described for wolves, i.e., submissive gestures, dominance displays, and aggressive behaviour (see Cafazzo et al., 2010, for a detailed description). Submissive behaviour was recorded both during greeting ceremonies (affiliative submissions) and in response to aggressive and dominance displays (agonistic submissions). Based on the directionality of these behavioural patterns within dyads, it was possible to demonstrate the presence of a statistically significant linear hierarchy in a pack of 27 dogs (‘Corridoio pack’) studied during a 1-year period (Cafazzo et al., 2010). Data on social interactions collected for this pack during 2005–2006 were sufficiently numerous to show that the dominance rank order was consistent across different contexts (i.e., competition for food; competition for mates; absence of any sources of competition). Although the values obtained for h were not high (range 0.3–0.65, depending on the behaviour used to assess the hierarchy and on competitive context), this was clearly due to the relatively low coverage and not to the presence of circular triads (Table 3-1). As in wolves, submissive gestures proved to be more useful to assess the hierarchy when compared to dominance and aggressive gestures because they had higher directional consistency (i.e., higher frequency with which the behaviour occurred in its more frequent direction within dyads relative to the total number of times the behaviour occurred; see van Hoof & Wensing, 1987) and higher coverage (Cafazzo et al., 2010; Table 1). Moreover, affiliative submissions showed complete unidirectionality

TABLE 3-1 Submissive Behavioural Acts Recorded in the 'Corridoio Pack' in 2005–2006, Both in Affiliative and Agonistic Contexts*

Signaler	Receiver																											
	Mer	Gas	Pip	Leo	Gol	Lan	May	Nan	Iso	Dia	Sim	Pon	Sem	Kim	Mor	Ste	Han	Cuc	Mam	Dot	Gon	Gre	Bro	Eol	Emy	Mag	Pis	
Mer	-																											
Gas	95	-																										
Pip	37	49	-																									
Leo	13		3	-																								
Gol	24	13	10	6	-		1		2		3		1															
Lan	7	10	14		5	-																						
May	5	2	5	1	1	3	-	1					1															
Nan	8		1				3	-																				
Iso	2	2	1		3	5	1	2	-																			
Dia	1				1				1	-			2	1														
Sim	59	34	25	16	19	18	8	6	1	3	-	12					1											
Pon	14	30	26	4	13	9	7	1	3	1	13	-	1	3	2		1											
Sem	20	23	34		26	18	9	3	23		98	8	-	5	1										3			
Kim	1	5	10	3	3	10	16	3	2		3	4	5	-														
Mor	15	5	7		1	7	7	3	7			1	3	1	-													

Continued

TABLE 3-1 Submissive Behavioural Acts Recorded in the 'Corridoio Pack' in 2005–2006, Both in Affiliative and Agonistic Contexts* – cont'd

Signaler	Receiver																											
	Mer	Gas	Pip	Leo	Gol	Lan	May	Nan	Iso	Dia	Sim	Pon	Sem	Kim	Mor	Ste	Han	Cuc	Mam	Dot	Gon	Gre	Bro	Eol	Emy	Mag	Pis	
Ste	11		2		2	3	10		8			1		3		-												
Han	13	7	10	11	4	5	7	7		1	9	6		3	3	2	-	2		1	3					1		
Cuc	5	4	3		5	8	16		9		5		15	9	11	2	4	-										
Mam	4	5	3	3	6	9	11	1	8		1	2	11	3	6	1			8	-		2				2		
Dot	12	9	2		17	31	10		12		4	1	22	2	4					9	3	-						
Gon	12	1	8	1	5	27	10		7		13	3	13	4	13		1	6	1	4	-							
Gre	11				2	4	4	12			2	5					1		1	1		-						
Bro	12		4		9	4	9	1	8		4	1	7	1	7	1		4	3	7	9						-	
Eol	16	5	6	3	12	19	11	1	19		4	1	8	4	6	1	3	4	4	5	5				5	-		
Emy	2				11	10	5		12		4		10		4	2	1	1	1	1	2			2	7	-		
Mag	3	3	1		3	11	8		15		3	1	33	2	3	1		2		4	1					11	-	
Pis	6		2	3	6	5	11	3	8			2	8	2	7		1	2	4	1	1	1	1	2	5			-

*Performers on the vertical axis and receivers on the horizontal one. Improved linearity test (de Vries, 1995): $h' = 0.65$, $P = 0.00001$. Directional consistency index (DCI) = 0.96. The dominance order was built following de Vries (1998). (This table has been modified from Cafazzo et al., 2010.)

(i.e., the behaviour was expressed by only one individual in all dyads), and thus they could indicate formal acceptance of subordination (for a similar argument in pet dogs, see [Bauer & Smuts, 2007](#); [Trisko, 2011](#)).

We studied the ‘Corridoio pack’ again in 2007–2008, when its size had shrunk to 11 individuals, and found that it was still possible to detect a significant linear hierarchy in it, based on the direction of submissive behaviour ([Bonanni, 2008](#)). On the other hand, for another group of 9 dogs studied in the same period, the ‘Curva pack’, the distribution of submissive signals resulted in a hierarchy whose linearity was just marginally significant ([Bonanni, 2008](#)). However, this lack of significant linearity was undoubtedly due to low coverage. In fact, this pack was studied in an undisturbed manner for just 5 months before its composition changed substantially (it was joined by another group of 5 dogs to form the ‘Fused pack’), and several members were sterilised by the Rome Municipality. Nonetheless, by summing all submissive interactions recorded before and after sterilisation, we achieved higher coverage and found a significant linear hierarchy in this pack as well ([Bonanni et al.](#), unpublished data). Finally, the distribution of submissive behaviours recorded in a group of 3 dogs, the ‘Piazza pack’, allowed to arrange its members in a perfect linear hierarchy ($h = 1$; [Bonanni, 2008](#)) although, due to the small size of this pack, it was not possible to demonstrate that linearity could not have arisen by chance (see [Appleby, 1983](#)).

Overall, in our packs the dominance rank order (built following [de Vries, 1998](#)) was positively correlated to age, with older dogs being dominant over younger ones ([Bonanni et al., 2010a](#); [Cafazzo et al., 2010](#)). Moreover, there was a tendency for males being dominant over females of similar age, although females were usually dominant over younger males ([Bonanni et al., 2010a](#); [Cafazzo et al., 2010](#)). Both results suggest that the structure of our dog packs was relatively similar to that of wolf family packs, in which the dominance order is also based on age and males tend to dominate females within a given age class ([van Hoof & Wensing, 1987](#); [Mech, 1999](#); [Packard, 2003](#)).

We stress that dominance hierarchies in dogs are not restricted to our study area. Work carried out by our collaborators, using our same methods, has found two significant linear hierarchies in a pack of six free-ranging dogs living in a different district of Rome ([Abis, 2004](#)) and in a group of eight dogs housed in a shelter in Southern Italy ([Barillari, 2004](#)). Furthermore, a significant linear hierarchy has recently been found in a large group of pet dogs housed at a daycare facility in North America ([Trisko, 2011](#)).

In an influential review, [Bradshaw et al. \(2009\)](#) re-examined a data set previously published by [Pal et al. \(1998\)](#) concerning the pattern of social interactions in two packs of Indian free-ranging dogs, and presented new data on dominance interactions in neutered male dogs. They applied David’s score ([Gammel et al., 2003](#)) in an attempt to arrange the dogs of all these groups in a rank order and, after finding some apparent inconsistencies, they rejected the usefulness of dominance as a construct to explain dog social behaviour. First of all, it should

be noted that, although David's score is a valuable tool in order to rank the members of a social group, it does not represent a test of the linearity of a hierarchy at all. Consequently, it cannot be used to reject a linear hierarchy model as applied to groups of domestic dogs. Second, we re-analysed the data published by [Pal et al. \(1998\)](#) using an improved linearity test developed by [de Vries \(1995\)](#), and found the following results: in the pack of eight dogs, outcomes of submissive interactions (see [Pal et al., 1998](#), p. 337, Table 3, LIG group) could be arranged in a hierarchy whose linearity was highly significant ($h' = 0.90$, $P = 0.0009$), thus contradicting the findings by [Bradshaw et al. \(2009\)](#); in the pack of five dogs, submissive interactions (see [Pal et al., 1998](#), p. 337, Table 3, HIG group) again resulted in a hierarchy whose degree of linearity was even higher ($h' = 0.95$) although, because this group comprised less than six individuals, there was no statistical power to demonstrate that this linearity could not have arisen by chance (see [Appleby, 1983](#)).

In summary, the finding of seven statistically significant linear hierarchies in large packs of domestic dogs, and of two hierarchies with very high indexes of linearity in small packs for which statistical testing of linearity was not applicable, suggests that hierarchies in this species are common, although it cannot probably be expected that every dog group will fit a hierarchy model. Hierarchies can be detected only by applying appropriate linearity tests, and mostly only after prolonged recording of social interactions necessary to achieve sufficient coverage. Our results strongly contradict previous claims about the presumed lack of a clear hierarchical structure in dog groups (e.g., [Boitani & Ciucci, 1995](#); [Boitani et al., 2007](#); [Bradshaw et al., 2009](#); [McGreevy et al., 2012](#)) and suggest instead that evolution in a domestic environment has not substantially altered the ability of dogs to form structured packs with conspecifics.

3.3.2 Leadership

Social animals have a strong tendency to do what their group companions are doing ([Epple & Alveario, 1985](#); [Glickman et al., 1997](#); [Ferrari et al., 2005, 2009](#)), and this holds for domestic dogs as well ([Ross & Ross, 1949](#); [Scott & Marston, 1950](#); [Range et al., 2011](#)). This coordination of group activities is fundamental in order to maintain group cohesion and eventually allow animals to get the benefits of social living ([Conradt & Roper, 2005](#)). However, group members are likely to vary in the degree to which they affect the behaviour of companions. For example, some individuals (usually referred to as 'leaders') can be more likely to make decisions about which activity the group will perform at a given time and companions will simply accept their decisions ([Conradt & Roper, 2005](#)).

In family groups of wolves, collective activities are usually led by the dominant breeders given that the offspring tend naturally to follow the initiatives of their parents ([Mech, 1999, 2000](#)). Parents usually make decisions about awakening at the den, initiation of foraging, and travelling direction, and also take

initiatives in hunting, territorial defense, etc. (Mech, 2000). In small family packs, leadership is shared by both the breeding male and the breeding female (Mech, 2000). However, in large family packs, containing multiple sexually mature individuals, dominant breeders usually lead movements during 60%–90% of travel time (Peterson et al., 2002), meaning that in a non-negligible minority of cases, subordinate offspring can also provide leadership. From a functional perspective, it is usually believed that young subordinates can benefit from accepting their parents' decisions because the latter are more experienced and thus have higher knowledge about the location of resources such as prey and refuges within the territory (Mech, 1999; Peterson et al., 2002; Packard, 2003). On the other hand, sharing leadership in large packs may allow dominant animals to take advantage of pooled knowledge of a territory, and also to reduce both energy expenditure and the risks associated with travelling at the front of the pack (Peterson et al., 2002).

Although leader–follower relationships have been observed and described also for free-ranging dogs (e.g., Beck, 1973, 1975; Nesbitt, 1975; Fox et al., 1975; Boitani et al., 1995), until recently quantitative data on social interactions in these animals were too scarce to allow any detailed comparison with the pattern found in their wild ancestors. In our study, we often observed free-ranging dogs of all packs engaging in coordinated collective movements (Figure 3-1) that usually occurred in correspondence with group activity shifts (e.g., from resting to travelling, from resting to feeding/drinking, etc.; see Bonanni et al., 2010a). This provided us with the opportunity to investigate leadership as a mechanism for promoting pack coordination, and also to assess how the individual tendency



FIGURE 3-1 The ‘Corridoio pack’ on the move. Dogs were often observed moving in a single file. See color plate section. (Photo by Simona Cafazzo.)

to lead the pack was influenced by social relationships. In particular, we focussed on leadership at group departure for two reasons: (1) it was not always possible to follow the group to its travel destination, and (2) studies on other species (Byrne, 2000) suggest that animals walking at the front of the group are *not necessarily* those who decide the direction of travel. Operationally, we defined a 'leader' as the first dog that, after leaving all other group members behind, moved along a direction followed by a minimum of two companions ('followers') within 10 minutes (see Bonanni et al., 2010a, for more details). Note that wolf researchers in the past have measured leadership both at group departure and as the frequency/duration of staying at the front of the pack during travelling, and that these two different measures have provided very similar results (Mech, 2000; Peterson et al., 2002). So, for this reason and others (see below), we are quite confident that our definition of leadership provides a useful measure to allow a comparison with studies on wolves.

We found that in our studied packs, leadership was shared among group members, although not equally (Bonanni et al., 2010a). In other words, although every dog of at least 1 year of age could behave as a leader sometimes, i.e., it could successfully initiate a collective movement involving a minimum of three animals, each pack contained a limited number of individuals that could be classified as 'habitual leaders' (i.e., individuals that behaved more frequently as leaders than they behaved as followers). For example, in the largest pack studied ('Corridoio pack', 2005–2006), only 6 out of 27 dogs could be classified as 'habitual leaders', whereas there was just 1 habitual leader in the 'Corridoio pack', 2007–2008, and in the 'Curva pack', that comprised 11 and 9 dogs, respectively (Bonanni et al., 2010a). Habitual leaders could be both male and female, and overall, gender had no significant effect on the frequency of leading. Instead, the individual frequency of leading was strongly influenced by a linear combination of age and measures of dominance (e.g., proportion of submissive group companions; Bonanni et al., 2010a). Specifically, dogs that were old and high-ranking were much more likely to behave as leaders than young, low-ranking individuals (Figure 3-2). However, a multivariate statistical analysis revealed that receiving affiliative submissions, or formal recognition of dominance (Bauer & Smuts, 2007; Cafazzo et al., 2010; Trisko, 2011), was overall a better predictor of leadership than receiving agonistic submissions. Specifically, dogs that more frequently behaved as leaders usually received both affiliative and agonistic submissions by many companions, whereas dogs that received submissions by many companions *only* in agonistic contexts rarely behaved as leaders (Bonanni et al., 2010a). These results suggest that the development of an affiliative relationship between dominant and subordinate dogs could play a fundamental role in eliciting follower behaviour. In any case, the two kinds of submissions were highly and positively correlated during the period 2005–2006, but not in 2007–2008. This difference between the two phases of the research was partly due to the fact that the dog scoring highest for 'received agonistic submissions' in 2007–2008 actually scored 'zero' for

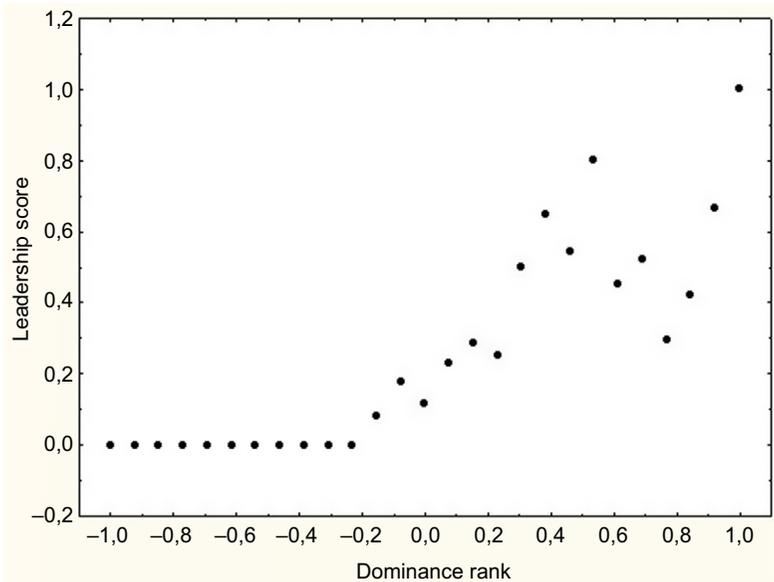


FIGURE 3-2 The relation between ‘leadership score’, as defined in [Bonanni et al. \(2010a\)](#), and ‘dominance rank’ for the members of the Corridoio pack during 2005–2006. Dominance rank is based on the directionality of both affiliative and agonistic submissions. Highest rank scored as +1 and lowest rank scored as -1. Spearman correlation between the two variables: $r_s = 0.92$, $P < 0.00001$.

‘received affiliative submissions’ ([Bonanni et al., 2010a](#)). This animal was a young adult male that was attaining higher positions in the dominance hierarchy of the ‘Corridoio pack’, although he rarely behaved as a leader ([Figure 3-3](#)). This might have been simply due to insufficient time passing from the achievement of a high-rankings status and hence a lack of recognition of his leadership role by the other members of the pack. Alternatively, this animal may not have possessed the social skills necessary to develop affiliative relationships with his potential followers ([Bonanni et al., 2010a](#)). The latter seems to us the most likely explanation based on the observations we carried out on this pack in 2009–2010. Moreover, the affiliative nature of leader–follower relationships is also emphasised by our finding that, during resting times, followers spent more time in close proximity with the ‘habitual leaders’ of their pack than with other followers ([Bonanni et al., 2010a](#)). This suggests that leaders were usually regarded by companions as more ‘attractive’ social partners than non-leaders.

From a proximate perspective, collective movements in free-ranging dogs may arise from the effort of subordinates to maintain proximity with dominant individuals. A further interpretation is that followers tend to do what the leaders do (e.g., go to a given place when the leader goes to that place) because they pay higher attention to the leaders’ actions than to the actions of other companions, having a stronger affiliative relationship with the former. Consistent

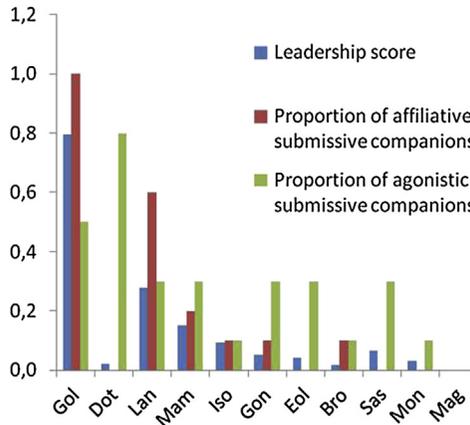


FIGURE 3-3 Distribution of ‘leadership score’, ‘proportion of affiliative submissive companions’, and ‘proportion of agonistic submissive companions’, respectively, for the members of the Corridoio pack during 2007–2008. Spearman’s correlation between ‘leadership score’ and ‘affiliative/agonistic submissive companions’: $r_s = 0.75$, $P < 0.008$; $r_s = 0.47$, $P = 0.14$, respectively. The latter failed to be statistically significant due to the behaviour of Dot. See color plate section. (Modified from Bonanni et al., 2010a.)

with this hypothesis, recent studies have shown that dogs pay more attention to the actions of their owners than to the actions of other familiar humans (Horn et al., 2013), indicating that in these animals attention is enhanced by affiliation. Moreover, Lockwood (1979) also proposed that the social organisation of his captive wolf packs could be described in terms of the differential attention that dominant animals received by companions.

So, based on our results, it can be argued that leadership in the free-ranging dogs of our population is mainly provided by old and dominant individuals (note that age and dominance are positively correlated), a pattern that seems to be relatively similar to that found in wolf family packs, in which parents lead activities and they are older than offspring and usually dominant over them (Mech, 2000; Peterson et al., 2002). However, from a functional perspective, it is unclear why dogs have retained the wolf trait of following the movements of experienced individuals because, unlike wolves, they subsist on food resources that are quite predictable in time and space. However, it remains possible that leaders may provide effective protection against common enemies (King et al., 2008) or know the better strategies and refuges to avoid them.

In wolves, the expression of both dominance and leadership closely corresponds to a ‘breeding status’, given that parents are in most cases the only breeding pack members, and they tend to suppress reproductive activity in their sexually mature offspring (Packard et al., 1985; Derix et al., 1993; von-Holdt et al., 2008). Conversely, packs of free-ranging dogs are known for containing often multiple breeding individuals of both sexes (Daniels & Bekoff,

1989a,b; Boitani et al., 1995; Macdonald & Carr, 1995; Pal et al., 1999; but see Gipson, 1983), and it has been argued that they lack those social mechanisms that allow dominant wolves to control the reproductive activity of subordinates (Boitani & Ciucci, 1995; Bradshaw et al., 2009). However, the latter is clearly a very questionable point because few data on dominance in free-ranging dogs have been published until the recent past and, consequently, the effect of social relationships on reproductive activities of group members has rarely, if ever, been tested. Our dog packs were similar to many others in that they contained multiple breeding individuals of both sexes. However, even if all sexually mature females mated and eventually gave birth, and several males of each group mated with oestrus females, in the pack for which analysis was possible (Corridoio pack, 2005–2006), both female reproductive success and male copulation rate were strongly influenced by leadership and dominance status (Cafazzo et al., submitted). In particular, high-ranking females that led the pack more frequently had a higher number of puppies surviving to sexual maturity, and high-ranking males that led the pack more frequently enjoyed a much higher copulation rate (Cafazzo et al., submitted). So, it seems that, at least in the Corridoio pack, leadership and dominance had a strong relationship with reproductive activity. Whereas in wolf packs there are usually just two ‘breeding’ individuals that consistently lead group activities, in our Corridoio pack multiple breeders could be ranked along a continuum from those that led frequently and had the highest reproductive success to those that rarely/never led and had the lowest reproductive success. Is the difference in the number of breeding individuals between wolf and dog packs an ‘adaptive’ consequence of the evolution of dogs in a domestic environment? We believe that this may be the case, and there are at least two possible reasons that packs of free-ranging dogs often contain multiple breeding individuals. First, as already pointed out by Lord et al. (2013), availability of food resources provided directly or indirectly by humans throughout the year allows dogs to reproduce in their first year of life. Conversely, wolves are much more food-limited than dogs and usually cannot breed before their second year of life (Lord et al., 2013). This means that young dogs can reproduce in their natal pack, whereas young wolves usually reproduce after dispersal. Second, abundant food resources in the domestic environment would presumably decrease feeding competition and nutritional stress in free-ranging dogs, and this may have favored the evolution of a social system in which dominant individuals would put less pressure over subordinates and would allow them to breed. This is also supported by the observation that wolf packs with multiple breeders are found where food resources are unusually abundant (Mech & Boitani, 2003). So, although much more data on the social regulation of reproduction in dogs are clearly needed, the interdependence of variables such as leadership, dominance, age, and reproductive activity, found both in studies of wolves and in our study on free-ranging dogs, suggests that some common organising mechanism may shape the social organisation of both species.

3.3.3 Cooperation

Cooperation can be defined as a joint action by two or more individuals to achieve a common goal (Boesch & Boesch, 1989). Moreover, in a broader sense, cooperation can also refer to prosocial behaviour by which an animal acts to benefit another one (e.g., de Waal et al., 2008). In wolves, social bonds among pack members have several functional consequences that include cooperation in hunting large prey (Mech, 1975; MacNulty et al., 2009, 2012), cooperation in territorial defence (Harrington & Mech, 1979; Mech, 1993; Mech & Boitani, 2003), and cooperation in breeding (Packard et al., 1992; Mech, 1999). Notably, wolf family packs are characterised by monogamous pair bonding, and by a division of *labour* system in which the breeding male leads hunts at places located several kilometers away from the den where the female remains to attend puppies (Mech, 1999, 2000). Subsequently, the breeding male and the older offspring come back to the den and provision the female and the puppies with food, by carrying pieces of prey and/or by regurgitating partially digested food (Mech, 1999, 2000). Conversely, many authors have stressed that domestication seems to have caused a reduction in cooperative tendencies in dogs, particularly because cooperative breeding and hunting seem to be greatly reduced in dogs relative to wolves (Boitani & Ciucci, 1995; Coppinger & Coppinger, 2001; Kubinyi et al., 2007; Miklósi, 2007a; Range et al., 2009; Brauer et al., 2013). For example, unlike wolves, free-ranging dogs have a primarily promiscuous mating system (Daniels, 1983b; Ghosh et al., 1984; Boitani et al., 1995; Pal et al., 1999; Pal, 2003), they rarely form monogamous pairs (for exceptions, see Gipson, 1983; Pal, 2005), and puppies are rarely fed by group members other than their mother (Macdonald & Carr, 1995; Boitani et al., 1995; Lord et al., 2013; but see Pal, 2005). According to Boitani et al. (1995), the lack of paternal care is one of the main reasons that feral dog populations suffer from very high infant mortality and are probably not self-sustaining. However, it should be stressed that many other authors have reported infant mortality rates for populations of free-ranging dogs, living in various environments, that fell within the range reported for wild populations of wolves (Scott & Causey, 1973; Nesbitt, 1975; Oppenheimer & Oppenheimer, 1975; Gipson, 1983; Daniels & Bekoff, 1989a,b; Butler & Bingham, 2000; Pal, 2001). This suggests that the apparent reduction in cooperative breeding in dogs is not necessarily a maladaptive trait. For example, Lord et al. (2013) have recently emphasised that the availability of food at dumps allows dog puppies to start foraging independently of parents at a much earlier age than wolf puppies (that have to learn to hunt). This might have favored the evolution in dogs of a decreased parental investment and of a consequent higher fertility (Lord et al., 2013). In populations that are close to the habitat carrying capacity, high fertility would lead to high infant mortality (e.g., Beck, 1973; Daniels, 1983a) but, on the other hand, it would allow fast recovery after increases in adult mortality (Lord et al., 2013). We add to these arguments the following considerations. First of all, human dumps are

likely to be much more predictable in time and space than mobile prey on which wolves subsist. This usually allows lactating female dogs to place their den in the vicinity of human food sources (e.g., [Gipson, 1983](#); [Boitani et al., 1995](#); [Macdonald & Carr, 1995](#)), and to feed without the need of waiting the return of any hunting companions while, at the same time, minimising the time in which puppies are left unattended. Consequently, in our opinion, allofeeding of mothers and puppies in free-ranging dogs does not happen frequently because it is not required by mothers, and it is probably not necessary in order to increase their reproductive success. Second, free-ranging dog populations are often characterised by much higher density than any wild canid species and by the lack of a clear reproductive season (e.g., [Beck, 1973](#); [Daniels, 1983a,b](#); [Boitani et al., 1995](#); [Butler & Bingham, 2000](#)). These conditions undoubtedly provide male dogs with the opportunity to court multiple oestrus females throughout the year while, at the same time, distracting them from any eventual caring for puppies. Consequently, these factors may have favoured the evolution from a monogamous mating system with prominent paternal care (like that of wolves) to a promiscuous mating system with reduced paternal care (like that of dogs). This seems to be supported by the fact that some wild canid species can switch from a monogamous to a polygynous/promiscuous mating system when population density increases (reviewed in [Hennessy et al., 2012](#)).

In our study population, we had limited possibilities to assess the level of cooperative breeding because dens with puppies were often well concealed in the dense vegetation and not easy to locate. On one occasion we did observe a neutered male dog regurgitating food for puppies that were past their weaning age. Moreover, on a number of occasions, we observed several members of a given pack gathering around a den location, or a male associating with a lactating female ([Cafazzo, 2007](#)); hence, we cannot rule out the possibility that certain adult dogs, other than the mother, regurgitated food to puppies. However, lactating females were frequently observed coming to the feeding stations to feed together with their group companions and then going back to the nature reserve to feed their pups without being followed by the rest of the pack. Another point is that we also observed some pregnant females leaving the Corridoio pack before giving birth and never coming back ([Cafazzo, 2007](#)). Notably these females, which presumably raised their puppies alone, had a reproductive success that was lower than that of the top-ranking female of the Corridoio pack, although still higher than that of non-dispersing subordinate females ([Cafazzo et al., submitted](#)). So, although these data are very limited, we hypothesise that (1) either any potential cooperative breeding effort concentrated mainly on the top-ranking female, or (2) it had no major impact on female reproductive success.

However, the fact that male dogs do not frequently regurgitate food to their companions does not, in our opinion, imply that dogs are not cooperative carnivores or that they are unable to display prosocial behaviour towards conspecifics. For example, free-ranging dogs, including males, can provide parental care

by guarding puppies against enemies (Nesbitt, 1975; Pal, 2003, 2005; Cafazzo, 2007; Guenther Bloch, personal communication), or can defend collectively an injured companion against approaching humans (Macdonald & Carr, 1995). Moreover, large dogs have been sometimes observed knocking over garbage cans to make food available for smaller dogs (Beck, 1973). Furthermore, in our opinion, cooperation should not be seen as a unitary trait. To give an example, cooperative breeding in wolves seems to be promoted by a spring peak in the secretion of prolactin (Kreeger et al., 1991; Asa, 1997; Asa & Valdespino, 1998). However, wolves also cooperate in hunting and in territorial defence at times other than spring (Mech & Boitani, 2003; MacNulty et al., 2012), indicating that different proximate mechanisms may underlie different kinds of cooperation. So, although group-living free-ranging dogs seem to show an overall reduction in cooperative breeding and hunting relative to wolves, they frequently engage in cooperative defence of territory and food resources against rival dogs (Fox et al., 1975; Font, 1987; Daniels & Bekoff, 1989b; Macdonald & Carr, 1995; Boitani et al., 1995; Pal et al., 1998). This is usually accomplished by several pack members joining forces to threaten or chase dogs belonging to stranger packs and often do not involve physical contact because the weaker opponents retreat without a fight. In our population, intergroup competition for food and space was very frequent. We were interested in assessing which variables influenced cooperation among group companions and individuals' active participation in conflicts against stranger packs. Active participation was defined as approaching opponents aggressively (e.g., barking, snarling, staring at the opponents with a tense body posture while keeping the tail high) by moving forward a minimum distance of 10 m, although we also recorded which dogs came closest to the opponents during an intergroup conflict or eventually in aggressive physical contact (e.g., biting, scratching, jumping upon) with them (see Bonanni et al., 2010b, for more details). Our results suggest that affiliative relationships between pack members promoted cooperation. Specifically, individuals that were more likely to actively participate in intergroup contests were those with the higher proportion of adult companions with whom they exchanged affiliative gestures (Figure 3-4; Bonanni et al., 2010b). From a functional perspective, cooperation with affiliative partners may ensure long-term reciprocation of social support and limit exploitation by cheaters (de Waal, 2008; Schino & Aureli, 2009; Berghanel et al., 2011). Surprisingly, we found that high-ranking dogs tended to participate more only in contests against groups that were larger than their own, although they did not stay at the front of the pack more often than subordinates (Bonanni et al., 2010b). Importantly, the coordinated aggressive behaviour exhibited by group companions appeared to be functional with respect to the competitive outcome because larger packs (those containing the higher number of participating individuals) were more likely to elicit a retreat response in the opposing groups (Bonanni et al., 2011).

From a socio-cognitive perspective, it would be interesting to assess whether these coordinated threatening displays observed in free-ranging dogs actually

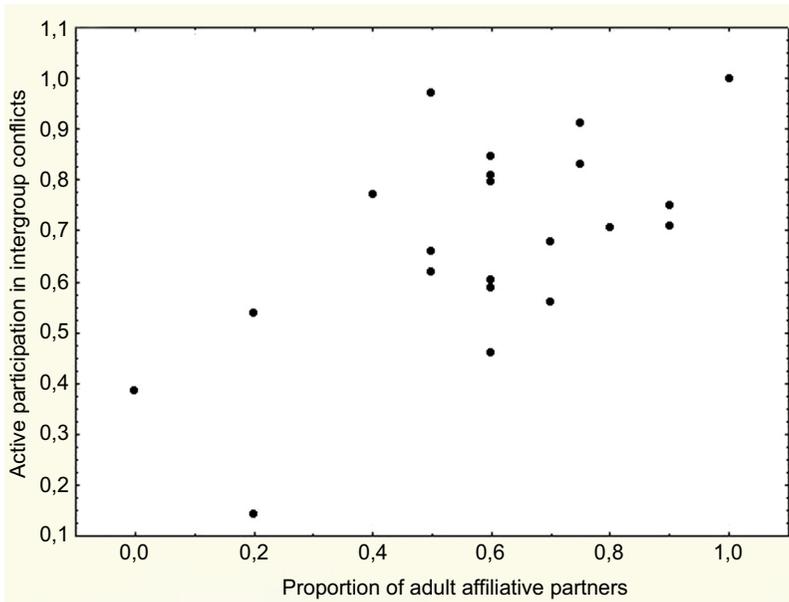


FIGURE 3-4 The relation between ‘relative frequency of active participation in intergroup conflicts’ and ‘proportion of adult affiliative companions’ for the members of three packs studied in 2007–2008. Pearson’s correlation between the two variables: $r = 0.63$, $P = 0.002$. (Modified from [Bonanni et al., 2010b](#).)

represent cooperation in a strict sense (see [Boesch & Boesch, 1989](#)). In other words, do dogs adjust their behaviour to that of companions so as to make coordination possible, or are they simply reacting to strangers simultaneously and independently of each other? For example, recently [Brauer et al. \(2013\)](#) found that even if pet dogs successfully coordinated their actions in a problem-solving task, there was no obvious indication that they attended to each other during the experiment, although the authors admitted that monitoring the partner may not have been necessary to solve the task. Although a compelling demonstration that dogs take their partner’s role into account should be based on controlled studies, our results provide some indications that free-ranging dogs were *not* acting independently of each other when engaging in coordinated aggressive displays. First of all, in our study, dogs were more likely to behave aggressively when their own pack outnumbered the opposing group ([Bonanni et al., 2011](#)), which suggests that dogs took their companions’ presence into account as if they were expecting to receive support from them during conflicts. Second, the previously mentioned correlation between individual participation in conflicts and measures of affiliative integration is, in our opinion, unlikely to emerge unless dogs are also attending to which companions participated in conflicts, and not just reacting to the opponents. For example, the first dogs that detect the presence of strangers will usually start challenging them (conditionally to

an assessment of relative group size), and this may facilitate the activation of similar motor patterns and similar emotional states in their companions (sensu Preston & de Waal, 2002); the latter, in turn, may happen with a higher probability, the closer the social relationship between the animals involved. Affiliative partners either may be more motivated to act together or simply pay higher attention to the actions of companions.

Moreover, during intergroup conflicts, we observed dogs displaying behavioural patterns indicating that they could take into account the behaviour of partners. For instance, we frequently observed dogs glancing at companions as if they were checking their position, although systematic recording of this behavioural pattern was prohibitively difficult because typically many dogs moved fast all together. However, on some occasions when dogs approached opponents slowly, we could observe some individuals monitoring the position of companions (e.g., by turning their heads backwards) and then stopping the approach until other dogs also started moving forward. So, we had the feeling that looking at companions could be used to check whether they would join the collective action and/or as a way to recruit them (see Fox et al., 1975, for a similar description). Finally, when groups of dogs chasing a lone opponent succeeded in reaching the opponent, they frequently encircled it, a behaviour indicating that dogs were adjusting their movements to those of companions.

In contrast, we almost never observed our studied dogs engaging in cooperative hunting, aside from an unsuccessful attempt at chasing a red fox (*Vulpes vulpes*), although they were suspected to have killed a crested porcupine (*Hystrix cristata*), some sheep (*Ovis aries*), and a donkey (*Equus africanus asinus*). It is probable that dogs had low opportunities to find suitable prey in the area, and the possibility of feeding on food provided by humans may have decreased their motivation to hunt and hence to cooperate in hunting. More generally, dogs have smaller teeth and less powerful jaws than wolves (Coppinger & Coppinger, 2001), and thus, they are likely to be less effective than wolves in killing large prey. Even so, in our opinion, evolution in a domestic environment does not necessarily imply that dogs have lost their predatory motivation or the ability to hunt cooperatively. Notably, this environment also contains several other species that were commensal of humans and potential prey for dogs during their evolution, including several ungulates (Zeder, 2012), and this may have contributed to maintain selective pressures for predatory motivation. Studies on free-ranging dogs' diet confirm that most of them subsist primarily on human waste and carrions, but they can also prey on small- and medium-sized animals such as reptiles (e.g., *Amblyrynchus cristatus*), birds (e.g., *Apterix australis*), mice (*Peromyscus* spp.), rabbits (*Sylvilagus* spp.), hares (*Lepus* spp.), white-tail deer (*Odocoileus virginianus*), roe deer (*Capreolus capreolus*), gazelles (e.g., *Procapra gutturosa*, *Gazella gazella*), impala (*Aepyceros melampus*), goats (*Capra hircus*), and sheep (Scott & Causey, 1973; Nesbitt, 1975; Kreeger, 1977; Lowry & MacArthur, 1978; Causey & Cude, 1980; Gipson, 1983; Boitani, 1983; Butler et al., 2004; Vanak & Gompper, 2009; Young et al., 2011). Although

systematic recording of how many dogs were involved in killing these prey was almost never carried out, these studies report that on a number of occasions two to four dogs participated in killing (e.g., Kreeger, 1977; Butler et al., 2004), indicating that free-ranging dogs can hunt cooperatively. Moreover, we were personally shown a series of pictures, taken by a game warden in Italy, showing a group of six free-ranging dogs chasing a herd of wild boars (*Sus scrofa*) and succeeding in isolating one of the juveniles and in killing it. In our view, it is realistic to suggest that most domestic dogs are less specialised than wolves in preying on large herbivores, but they can easily hunt medium-sized animals, including some ungulates, and can do this cooperatively. Although it has been suggested that free-ranging pets kill ungulates more frequently than unowned dogs (e.g., Kreeger, 1977; Lowry & MacArthur, 1978), this may be simply due to the fact that the former were more numerous in the areas where those predation events were recorded. It is plausible that unowned dogs are more likely to engage in cooperative hunting where suitable prey are available and food resources provided by humans are less abundant.

To summarise this part, our belief is that ecological pressures experienced by dogs in the domestic environment have led to the evolution of a promiscuous mating system characterised by a reduction in cooperative breeding relative to wolves, and of a feeding strategy primarily based on scavenging and predation of small- or medium-sized animals, still involving some degree of cooperative hunting. However, defending food resources collectively against conspecifics seems to be still advantageous in dogs, at least when these are abundant enough to allow pack living, and this might have provided selective pressures for the ability to develop a complex social structure, relatively similar to that of wolves.

3.4 INTERGROUP RELATIONSHIPS: SPACING PATTERN

A territory can be defined as a defended area from which competitors are actively excluded (reviewed in Maher & Lott, 1995, 2000). Wolves are usually depicted as highly territorial carnivores because packs live in more or less exclusive areas usually showing little overlap with areas occupied by neighbouring packs (Peters & Mech, 1975; Harrington & Mech, 1979; Harrington & Asa, 2003; Mech & Boitani, 2003). Moreover, such areas are defended both directly, i.e., through attacks against trespassing wolves, and indirectly through scent marking and howling (Peters & Mech, 1975; Harrington & Mech, 1979; Harrington & Asa, 2003; Mech & Boitani, 2003). Scent marking is accomplished mainly through raised-leg urinations (in males), flexed-leg urinations (in females), and ground scratching, all of which are usually performed only by the dominant breeders (Peterson et al., 2002; Harrington & Asa, 2003). Scent marks are released at higher rates along the boundaries of territories than in the interior parts, and there is some evidence that they can deter intruders from trespassing, and that trespassing wolves usually suspend marking (Peters & Mech, 1975; Mech & Boitani, 2003). Howling can also be used to advertise a pack's presence

in a given area, although it seems to be independent of location (Harrington & Mech, 1983). In any case, both marking and howling appear to be functional in order to space different packs and to reduce the probability of interpack encounters. Nevertheless, territorial competition in wolves can become more intense during the mating season, and interpack conflicts are actually one of the main causes of wolf mortality (Mech & Boitani, 2003).

However, the degree of territoriality exhibited by a given species is known to vary with ecological conditions (Maher & Lott, 2000). For instance, wolf territories may overlap more when food resources become more abundant, population density increases, and the habitat becomes saturated (Peterson, 1979; Mech & Boitani, 2003). More in general, when population density increases above a given threshold, intruder pressure may become so intense that territories would no longer be economically defensible, leading animals to switch to alternative competitive strategies (Brown, 1964; Maher & Lott, 2000). So, since free-ranging dogs often subsist on abundant food resources and, as a consequence, live at much higher densities than wolves, it may be expected that overall they will be less territorial than their wild ancestors. For example, in some high-density urban populations, free-ranging pets seem to defend their household as a territory but, when outside, their small home ranges greatly overlap with those of other dogs, indicating that they are not defending exclusive areas (e.g., Berman & Dunbar, 1983; Daniels, 1983a; Daniels & Bekoff, 1989a). Conversely, packs of unowned free-ranging dogs living in low-density rural areas have often been described as territorial (Nesbitt, 1975; Gipson, 1983; Daniels & Bekoff, 1989a,b; Macdonald & Carr, 1995; Boitani et al., 1995). On the other hand, there are also reports of territorial pack-living dogs in urban areas (Fox et al., 1975; Font, 1987; Pal et al., 1998) and of non-territorial packs in low-density rural areas (e.g., Scott & Causey, 1973). So, it appears that between-population variation in territoriality is affected by multiple variables in free-ranging dogs, which could possibly include density, abundance, distribution, and predictability of food resources as well as the degree of relatedness to certain breeds selected for higher/lower territoriality, etc. (see next section).

Moreover, free-ranging dogs' territories are usually much smaller than those of wolves, the former ranging from 0.1 ha in urban areas (Daniels, 1983a) to 70 km² in Alaska (Gipson, 1983), and the latter ranging from 30 to more than 6,000 km² (Mech & Boitani, 2003). Clearly, the size of wolf territories will be inversely related to prey biomass (Mech & Boitani, 2003), whereas dogs' territories presumably just need to embrace human food sources and are unlikely to be strongly influenced by highly mobile prey. There is no evidence that free-ranging dogs rely on howling to space each other as wolves do, although there is some indication that they can use collective barking to intimidate rival packs even at considerable distance and to keep them away from dumps (Daniels & Bekoff, 1989b; Macdonald & Carr, 1995). Overall, it appears that free-ranging dogs are usually less spaced than wolves (because they live at higher densities, in smaller territories), and that interpack conflicts are much more frequent, although rarely escalating into fatal aggression (Daniels & Bekoff, 1989b; Boitani et al., 1995;

Bonanni et al., 2010b, 2011; for exceptions, see Gipson, 1983; Macdonald & Carr, 1995).

There are somewhat ambiguous indications that dogs in our study population were defending territories. For example, based on the locations of intergroup contests, the Corridoio pack in 2005–2006 appeared to be defending an area of about 22 ha, comprised within a larger home range of about 60 ha (Cafazzo et al., 2012). Members of this pack scent marked (using the same behavioural patterns described previously for wolves) more frequently along the territorial boundary and within the territory than outside (Cafazzo et al., 2012). Moreover, they marked more frequently during interpack than during intrapack agonistic interactions (Cafazzo et al., 2012). Unlike wolves, in dogs marking was not restricted to the highest-ranking male and female, although there was a very high positive correlation between marking rate and dominance rank both in males and females (Figure 3-5; Cafazzo et al., 2012; Bonanni et al., unpublished data). Nevertheless, in 2007–2008 we found that the areas marked with raised-leg urinations by the members of three competing packs overlapped to a considerable extent (45%–75% of the total area), indicating that marking was not really effective in deterring strangers from entering a given area (Bonanni et al., 2011). However, the larger packs were usually able to keep the smaller ones away from a given feeding site at least temporarily (Bonanni et al., 2011), and the smaller packs often could feed at a given site only when the larger groups were elsewhere (Bonanni et al., unpublished data). It is likely that the spacing pattern observed in our population was a reflection of the way in which people distributed the food, that led several packs to concentrate their activities around the central road. However, the situation might have been different in 2005–2006, when the Corridoio pack was much bigger than all the other groups in the area, and might have been also more effective in keeping strangers away from its territory.

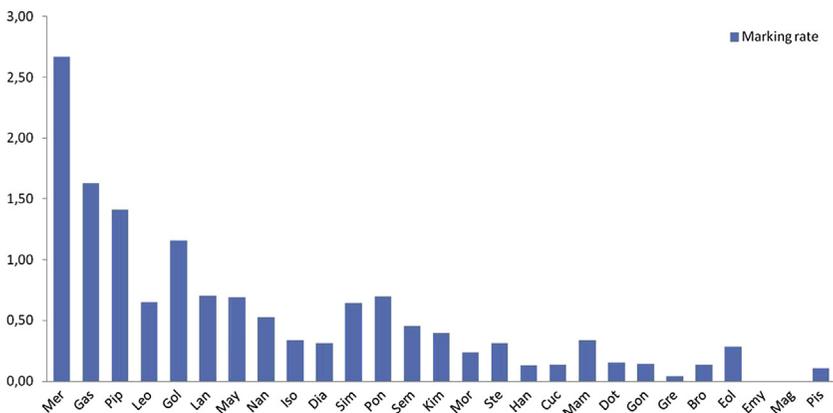


FIGURE 3-5 The relation between ‘marking rate’ and ‘dominance rank’ for the members of the Corridoio pack during 2005–2006. Spearman rank correlation between the two variables: $r_s = 0.92$, $P = 0.0001$. Individuals are ordered from the highest (on the left) to the lowest dominance rank.

Whereas in wolves marking and territorial defence seem to increase during mating periods (Mech & Boitani, 2003), the opposite seems to hold for free-ranging dogs. During the oestrus period, male dogs can frequently trespass into other packs' territories and succeed in mating with females (Boitani et al., 1995; Pal et al., 1998, 1999; Cafazzo et al., submitted). Consistent with these observations, in our population, males of the Corridoio pack marked less frequently in the presence of oestrus females than at other times (Cafazzo et al., 2012). Furthermore, the oestrus period in dogs can also provide opportunities to recruit strangers into resident packs (Boitani et al., 1995; Macdonald & Carr, 1995; Cafazzo, 2007). It has been suggested (Macdonald & Carr, 1995) that recruitment of immigrant dogs would be more probable during periods in which the structure of packs is highly perturbed by human-caused mortality (e.g., car accidents, capturing, killing). Conversely, when stable affiliative and kinship ties develop among the members of a pack, the chances of unrelated immigrants being recruited will probably diminish (Macdonald & Carr, 1995). More generally, we believe that recruitment of immigrant dogs would be functional for relatively small packs that need to increase in size to face intergroup competition for resources.

Overall, it seems that the pattern of abundance and distribution of food resources in the domestic environment has led to an increase in the frequency of interpack encounters and to a higher degree of interpack tolerance in dogs relative to wolves.

3.5 VARIATION IN DOG SOCIETY

Our studies have shown that a population of free-ranging dogs living in a suburban area of Rome exhibited a complex degree of social organisation. Nevertheless, the social organisation of our dogs apparently was very different from that reported by several other authors who claimed that free-ranging dogs either rarely form stable social groups (Beck, 1973, 1975; Rubin & Beck, 1982; Berman & Dunbar, 1983; Daniels, 1983a; Coppinger & Coppinger, 2001; Butler et al., 2004; Ortolani et al., 2009) or, if they do, they lack a clear hierarchical structure (Boitani & Ciucci, 1995; van Kerkhove, 2004; Boitani et al., 2007; Bradshaw et al., 2009). Consequently, it appears of paramount importance to unravel which variables are likely to explain the observed variation in the social organisation of dogs, and to assess to what extent the findings from our population can be extended to other dog populations.

First of all, differences in the results of different studies on free-ranging dogs can partly arise from differences in the methodologies employed. For example, in our opinion, previous claims about the presumed lack of social structure in dog packs were not justified due to very limited quantitative data on social interactions (see the previous discussion about dominance). Moreover, methodology may also affect whether or not dogs are depicted as solitary *versus* social animals. In our study, we concluded that dogs were living in stable packs

after observing the animals continuously for several weeks. For example, in 2005 we took about 6 weeks to recognise individually all members of the ‘Corridoio’ pack and to conclude that they belonged to the same group, although the time necessary to assess the composition of a given pack will inevitably vary depending on group size, population density, and visibility. On the other hand, in most studies claiming that urban free-ranging dogs are semi-solitary carnivores (Beck, 1973; Berman & Dunbar, 1983; Daniels, 1983a; Daniels & Bekoff, 1989a; Ortolani et al., 2009), sociality was assessed by recording the frequencies of group sizes during population surveys, and then by comparing them with the expected frequencies generated by a zero-truncated Poisson distribution, under the hypothesis of random grouping. This method always led to the finding that solitary dogs comprised 50%–80% of the total population and that they were more frequent than expected. However, as pointed out by Font (1987), this method does not involve prolonged and continuous observations of animals, and it can lead to an overestimation of the proportion of solitary individuals in cases in which members of social groups are solitary foragers. Actually, prolonged focal observations of free-ranging dogs living in urban areas and in villages have revealed that they can form stable social groups that defend territories collectively, although they spend considerable time foraging alone (Font, 1987; Macdonald & Carr, 1995). Consequently, the applicability of the previously described method to investigate dog sociality may be questionable.

Whether free-ranging dogs forage alone or in groups or, more in general, whether they live solitary or in packs is likely to be affected by local ecological conditions, particularly by the abundance and distribution of food resources. Theories concerning the ecology of carnivore sociality predict that the size of social groups will be positively correlated to food biomass during periods of minimum availability (Macdonald, 1983). For example, it has been argued that where food resources are dispersed in small packages (e.g., handouts, scraps from restaurants, dustbins), as in many urban areas and villages, that are usually insufficient to satiate more than one individual at a time, dogs will often forage alone (Daniels & Bekoff, 1989a; Macdonald & Carr, 1995; Coppinger & Coppinger, 2001). Conversely, when food resources provided by humans are clumped in large packages (e.g., garbage dumps), then group foraging becomes possible, and living in large packs probably allows dogs to increase access to food by outcompeting single dogs and smaller groups (Daniels & Bekoff, 1989a,b; Macdonald & Carr, 1995). In our study site, food dispensed by humans at each feeding site was probably abundant enough to support packs of an unusual size (we always saw group members feeding together). However, accurate measurements of food abundance in all these studies were not carried out, and so this hypothesis still awaits testing.

Free-ranging dogs that live in urban areas and in villages have been classified as ‘village dogs’ by several authors (Macdonald & Carr, 1995; Coppinger & Coppinger, 2001; Boitani et al., 2007; Ortolani et al., 2009). However, this category is very heterogeneous because it comprises both owned and unowned

dogs and, in our opinion, it is very important to distinguish dogs on the basis of both their ownership status and their degree of socialisation to people. For example, Daniels (1983a) found that free-ranging pets spent less time in association with other dogs, and had smaller home ranges, than unowned free-ranging dogs. Moreover, it should be noted that in virtually all the studies concluding that free-ranging dogs are semi-solitary animals, conducted both in urban and in rural environments, the population comprised a considerable proportion of free-ranging pets (Beck, 1973, 1975; Rubin & Beck, 1982; Berman & Durban, 1983; Daniels, 1983a; Daniels & Bekoff, 1989a; Butler et al., 2004; Ortolani et al., 2009). Conversely, all studies in which free-ranging dogs formed stable groups in urban (Fox et al., 1975; Font, 1987; Pal et al., 1998), suburban (Bonanni et al., 2010a,b; Cafazzo et al., 2010, 2012), and rural/wild environments (Scott & Causey, 1973; Nesbitt, 1975; Causey & Cude, 1980; Gipson, 1983; Daniels & Bekoff, 1989b; Boitani et al., 1995; Macdonald & Carr, 1995) concerned unowned animals that were probably to a large extent non-socialised to humans (based on their avoidance/aggressive response to people) or with a minority of abandoned/escaped dogs recruited into packs. So, why do free-ranging pets seem to be less likely to live in packs than unowned free-ranging dogs? The question seems particularly intriguing because many pet dogs undoubtedly possess the potential to engage in complex social interactions with conspecifics (Bauer & Smuts, 2007; Cools et al., 2008; Ward et al., 2008, 2009; Trisko, 2011). We propose the following potential explanations: one possibility is that some free-ranging pets may actually form groups, but these may go undetected because these dogs can forage alone for considerable amounts of time (see previous discussion); a second possibility is that, depending on the degree of restraint placed by their owners, free-ranging pets may have limited chances of coordinating their actions with those of potential companions, hence reducing the likelihood of group formation; third, depending on the timing and amount of socialisation to humans relative to timing and amount of socialisation to conspecifics, some free-ranging pets may be less motivated to develop social relationships with other dogs (see Scott & Fuller, 1965), considering humans their primary relationship partners; finally, free-ranging pets that do not share their home site with other dogs may have limited experience/social skill in interactions with conspecifics (see Daniels & Bekoff, 1989a). Note that, if one of the last two hypotheses is correct, one should expect that even 'abandoned dogs', which are socialised to humans, will be on average less skilled at interacting with conspecifics than 'non-socialised dogs'. In partial support for this, Daniels and Bekoff (1989b) found that abandoned dogs had fewer social contacts with conspecifics, and much smaller home ranges, than non-socialised dogs, although some of them were also recruited into packs of non-socialised animals.

Some authors have stressed that the behaviour of free-ranging dogs is likely to be influenced also by the effects of artificial selection (e.g., Boitani & Ciucci, 1995; Macdonald & Carr, 1995). Although 'pure breed' dogs are rarely found in free-ranging groups (Boitani & Ciucci, 1995), it is believed that differential

genetic relatedness with specific breeds may contribute to explain the observed variation in free-ranging dog behaviour. For example, [Boitani and Ciucci \(1995\)](#) suggested that higher territoriality in a given group/population may depend on relatedness of its members with breeds artificially selected to guard livestock and other human property. Moreover, differential relatedness with specific breeds can also affect body size and physiology which, in turn, will affect the energetic and ecological requirements of a given population of free-ranging dogs and eventually their fitness in a given environment. For example, a pack of free-ranging dogs studied in Alaska showed excellent survival at extreme low temperatures, and most of its members apparently were related to breeds specifically selected in cold latitudes ([Gipson, 1983](#)). On the one hand, we agree that the effects of artificial selection will complicate the adaptive interpretations of dog behaviour and will probably increase its variability relative to that of their wild ancestor. On the other hand, we believe that predicting the behaviour of free-ranging dogs based on their degree of relatedness to specific breeds is a very difficult task. First of all, hybridisation studies suggest that the behaviour of crossbred dogs usually differs from that of both parental breeds ([Scott & Fuller, 1965](#)). Moreover, free-ranging dogs could differ from genetically related breeds, not just with respect to their genetic sequences, but also with respect to patterns of gene expression mediated by different environmental stimuli (*sensu* [Saetre et al., 2004](#); [Crews, 2011](#)). Aside from all these considerations, we also caution against arguing that the complex sociality observed in some free-ranging dogs is a mere consequence of artificial selection. We stress, instead, that some of the salient features of dog sociality that emerged in our and in other studies on free-ranging dogs (e.g., dominance, cooperation) appear to be shared by multiple breeds and also by the primitive Indian dogs, suggesting a possible derivation by a common ancestor. For example, a recent study found a linear dominance hierarchy in a large group of pet dogs comprising 18 different breeds ([Trisko, 2011](#)). Moreover, cooperative behaviours such as coalitions to intimidate/attack common targets, observed by us and other researchers in free-ranging dogs, have been described also in several breeds of both large and small size ([Scott & Fuller, 1965](#); [Borchelt et al., 1983](#)). Most important, Indian free-ranging dogs, which are presumably genetically closer to the most primitive dogs than Western free-ranging dogs ([Clutton-Brock, 1995](#); [Gonzalez, 2012](#); [Crapon de Caprona & Savolainen, 2013](#)), display a social organisation that shares several features with the dogs of our population, i.e., stable social groups with hierarchical structure, cooperation in intergroup conflicts, and a promiscuous mating system ([Pal et al., 1998, 1999](#); see also the previous section on dominance).

In summary, we suggest that all the previously cited factors could contribute to explain variation in the social organisation of free-ranging dogs. However, we predict that stable packs are more likely to develop when unowned free-ranging dogs, and especially those that are not socialised to humans, can subsist on abundant and non-dispersed food resources.

3.6 CONCLUSIONS

Our results suggest that domestic dogs possess the potential to develop long-term, complex social bonds with their conspecifics and not just with humans. Under the appropriate ecological conditions, free-ranging dogs can form stable packs whose organisation resembles that of wolf packs with respect to several aspects, including age-based dominance hierarchies, leader–follower relationships, social regulation of reproductive activities, and cooperation in resource defence. Differences between their social organisation and that of wolves can be reasonably explained as an adaptation to the domestic environment. Finally, the fact that some dogs do not form stable groups should not be interpreted as an indication that domestication has drastically reduced their intraspecific sociality, but rather as a flexible response to specific ecological conditions and higher dependency on humans.

Future Directions

- Our finding that affiliative relationships seem to promote coordination and coalition formation in free-ranging dogs is based on correlational evidence only. However, the existence of a causal link between affiliative and cooperative interactions could be tested by administering substances that in other species are related to both behaviours (e.g., ‘oxytocin’; [De Vries et al., 2003](#); [Madden & Clutton-Brock, 2011](#)) to domestic dogs.
- What is the effect of kinship on social relationships in dogs? We currently do not know whether the social organisation of packs composed primarily by relatives differs from that of packs made up of unrelated individuals.
- Why do male dogs rarely regurgitate food for puppies? In wolves, cooperative breeding seems to be promoted by a seasonal prolactin peak, coinciding with the birth of puppies ([Kreeger et al., 1991](#); [Asa, 1997](#); [Asa & Valdespino, 1998](#)). However, little is known about variations of prolactin and parental behaviour in dogs, especially in males.
- Is pack living in dogs a trait maintained by natural selection? Although it has been shown that larger packs of free-ranging dogs outcompete smaller packs and lone individuals over access to resources ([Daniels & Bekoff, 1989b](#); [Macdonald & Carr, 1995](#); [Bonanni et al., 2011](#)), there are currently no data about the effect of pack size on reproductive success of free-ranging animals.
- It is fundamental to replicate studies on the social organisation of free-ranging dogs using methods based on continuous observations of animals (e.g., *focal animal sampling*; [Altmann, 1974](#)), which would be also useful in order to assess the degree of human influence on their behaviour (e.g., ownership, socialisation to people).
- It is useful to conduct studies on the intraspecific social behaviour of pure breeds. In the absence of more information about this topic, any attempt at interpreting the behaviour of free-ranging dogs on the basis of their genetic relatedness to specific breeds would be highly speculative.

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