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Articles

Effect of affiliative and agonistic relationships on leadership behaviour in free-ranging dogs

Roberto Bonanni [a,*], Simona Cafazzo [b,1], Paola Valsecchi [a], Eugenia Natoli [c,2]

[a] Dipartimento di Biologia Evolutiva e Funzionale, Università di Parma
[b] Dipartimento di Protezione e Valorizzazione Agroalimentare, Università di Bologna
[c] Azienda USL Roma D, Area Dipartimentale Sanità Pubblica Veterinaria

Consensus decisions about the nature and timing of group activities allow animals to maintain group cohesiveness, but also entail costs because individuals often differ with respect to their optimal activity budgets. Two mechanisms whereby animals reach a consensus include 'consistent leadership', in which a single dominant individual makes the decision, and 'variable leadership' in which several group members contribute to the decision outcome. Sharing of consensus decisions is expected to reduce consensus costs to most group members. Both patterns are thought to emerge from the complexity of social relationships of group members. We investigated the distribution of leadership during group departures in two packs of free-ranging dogs, Canis lupus familiaris, and tested how its distribution between individuals was affected by dominance rank-related affiliative and agonistic relationships. Although leadership was not entirely concentrated on a single group member, both packs had a limited number of habitual leaders. In the largest pack, the pattern of leadership changed from 'variable' to nearly 'consistent' after its size had shrunk. Habitual leaders were usually old and high-ranking individuals. However, high-ranking dogs that received affiliative submissions in greeting ceremonies were more likely to lead than dominant dogs receiving submissions only in agonistic contexts. During resting times, habitual followers associated more closely with habitual leaders than with other followers. These results suggest that in social species collective movements may arise from the effort of subordinates to maintain close proximity with specific valuable social partners.
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To benefit from sociality, animals need to maintain group cohesiveness and make collective consensus decisions about which activities to perform and when to perform them (Conradt & Roper 2000, 2003, 2005). Two extreme mechanisms that have been proposed to allow animals to reach consensus decisions are 'consistent leadership' and 'variable leadership' (Conradt & Roper 2003, 2005). Leaders (or decision makers) are those individuals that, even when animals decide collectively, are more influential with respect to the decision outcome whereas the others will simply accept their decision. Consistent leadership (also termed 'despotic', or 'unshared leadership') refers to the same individual, usually the highest ranking or the oldest and most experienced member of a social group, being the one that always leads group

actions (Conradt & Roper 2005). Conversely, variable leadership (also termed 'democratic' or 'shared leadership') refers to social situations where different group members contribute to the decision outcome on different or on the same occasions (Conradt & Roper 2005). An empirical example of consistent leadership is provided by a cooperative breeding carnivore such as the dwarf mongoose, *Helogale parvula*, in which the breeding and dominant female determines foraging initiation, route taken, distance travelled and selection of resting sites for the entire group (Rasa 1987). Variable leadership can be found in white-faced capuchin monkeys, *Cebus capucinus*, in which virtually all group members can successfully initiate a collective movement (Leca et al. 2003). Variable leadership can involve either an 'equally shared consensus decision', where all group members contribute to the decision outcome, or a 'partially shared consensus decision' in which a given proportion of group members, usually a demographic subset, contribute to decision outcome (Conradt & Roper 2005). An example of the last pattern may be seen in another cooperatively breeding carnivore, the wolf, *Canis lupus*, in which group activities are predominantly led by both members of the dominant breeding pair (Mech 2000; Peterson et al. 2002).

* Correspondence: R. Bonanni, Dipartimento di Biologia Evolutiva e Funzionale, Università di Parma, Viale Usberti 11/A, 43100 Parma and via Giuseppe Donati 32, 00159 Roma, Italy.
E-mail address: roberto.bonanni@inwind.it (R. Bonanni).
[1] S. Cafazzo is at the Dipartimento di Protezione e Valorizzazione Agroalimentare, Università di Bologna, via Fratelli Rosselli 107, 43100, Reggio Emilia, Italy.
[2] E. Natoli is at Azienda USL Roma D, Area Dipartimentale Sanità Pubblica Veterinaria, Ospedale Veterinario, via della Magliana 856, 00148 Roma, Italy.

However, consensus decisions often involve considerable conflict of interest between group members, termed consensus costs (Conradt & Roper 2000). This is because individuals, and especially those belonging to different age/sex classes, usually differ with respect to their optimal activity duration, or their preferred travel destination, and thus the actual group decision outcome may differ from an individual's optimal decision outcome (Gompper 1996; Ruckstuhl 1999; Conradt & Roper 2000). Consensus costs will also be affected by how group members contribute to the decision outcome: theoretical models predict that for most group members equally shared consensus decisions should result in lower synchronization costs than unshared decisions (Conradt & Roper 2003). Subordinates will not benefit by accepting a despotic decision of a single dominant and experienced leader unless group size is small and there is a large asymmetry in information about the environment (e.g. location of resources, predation risks) between the dominant leader and the subordinates themselves (Conradt & Roper 2003; Lusseau & Conradt 2009). Consequently, shared decision making should be more likely to occur in nature given that many subordinates together can invest more energy in resisting a despot's decision than a single despot can invest in coercion (Conradt & Roper 2003, 2005). However, King et al. (2008) suggested that the long-term benefits of affiliative relationships with dominant leaders may often outweigh consensus costs and thus result in subordinates accepting despots' decisions and following their movements. For instance, in female chacma baboons, *Papio hamadryas ursinus*, these benefits may consist of increased protection from predators and from infanticidal males as a consequence of close association with male dominant leaders (King et al. 2008; Stueckle & Zinner 2008). Although it is widely recognized that group decision making arises from complex interactions and social relationships between group members (Dunbar 1983; Lamprecht 1992; Byrne 2000; Couzin & Krause 2003; Couzin et al. 2005; Fischhoff et al. 2007; Dyer et al. 2009), few studies have explored the link between leadership and affiliative relationships in social groups (Byrne et al. 1990; King et al. 2008; Ramseyer et al. 2009a, b). These studies reveal that, in species in which consensus decisions are not equally shared, individual variation in leadership is not a simple function of social dominance or experience, given that follower behaviour is often determined by social bonds to the leader.

In this study we investigated the pattern of individual variation in leadership during group departures in two packs of free-ranging dogs, *Canis lupus familiaris*, and how this variation was affected by affiliative and agonistic relationships. Free-ranging dogs form packs which comprise individuals belonging to different age/sex classes (Font 1987; Daniels & Bekoff 1989a, b; Macdonald & Carr 1995; Boitani et al. 1995; Boitani & Ciucci 1995; Pal et al. 1998; Cafazzo et al., in press). Recent studies (Cafazzo et al., in press) have demonstrated that they show a complex level of social organization in which dominance relationships are expressed both in the outcome of agonistic interactions (agonistic dominance, de Waal 1989) and in greeting ceremonies in which subordinates signal the acceptance of their lower social status to dominant animals (formal dominance, de Waal 1989). Moreover, consensus decision making appear to constitute a basic feature of the dogs' social organization since packs travel as cohesive units and are highly cooperative in conflicts against conspecifics (Bonanni et al. 2010). Keeping the pack cohesive would be functional since large packs dominate smaller ones in intergroup conflicts and lone dogs that are temporarily separated from their own pack are the most likely to be attacked by strangers (R. Bonanni, E. Natoli, S. Cafazzo & P. Valsecchi, unpublished data).

Here, we aimed first at describing the pattern of leadership during group departures in two free-ranging dog packs, and at placing it along the continuum from unshared, via partially shared, to equally shared decision making. Then, we assessed the effect of dominance rank on individual variation in leadership by focusing in particular on a pack that underwent a reduction in size during the study, and a partial rearrangement of dominance relationships. We examined the effect of formal dominance and agonistic dominance separately because the acquisition of formal dominance (but not of agonistic dominance) appears to be closely related to the development of affiliative relationships between dominant and subordinate animals (de Waal & Luttrell 1985; de Waal 1986). We also examined social proximity as a measure of affiliation (Hill & van Hoof 1994). The following predictions should hold if affiliative relationships with dominant leaders play a role in mediating follower behaviour: (1) formal dominance should be a more consistent predictor of leadership than agonistic dominance, that is high-ranking dogs that receive submissions during greeting ceremonies should be more likely to lead than high-ranking dogs receiving submissions only during agonistic interactions; (2) followers should maintain closer spatial associations with leaders than with other followers.

METHODS

Study Area

The research was carried out in a suburban environment situated in the southwestern outskirts of Rome, Italy. The study area was about 300 ha and was delimited to the north, west and south by roads with heavy traffic and to the east by cultivated areas. The southwest sector was urbanized although not densely populated. The northeast sector was mainly occupied by a nature reserve called 'Tenuta dei Massimi'. The habitat in the reserve consisted mainly of open grasslands with some interspersed wooded areas.

Free-ranging dogs had free access to virtually every part of the study area. They used the reserve mainly to find resting sites, refuges and dens for puppies in the dense vegetation of the wooded areas. However, they frequently approached a central road crossing the study area, especially in the early morning, to feed on the food (mainly meat from a slaughterhouse) brought every day by volunteer dog caretakers.

Packs Studied

Dogs studied belonged to a population of about 100 adult animals inhabiting the study area. All dogs were medium-sized to large mongrels (Cafazzo 2007). Those that travelled, rested and defended resources as a cohesive unit (Cafazzo 2007), thus fitting the definition of a canid pack (Mech 1970), were considered to belong to the same group. With very few exceptions, dogs were not socialized to humans although they were dependent on humans for food provisioning.

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

The research was conducted in two phases. In the first part, which encompassed the period April 2005 to May 2006, we focused on a group called the 'Corridoio pack' whose size ranged from 40 to 25 individuals throughout the study period. However, for the purposes of this study data were collected on 27 individuals. The remaining 13 individuals had been members of this pack for a limited time before their dispersal (or disappearance) and thus were never observed to take part in any collective movement. In the second part of the study, which encompassed the period May 2007 to September 2008, we focused on two packs. These included the

Corridoio pack (whose size had shrunk to 11 individuals in the meantime, Corridoio pack II henceforth) and the 'Curva pack' which comprised nine individuals (see Table 1 for details of the composition of the packs). Nine dogs (six males and three females) that were members of the Corridoio pack during the first phase of the study were still in the same pack during the second phase, whereas two males and a female had dispersed in the Curva pack.

Between November 2007 and March 2008 two males and three females of the Curva pack were sterilized by the Rome Municipality. Given that sterilization seems to cause considerable behavioural changes in dogs (Maarschalkerweerd et al. 1997), we did not analyse the data collected, for this pack after October 2007, and this caused a considerable reduction in the data set available for this pack on leadership behaviour. All the neutered dogs in the studied packs that were included in the analysis of individual behaviour had been sterilized between 6 and 12 months before the beginning of the study.

Leadership

Observations on dogs' behaviour were conducted daily, usually between 0600 and 1700 hours to cover, when possible, all the daylight period. To locate the dogs we walked on foot along a circuit and tried to observe each group on a rotational daily basis when possible. Dogs were observed from distances of 20–150 m using 10 × 50 binoculars. Altogether, we carried out 630.4 h of observation in the field in the first part of the study and 1147.2 h in the second.

Data on leadership were collected ad libitum (Altmann 1974). Upon locating a pack, we monitored continuously all group members that were within 50 m of each other. Dogs do not display obvious signals to advertise an intention to move. Every time we observed a dog that initiated a movement of at least 10 m so as to leave all other group members behind, we checked whether at least two other dogs moved in the same direction within 10 min; if this was the case we recorded the initiator as a leader and the others as followers and if this was not the case, that is the initiator was either followed by no more than one dog or not followed at all, we recorded the initiator's movement as an unsuccessful attempt at leaving. Followers were regarded as walking in the same direction as the leader if they directly followed the initiator, or if they converged towards it, or if they walked in a direction parallel with and not more than 10 m distant from that of the initiator. Collective movements concerned the following activity shifts: from resting to travelling; from resting to feeding or drinking; from resting in an area exposed to the sun to a shaded area; from resting in an open area to resting in the dense vegetation. With the exception of the first, all activity shifts sometimes involved short movements (10–50 m). In this case, followers had to move for at least half the distance travelled by the leader for their behaviour to be scored as following. We did not include here either collective movements related to conflicts against other packs (these were examined in Bonanni et al. 2010) or movements occurring during courting activities (because leading in this case was biased in favour of the oestrous female). Successive movements were scored as independent if they were separated by an activity change lasting at least 10 min (for instance, two different travelling bouts separated by resting for 10 min).

We calculated for each individual a 'leadership score' as follows: for each dog we divided the total number of times it behaved as leader by the sum of the total number of times it behaved as follower and the total number of time it behaved as leader. We used this score instead of the total number of leadership events to avoid biasing our data in favour of the more visible individuals. We defined as 'habitual leader' an individual that behaved as leader more frequently than it behaved as follower (conversely, 'habitual follower' was an individual that behaved as follower more frequently than it behaved as leader). Additionally, we calculated

Table 1
Identity, pack, birth year and gender of the dogs studied during the first and second phases of the research

First phase				Second phase			
Dog identity	Pack	Birth year	Gender	Dog identity	Pack	Birth year	Gender
MER	Corridoio	Very old	Male	GOL	Corridoio II	Before 2004	Male
GAS	Corridoio	Before 2004	Male	DOT	Corridoio II	2005	Male
PIP	Corridoio	Before 2004	Male	LAN	Corridoio II	Before 2004	Neutered male
LEO	Corridoio	Very old	Male	MAM	Corridoio II	Before 2004	Female
GOL	Corridoio	Before 2004	Male	ISO	Corridoio II	Before 2004	Neutered female
LAN	Corridoio	Before 2004	Male	GON	Corridoio II	2005	Male
MAM	Corridoio	Before 2004	Female	EOL	Corridoio II	2005	Neutered male
NAN	Corridoio	Before 2004	Female	BRO	Corridoio II	2005	Male
ISO	Corridoio	Before 2004	Female	SAS	Corridoio II	2006	Female
DIA	Corridoio	Before 2004	Female	MON	Corridoio II	2006	Neutered female
SIM	Corridoio	2004	Male	MAG	Corridoio II	2005	Neutered female
PON	Corridoio	2004	Male	PON	Curva	2004	Male
SEM	Corridoio	2004	Male	GAS	Curva	Before 2004	Male
KIM	Corridoio	2004	Male	MOR	Curva	2004	Female
MOR	Corridoio	2004	Female	MUS	Curva	2004	Male
STE	Corridoio	Before 2004	Neutered female	NER	Curva	2006	Neutered male
CUC	Corridoio	2005	Female	JOS	Curva	2006	Male
DOT	Corridoio	2005	Male	FRA	Curva	2007	Female
GON	Corridoio	2005	Male	DAN	Curva	2007	Female
MAL	Corridoio	2005	Male	PAS	Curva	2007	Male
HAN	Corridoio	2005	Male	GIO	Curva	2007	Female
GRE	Corridoio	2005	Female				
BRO	Corridoio	2005	Male				
EOL	Corridoio	2005	Female				
EMY	Corridoio	2005	Female				
MAG	Corridoio	2005	Female				
PIS	Corridoio	2005	Female				

Individuals within each pack are ordered from the highest (upper) to the lowest dominance rank, with the exception of PON whose rank in the Curva pack could not be assessed. The assessment of dominance rank is based on directionality of both formal and agonistic submissions.

the proportion of movements away from the pack in which each individual was successful in recruiting at least two followers, in relation to the total number of attempts at leaving.

Formal Dominance

We recorded ad libitum two behavioural patterns displayed by dogs during ritualized greeting ceremonies which usually occur when group members meet after a period of separation: licking the muzzle of another dog (or simply pushing the muzzle of the other dog with the nose) and wagging the tail while holding the tail down. Both the behavioural patterns were defined by Schenkel (1967, page 324) as active submission: 'the impulse and effort of the inferior towards friendly harmonic social integration'. However, here we examined their effects separately because they seem to differ with respect to their dyadic directional consistency (Cafazzo 2007; R. Bonanni, unpublished data). In particular, 'muzzle licking' shows a perfect directional consistency (within each dyad it has a completely fixed direction) and may thus fulfil the criterion for 'formal submission', that is, acceptance of the dominance relationship by subordinates (Cafazzo et al., in press). 'Tail wagging' conveys affiliative intentions (Schenkel 1967), but is probably less important for the communication of asymmetries in social status.

For each dog we calculated the number of companions from which it received at least one instance of muzzle licking and tail wagging, and divided it by the total number of available companions in its pack to allow comparison between individuals belonging to packs of different size.

Agonistic Dominance

To assess agonistic relationships we also recorded ad libitum all submissions shown by dogs in response to aggression and dominance displays, which were termed 'agonistic submissions'. These included: avoiding eye contact, lowering the head, lowering the tail between the hindlegs, lying down on the back, yelping, fleeing, withdrawing, interruption of feeding (in the feeding context). Unlike formal submissions described above, agonistic submissions do not necessarily imply a friendly relationship between interacting animals, that is, acceptance of lower social status by subordinates and tolerance by dominant animals (Cafazzo et al., in press).

We calculated for each individual the number of companions from which it received at least one instance of agonistic submission, and divided it by the total number of available companions in its pack to allow comparison between individuals belonging to packs of different size.

By using data on both formal and agonistic submissions we could arrange the dogs in a linear dominance hierarchy whose details are described elsewhere (Cafazzo et al., in press).

Pattern of Spatial Association

We also recorded proximity among individuals as a measure of affiliative relationships (see Hill & van Hoof 1994). To this aim we used focal animal sampling sessions (Altmann 1974), carried out when pack members were resting and we were not collecting data on leadership (175.35 h of observation in the first part of the study and 221.4 h in the second one), and recorded which individuals were within 1 m of the focal animal (instantaneous sampling method, 60 s interval, Altmann 1974). Then we calculated dyadic association indexes (DAI) using the following formula (Clutton-Brock et al. 1982): $N_{ab}/(N_a + N_b + N_{ab})$, where N_{ab} refers to the number of instances in which individuals a and b were seen within 1 m of each other, N_a refers to the number of instances when individual a was

seen without individual b, and N_b refers to the number of instances when individual b was seen without individual a.

Statistical Analysis

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

To explain individual variation in leadership we used the following predictor variables: proportion of companions from which each dog received at least one instance of agonistic submission, age, proportion of companions from which each dog received at least one instance of muzzle licking, and proportion of companions from which each dog received at least one instance of tail wagging. Since we expected that some of these variables were correlated, we applied a principal components analysis (PCA) to check whether or not the predictor variables (particularly agonistic and formal submissions) varied in the same direction. This analysis allowed us to replace the original correlated variables with new uncorrelated component variables, linear combinations of the original variables, called principal components or factors. Then we ran a general linear model with 'leadership score' as the dependent variable and the two PCA components that explained most of the variation in the data as independent variables. We also included gender as a factor in the model and ran two different models, one for each phase of the study. Model residuals were tested for normality using the Kolmogorov–Smirnov test. All statistics were performed using Statistica Release 7 (StatSoft Inc., Tulsa, OK, U.S.A.).

Although the analyses concerning the two phases of the research were not independent, rearrangements of both dominance relationships and distribution of leadership among individuals were highly expected in the Corridoio pack after its marked reduction in size. So we used Pearson correlation to compare leadership scores of dogs that were studied during both phases of the research.

Because of the symmetrical nature of spatial associations (which lack the directionality of submissions), a strong correlation between 'leadership score' and number of close associates was not expected, and consequently we did not include measures of proximity in the model developed to explain individual variation in leadership. Rather, for each individual that behaved as 'habitual follower' we calculated its median DAI with respect to companions that played the 'role' of habitual leaders and its median DAI with respect to companions that behaved as habitual followers. Then we compared the median values obtained using a Wilcoxon signed-ranks test, given that DAI were not normally distributed.

We defined adult dogs as those that were at least 2 years old, subadult dogs as those that were 1–2 years old and juveniles as those that were younger than 1 year. For the purposes of statistical analysis, dogs were assigned to the following age classes: the first class included two individual dogs that showed obvious signs of old age (presence of grey muzzle hair and worn teeth); the second class included dogs that were fully grown at the time when the study began (April 2005) but did not show signs of old age; the third class comprised individuals that were juveniles at the beginning of the study (on the basis of allometry and body size) and thus were presumably born in 2004; the other classes comprised dogs that were observed to be born in 2005, 2006 and 2007, respectively.

Interobserver Reliability

Interobserver reliability was assessed between two of us (R.B. and S.C.) by calculating 'leadership scores' for eight dogs belonging to the Corridoio pack (which was studied by both observers) across 12 collective movements. Pearson correlation between the leadership scores obtained by the two observers was $r_6 = 0.98$.

RESULTS

Distribution of Leadership within Packs

In the Corridoio pack ($N = 133$ collective movements) leadership was clearly not restricted to a single dog. As shown in Fig. 1a, every adult and subadult individual could be successful in
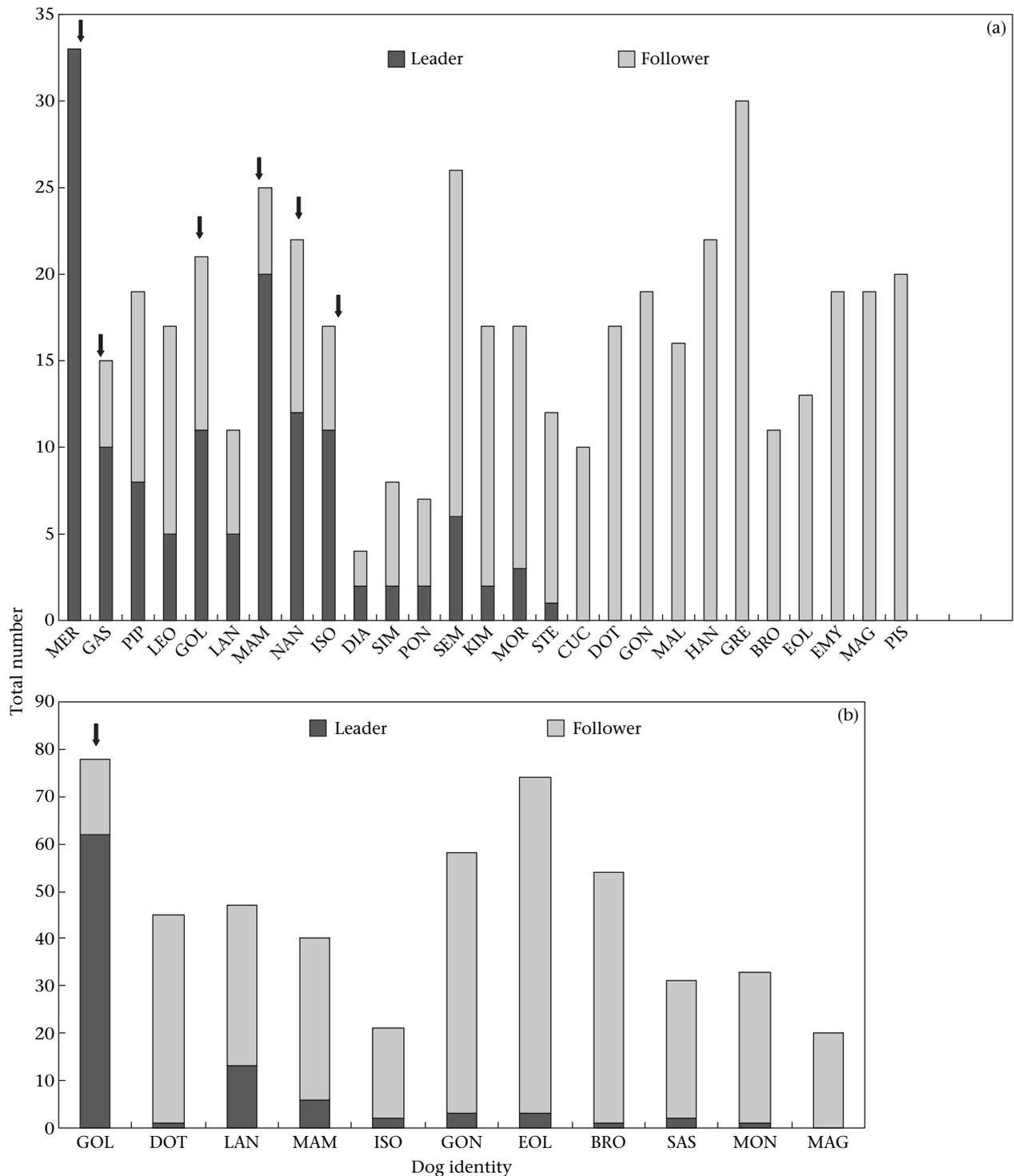

Figure 1. Corridoio pack: total number of events in which each dog behaved as leader and follower during (a) the first and (b) the second phase of the study. Individuals are ordered from the highest (on the left) to the lowest dominance rank. Black arrows indicate habitual leaders.

recruiting at least two followers, whereas juveniles never behaved as leaders. However, individual differences in the frequency of leadership were significantly greater than expected by chance even when we restricted the analysis to adults and subadults ($\chi^2_{15} = 84.94$, $P < 0.0001$). Altogether there were 275 attempts at leaving the pack, and the proportion of successful attempts was highly and positively correlated with leadership score (Pearson correlation: $r_{25} = 0.88$, $P = 0.0001$). So, dogs that behaved more frequently as leaders were those that were more successful at recruiting followers.

Individual differences in the tendency to lead deviated significantly from an even distribution ($\chi^2_{10} = 241.55$, $P < 0.0001$) also in the Corridoio pack II ($N = 94$ collective movements). However, in this case, there was just one dog (the highest ranking male) out of 11 (9%) that behaved more frequently as leader than he behaved as follower, whereas in the first phase six of 27 dogs (22.2%) behaved as habitual leaders (Fig. 1a, b). The dog that played the role of single habitual leader in the Corridoio pack II (GOL) had been a habitual leader during the first part of the research as well (Fig. 1a, b). The proportion of successful attempts at leaving was still positively correlated with leadership score (Pearson correlation: $r_9 = 0.74$, $P = 0.01$; total number of start attempts = 149).

In the Curva pack ($N = 17$ collective movements) one male (PON) was the consistent leader before his dispersal from the pack 1 month into the study (Fig. 2a). After that dispersal event (the male was excluded from the subsequent models because of insufficient information on his social status and relationships), leadership was more variable although a female (MOR) was the only habitual leader (Fig. 2b). This female had dependent puppies and did not

travel with the pack during the period in which it was led by the above-mentioned male. Both individuals (PON, MOR) had been members of the Corridoio pack during the first part of the research and were not habitual leaders at that time (Fig. 1a). Conversely, one dog (GAS) that was previously a habitual leader in the Corridoio pack (Fig. 1a) did not behave so when he became a member of the Curva pack (Fig. 2a, b).

Here the chi-square test could not be applied because more than 20% of the expected frequencies were smaller than 5 (see Siegel & Castellan 1988). In this pack we observed 46 start attempts involving almost exclusively adult dogs and the proportion of successful attempts was again positively correlated with leadership score (Pearson correlation: $r_4 = 0.93$, $P = 0.008$; only individuals that made more than one attempt included).

Individual Variation in Leadership

For the Corridoio pack, the first factor of the PCA alone explained 85.3% of the total variance in the data and was highly and negatively correlated with all of the original explanatory variables (Fig. 3): dogs characterized by high negative scores on this factor were old individuals and received both formal and agonistic submissions, as well as tail wagging, from many partners. The second factor of the PCA explained just 8.4% of the variance, but none of the original variables showed a high correlation with it (Fig. 3).

The general linear model developed for 'leadership score' was significant ($R^2 = 0.83$, $F_{3,23} = 37.56$, $P < 0.0001$), and showed that the first factor of the PCA was a significant predictor of leadership
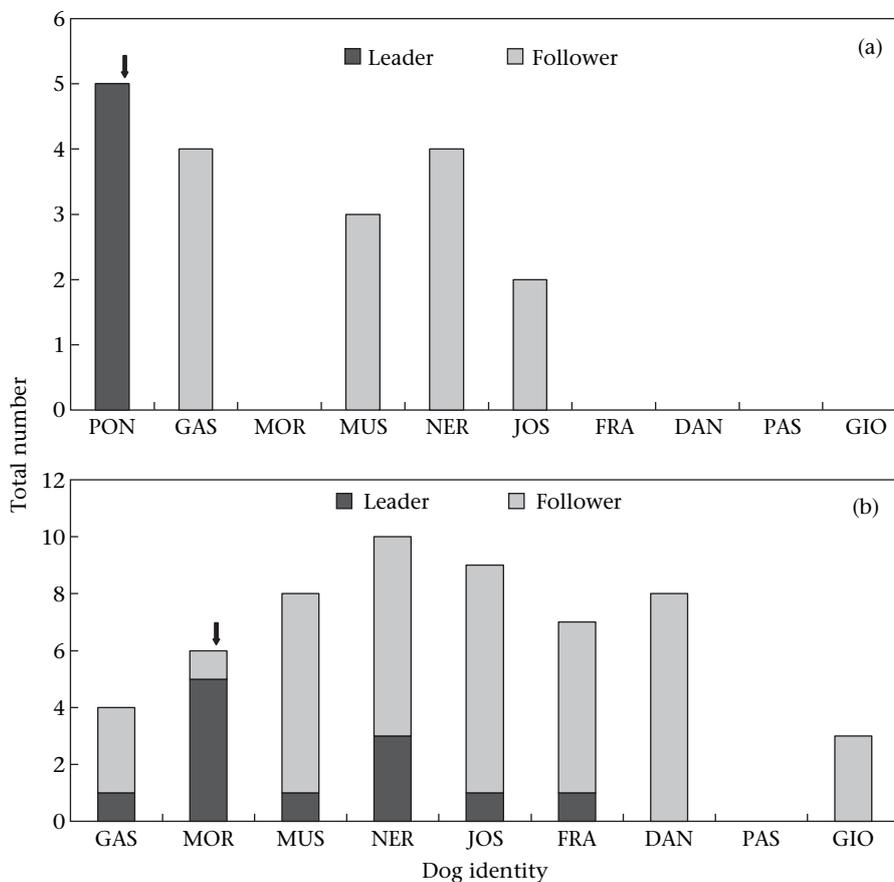

Figure 2. Curva pack: total number of events in which each dog behaved as leader and follower (a) before and (b) after the dispersal of the male PON. Individuals are ordered from the highest (on the left) to the lowest dominance rank with the exception of PON. Black arrows indicate habitual leaders.
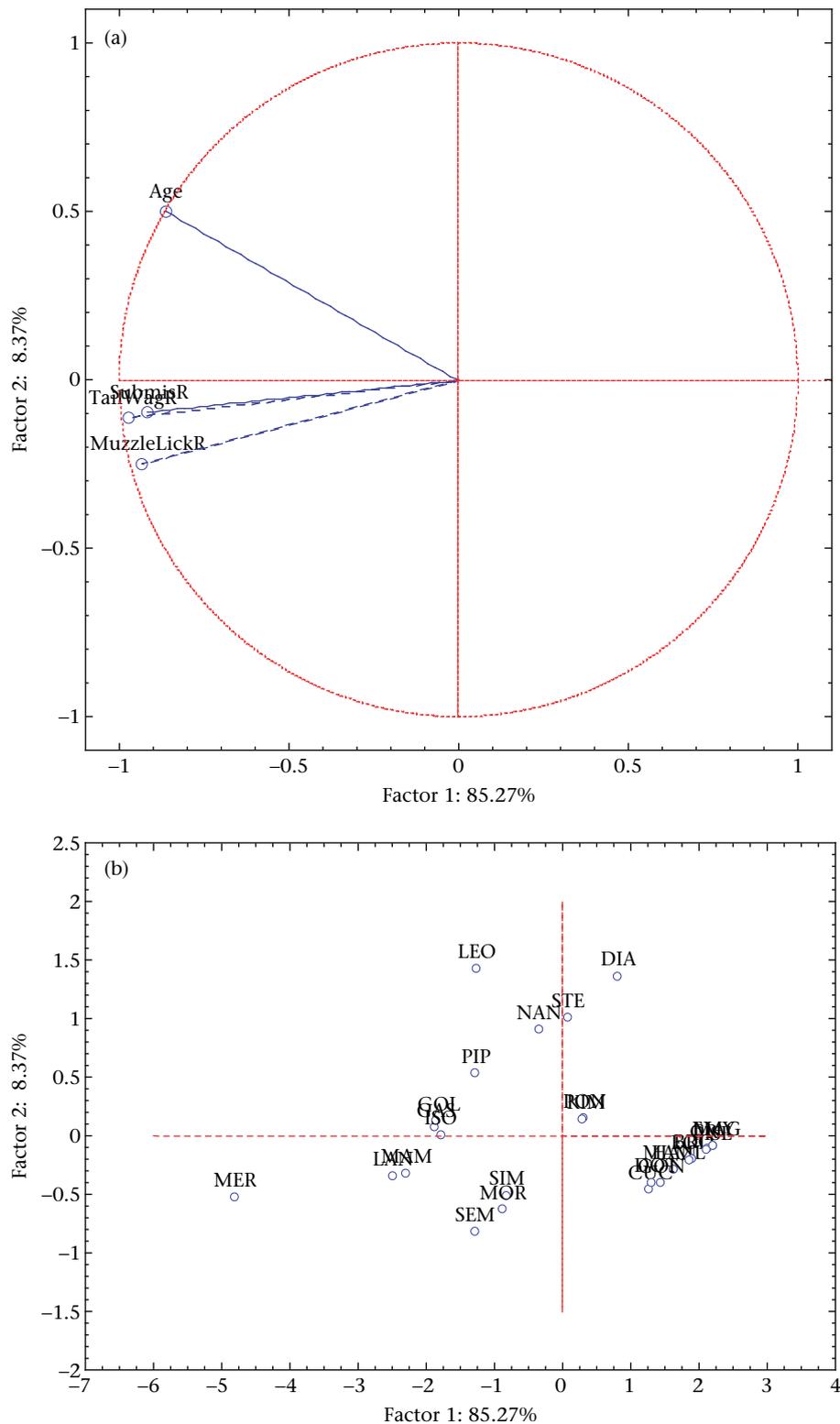
Figure 3. Principal components analysis (PCA) results for the Corridoio pack. (a) The circle shows the correlation between the original variables and the two new components. (b) The scatter plot shows the position of the dogs on the plain and can be interpreted in relation to the corresponding position of the variables on the correlation circle. Muzzle-LickR = proportion of companions from which each dog has received at least one instance of muzzle licking. TailWagR = proportion of companions from which each dog has received at least one instance of tail wagging. SubmisR = proportion of companions from which each dog has received at least one instance of submissive behaviour elicited by aggression or dominance displays. Pearson correlations between factor 1 of the PCA and the original variables were: −0.86 (Age), −0.93 (MuzzleLickR), −0.92 (SubmisR), −0.98 (TailWagR); Pearson correlations between factor 2 and the original variables were: 0.50 (Age), −0.25 (MuzzleLickR), −0.10 (SubmisR), −0.11 (TailWagR).

(coefficient $= -0.15 \pm 0.01$, $t = -10.41$, $P < 0.0001$): dogs with high negative scores on this factor were more likely to behave as leaders. There was also a nonsignificant tendency for females leading more frequently than males when all the other variables were kept equal (coefficient $= 0.05 \pm 0.03$, $t = 1.73$, $P = 0.097$).

For the Corridoio II and the Curva packs, the first factor of the PCA explained 66.8% of the total variance in the data and was negatively correlated with all the explanatory variables, although the correlation was lower for the proportion of partners from which each dog received agonistic submissions (Fig. 4). This variable was indeed the only one to show a high correlation with the second factor of the PCA which explained 19.8% of the variance. So, dogs with high negative scores on the first component were old individuals that received muzzle licking, tail wagging and, to a lesser extent, agonistic submissions from many partners. However, dogs with high positive scores on the second factor received agonistic submissions from many companions, but did not receive muzzle licking and tail wagging very often (Fig. 4). Moreover, these dogs were also younger, on average, than those that had high negative scores on the first component.

The general linear model of 'leadership score', for the second phase of the study, was also significant ($R^2 = 0.70$, $F_{3,15} = 11.52$, $P < 0.0004$) and revealed that the first component of the PCA was a significant predictor of the dependent variable (coefficient $= -0.13 \pm 0.02$, $t = -5.86$, $P < 0.0001$; Fig. 5a), whereas the second one was not (coefficient $= 0.01 \pm 0.04$, $t = 0.34$, $P = 0.74$; Fig. 5b): older dogs that received muzzle licking and tail wagging from many partners behaved frequently as leaders, but younger high-ranking dogs receiving submissions only in agonistic interactions were unlikely to lead the group. There was again a nonsignificant tendency for males leading less often than females (coefficient $= -0.07 \pm 0.04$, $t = -1.85$, $P = 0.08$).

Finally, leadership scores of 11 dogs that were studied during both phases of the research were not significantly correlated (Pearson correlation: $r_9 = 0.24$, $P = 0.47$).

Leadership and Pattern of Interindividual Association

In all the packs studied 'habitual followers' developed significantly closer spatial associations during resting with 'habitual leaders' than they did with other habitual followers (Wilcoxon signed-ranks test: Corridoio pack: $T = 29$, $N = 21$, $P < 0.003$, median score follower–leader $= 0.086$, median score follower–follower $= 0.042$; Corridoio pack II: $T = 1$, $N = 10$, $P < 0.007$, median score follower–leader $= 0.101$, median score follower–follower $= 0.014$; Curva pack: $T = 2$, $N = 7$, $P < 0.05$, median score follower–leader $= 0.081$, median score follower–follower $= 0.014$; Fig. 6).

DISCUSSION

In this study we found that leadership during group departures in free-ranging dogs was not entirely concentrated on a single individual. Every adult and subadult individual within a given pack could successfully initiate a collective movement involving a minimum of three animals, whereas dogs younger than 1 year rarely succeeded in doing so. However, in all packs studied some individuals behaved as habitual leaders and others as habitual followers. In the two packs for which testing was possible, the distribution of leadership among individuals was significantly different from an even one. Since the overall frequency of leading the pack (leadership score) was highly correlated with the proportion of successful attempts at leaving, it seems that individuals that led more frequently did so because they were more successful at recruiting partners when they moved away from the

pack, and not just because they left the pack more often than others. In the Corridoio pack, the pattern of group decision making at group departure changed from 'partially shared' during a period when its size was 27 individuals and there were six habitual leaders, to nearly 'unshared' at the time when its size was 11 individuals and there was just one habitual leader. Moreover, a pattern approaching 'unshared decision making', with one habitual leader, was also found in the relatively small Curva pack. So, although the number of packs studied here is limited, these results seem to suggest that in larger groups it may actually be more difficult for despots to influence the behaviour of many followers in their favour (see Conradt & Roper 2003). On the other hand, in the Corridoio pack the distribution of leadership among individuals was still uneven at the time when its size was probably close to or above the optimal (this pack was one of the largest canine packs ever observed; see Mech & Boitani 2003 for a review of the largest canine packs observed in the wild), a condition that should favour the evolution of equal sharing of consensus decisions in animals (Conradt & Roper 2007).

To provide an explanation for the occurrence of unequal sharing of decisions in animal societies, it seems important to investigate factors affecting individual variation in leadership tendencies. We have found that individual variation in leadership in free-ranging dogs at the time of group departure was significantly affected by dominance relationships. Dogs that behaved more frequently as leaders were old and high-ranking individuals that received submissive behaviour, both in greeting ceremonies and in agonistic contexts, from many partners. There was also a nonsignificant tendency for females leading more than males when all other variables were kept constant.

We also investigated how the leading and following tendencies of individuals changed after a change in group composition (and in dominance relationships), or after dispersal to another pack. The lack of correlation that we found between the leadership scores of those individuals that were studied in both the first and the second phase of the research further stresses the importance of group composition, and consequently of social relationships, for leadership, and it also suggests that leadership is not an inherent property of individuals. Moreover, the PCA has shown that there were some differences between the two phases of the research with respect to the variables affecting leadership. In particular, in the first phase all the original predictor variables were highly correlated (Fig. 3). Conversely, in the second phase the PCA clearly separated older high-ranking dogs that received formal submissions in greeting ceremonies from younger high-ranking dogs that received submissions only in agonistic interactions (Fig. 4). Most importantly, we showed that the former were likely to behave as leaders, whereas the latter were not (Fig. 5). One possible explanation for the differences we found is that packs studied during the second phase were experiencing a period of social instability, in which some dogs were attaining higher positions in the dominance hierarchy not recognized yet by subordinates by means of greeting ceremonies. This is exemplified well by the dog that had the highest score on factor 2 of the PCA (Fig. 4b). This male (DOT) was a low-ranking juvenile dog during the first phase, but he achieved the second highest position of the dominance hierarchy of the Corridoio pack II during the second phase, when he was a young adult dog (see Table 1). These results indicate that formal dominance in free-ranging dogs may be a more consistent predictor of leadership than agonistic dominance. Since the achievement of formal dominance appears to be indistinguishable from the establishment of affiliative relationships with subordinates in social mammals (de Waal & Luttrell 1985; East et al. 1993; Wittig & Boesch 2003), one interpretation of these results is that affiliative relationships between high-ranking leaders and subordinates would play a role
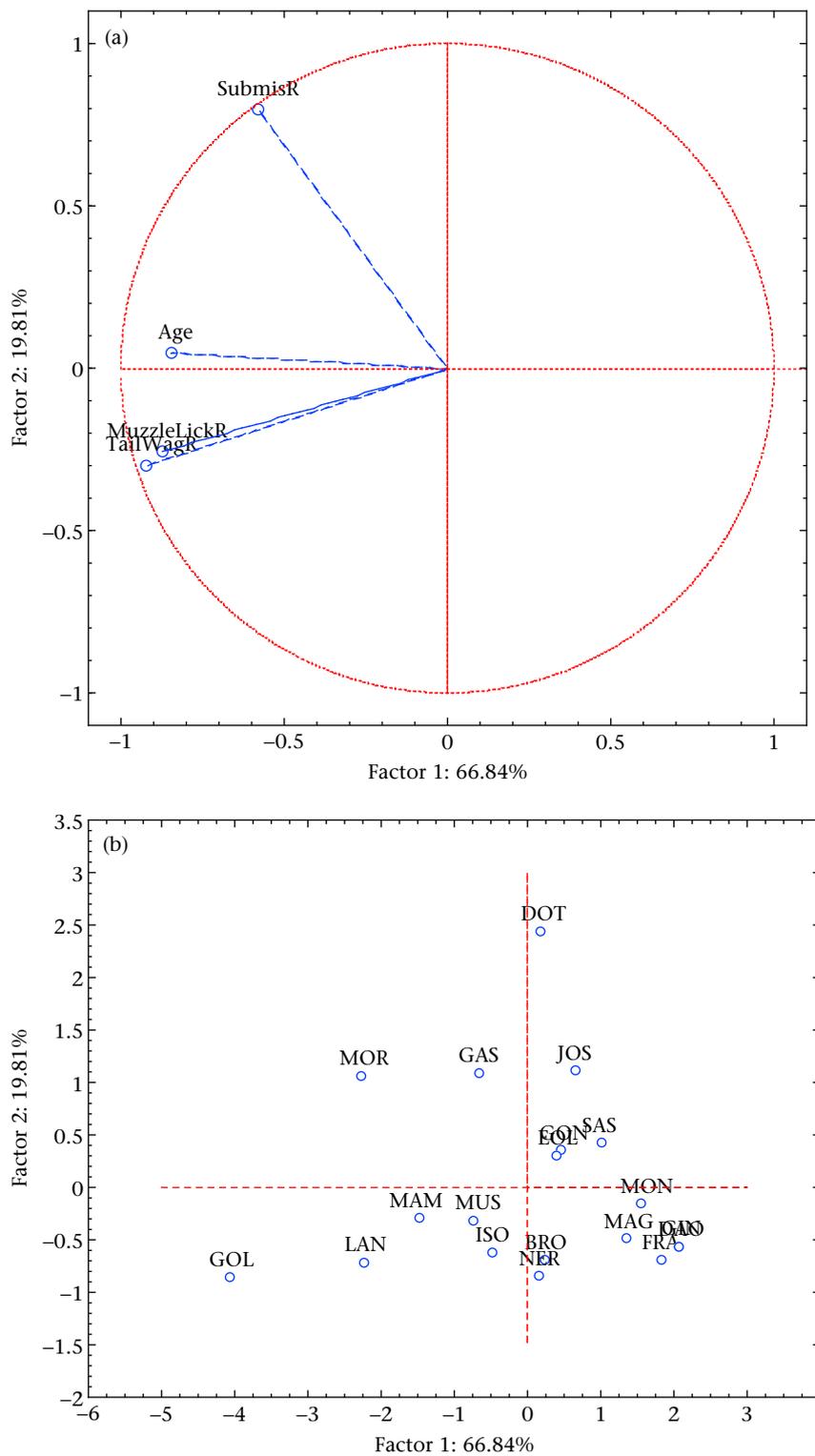
Figure 4. Principal components analysis (PCA) results for the Corridoio II and Curva packs. (a) The circle shows the correlation between the original variables and the two new components. (b) The scatter plot shows the position of the dogs on the plain and can be interpreted in relation to the corresponding position of the variables on the correlation circle. MuzzleLickR = proportion of companions from which each dog has received at least one instance of muzzle licking. TailWagR = proportion of companions from which each dog has received at least one instance of tail wagging. SubmisR = proportion of companions from which each dog has received at least one instance of submissive behaviour elicited by aggression or dominance displays. Pearson correlations between factor 1 of the PCA and the original variables were: −0.85 (Age), −0.87 (MuzzleLickR), −0.58 (SubmisR), −0.92 (TailWagR); Pearson correlations between factor 2 and the original variables were: 0.05 (Age), −0.26 (MuzzleLickR), 0.80 (SubmisR), −0.30 (TailWagR).

in eliciting follower behaviour in free-ranging dogs. Consistent with this interpretation, our analysis of the pattern of spatial associations during resting times has shown that, in both phases of the research, followers associated more closely with habitual leaders than with other followers (Fig. 6). This suggests that they had developed stronger affiliative relationships with leaders, or in
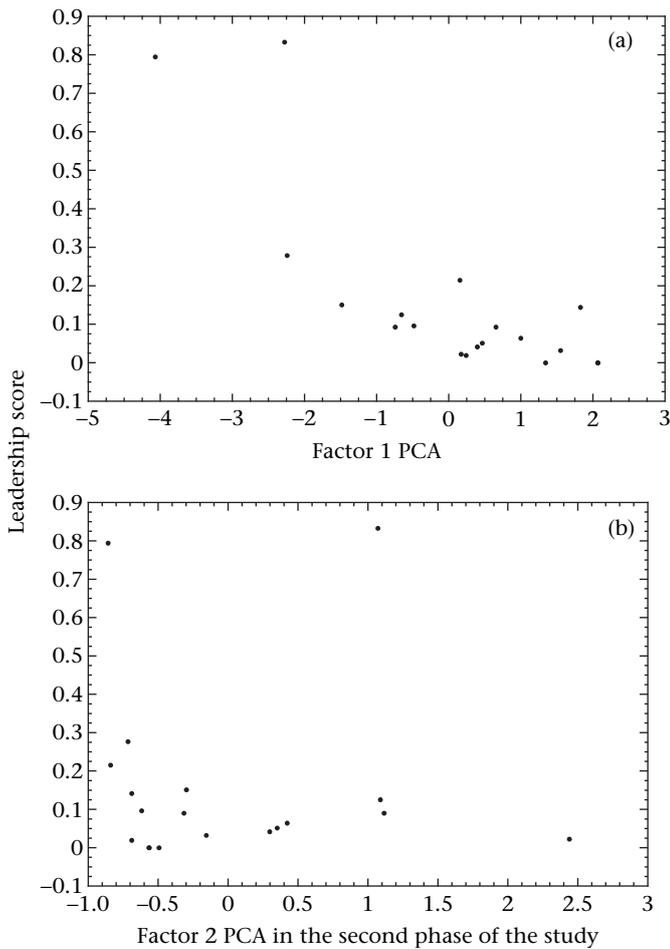
Figure 5. The relation between 'leadership score' and the first two factors of the PCA. In (a) higher negative values on factor 1 indicate older age and higher number of partners from which both muzzle licking and tail wagging were received; in (b) higher positive values on factor 2 indicate higher number of partners from which submissions were received in aggressive interactions.

other words that they regarded leaders as their preferred social partners. Possibly, young high-ranking dogs were not formally recognized as leaders because they did not possess the level of social skilfulness that would have been necessary to establish affiliative relationships with followers, and that could improve with age (see de Villiers et al. 1997 for a similar argument in African wild dogs, *Lycaon pictus*).

What kind of benefits might followers derive by maintaining close associations with dominant leaders? One possibility is that subordinates would benefit from following the movements of high-ranking animals because these are usually older and more experienced individuals (Figs 3, 4). Although in this population individual asymmetries in information about the environment were probably small (food resources were predictable in both time and space because they were provided by humans), it remains possible that dogs were behaving according to rules evolved in the original environment of adaptation, before domestication: domestic dogs evolved from wolves (Vilà et al. 1997), in which both juveniles and adult offspring usually follow their parents to exploit their superior experience in finding food (Mech 2000; Packard 2003).

In conclusion, this study emphasizes the occurrence of unequal sharing of consensus decisions in social animals. However, in free-ranging dogs leadership does not appear to be a simple function of dominance rank, and affiliation may play a role in mediating
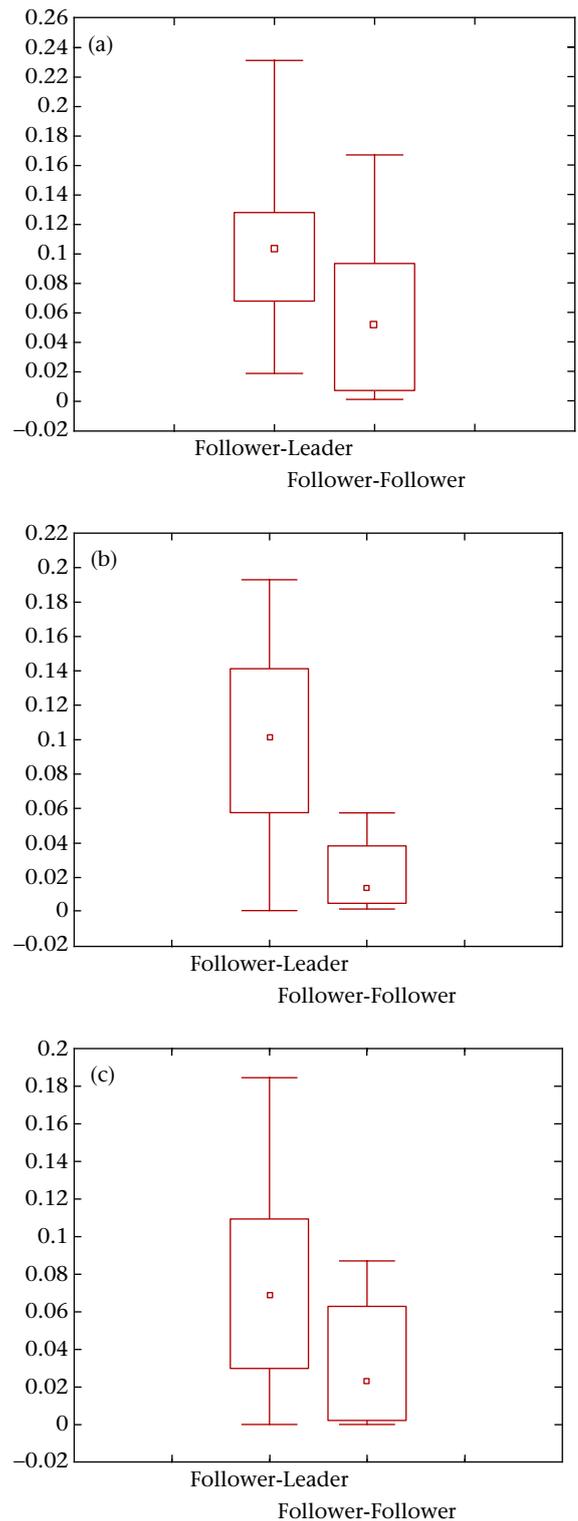

Figure 6. Comparison of the median dyadic association indexes (DAI) of 'habitual followers' with 'habitual leaders' and other 'habitual followers'. Boxes show the median and 25–75% interquartile range; whiskers indicate minimum and maximum values. Further explanations are given in the text. (a) Corridoio pack, (b) Corridoio pack II, (c) Curva pack.

follower behaviour. This result may provide some support for the hypothesis that subordinates would benefit from establishing social bonds with dominant leaders, and that these benefits would exceed consensus costs (King et al. 2008).

Acknowledgments

References

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–267.

Bekoff, M. 1979. Scent-marking by free-ranging domestic dogs. *Biology of Behavior*, **4**, 123–139.

Boitani, L. & Ciucci, P. 1995. Comparative social ecology of feral dogs and wolves. *Ethology, Ecology and Evolution*, **7**, 49–72.

Boitani, L., Francisci, F., Ciucci, P. & Andreoli, G. 1995. Population biology and ecology of feral dogs in central Italy. In: *The Domestic Dog: its Evolution, Behaviour and Interactions with People* (Ed. by J. Serpell), pp. 217–244. Cambridge: Cambridge University Press.

Bonanni, R., Valsecchi, P. & Natoli, E. 2010. Pattern of individual participation and cheating in conflicts between groups of free-ranging dogs. *Animal Behaviour*, **79**, 957–968.

Byrne, R. W. 2000. How monkeys find their way: leadership, coordination, and cognitive maps of African baboons. In: *On the Move: How Animals Travel in Groups* (Ed. by S. Boinski & P. A. Garber), pp. 491–518. Chicago: University of Chicago Press.

Byrne, R. W., Whiten, A. & Henzi, S. P. 1990. Social relationships of mountain baboons: leadership and affiliation in a non-female-bonded monkey. *American Journal of Primatology*, **20**, 313–329.

Cafazzo, S. 2007. Dinamiche sociali in un gruppo di cani domestici (*Canis lupus familiaris*) liberi in ambiente suburbano. Ph.D. thesis, University of Parma.

Cafazzo, S., Valsecchi, P., Bonanni, R. & Natoli, E. In press. Dominance in relation to age, sex and competitive contexts in a group of free-ranging domestic dogs. *Behavioral Ecology*.

Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982. *Red Deer, Behavior and Ecology of Two Sexes*. Chicago: University of Chicago Press/Edinburgh: Edinburgh University Press.

Conradt, L. & Roper, T. J. 2000. Activity synchrony and social cohesion: a fission–fusion model. *Proceedings of the Royal Society B*, **267**, 2213–2218.

Conradt, L. & Roper, T. J. 2003. Group decision-making in animals. *Nature*, **421**, 155–158.

Conradt, L. & Roper, T. J. 2005. Consensus decision making in animals. *Trends in Ecology & Evolution*, **20**, 449–456.

Conradt, L. & Roper, T. J. 2007. Democracy in animals: the evolution of shared group decisions. *Proceedings of the Royal Society B*, **274**, 2317–2326.

Couzin, I. D. & Krause, J. 2003. Self-organization and collective behaviour in vertebrates. *Advances in the Study of Behavior*, **32**, 1–75.

Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. 2005. Effective leadership and decision-making in animal groups on the move. *Nature*, **433**, 513–516.

Daniels, T. J. & Bekoff, M. 1989a. Spatial and temporal resource use by feral and abandoned dogs. *Ethology*, **81**, 300–312.

Daniels, T. J. & Bekoff, M. 1989b. Population and social biology of free-ranging dogs, *Canis familiaris*. *Journal of Mammalogy*, **70**, 754–762.

Dunbar, R. I. M. 1983. Structure of gelada baboon reproductive units IV. Integration at group level. *Zeitschrift für Tierpsychologie*, **63**, 265–282.

Dyer, J. R. G., Johansson, A., Helbing, D., Couzin, I. D. & Krause, J. 2009. Leadership, consensus decision making and collective behaviour in humans. *Philosophical Transactions of the Royal Society B*, **364**, 781–789.

East, M. L., Hofer, H. & Wickler, W. 1993. The erect 'penis' is a flag of submission in a female-dominated society: greeting in Serengeti spotted hyenas. *Behavioral Ecology and Sociobiology*, **33**, 355–370.

Fischhoff, I., Sundaresan, S. R., Cordingley, J., Larkin, H. M., Sellier, M. J. & Rubenstein, D. I. 2007. Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Animal Behaviour*, **73**, 825–831.

Font, E. 1987. Spacing and social organization: urban stray dogs revisited. *Applied Animal Behaviour Science*, **17**, 319–328.

Gompper, M. E. 1996. Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. *Behavioral Ecology*, **7**, 254–263.

Hill, D. A. & van Hoof, J. A. R. A. M. 1994. Affiliative relationships between males in groups of nonhuman primates: a summary. *Behaviour*, **130**, 143–149.

King, A. J., Douglas, C. M. S., Huchard, E., Isaac, N. J. B. & Cowlishaw, G. 2008. Dominance and affiliation mediate despotism in a social primate. *Current Biology*, **18**, 1833–1838.

Lamprecht, J. 1992. Variable leadership in bar-headed geese (*Anser indicus*): an analysis of pair and family departures. *Behaviour*, **122**, 105–120.

Leca, J. B., Gunst, N., Thierry, B. & Petit, O. 2003. Distributed leadership in semifree-ranging white-faced capuchin monkeys. *Animal Behaviour*, **66**, 1045–1052.

Lusseau, D. & Conradt, L. 2009. The emergence of unshared consensus decisions in bottlenose dolphins. *Behavioral Ecology and Sociobiology*, **63**, 1067–1077.

Maarschalkerweerd, R. J., Endenburg, N., Kirpensteijn, J. & Knol, B. W. 1997. Influence of orchiectomy on canine behaviour. *Veterinary Record*, **140**, 617–619.

Macdonald, D. W. & Carr, G. M. 1995. Variation in dog society: between resource dispersion and social flux. In: *The Domestic Dog: its Evolution, Behaviour and Interactions with People* (Ed. by J. Serpell), pp. 199–216. Cambridge: Cambridge University Press.

Mech, L. D. 1970. *The Wolf: the Ecology and Behavior of an Endangered Species*. New York: Natural History Press, Doubleday.

Mech, L. D. 2000. Leadership in wolf, *Canis lupus*, packs. *Canadian Field Naturalist*, **114**, 259–263.

Mech, L. D. & Boitani, L. 2003. Wolf social ecology. In: *Wolves: Behavior, Ecology and Conservation* (Ed. by L. D. Mech & L. Boitani), pp. 1–34. Chicago: University of Chicago Press.

Packard, J. M. 2003. Wolf behavior: reproductive, social, and intelligent. In: *Wolves: Behavior, Ecology and Conservation* (Ed. by L. D. Mech & L. Boitani), pp. 35–65. Chicago: University of Chicago Press.

Pal, S. K., Ghosh, B. & Roy, S. 1998. Agonistic behaviour of free-ranging dogs (*Canis familiaris*) in relation to season, sex and age. *Applied Animal Behaviour Science*, **59**, 331–348.

Peterson, R. O., Jacobs, A. K., Drummer, T. D., Mech, L. D. & Smith, D. W. 2002. Leadership behaviour in relation to dominance and reproductive status in gray wolves, *Canis lupus*. *Canadian Journal of Zoology*, **80**, 1405–1412.

Ramseyer, A., Petit, O. & Thierry, B. 2009a. Decision-making in group departures of female domestic geese. *Behaviour*, **146**, 351–371.

Ramseyer, A., Boissy, A., Dumont, B. & Thierry, B. 2009b. Decision-making in group departures of sheep is a continuous process. *Animal Behaviour*, **78**, 71–78.

Rasa, O. A. E. 1987. The dwarf mongoose: a study of behaviour and social structure in relation to ecology in a small, social carnivore. *Advances in the Study of Behavior*, **17**, 121–163.

Ruckstuhl, K. E. 1999. To synchronise or not to synchronise: a dilemma for young bighorn males? *Behaviour*, **136**, 805–818.

Schenkel, R. 1967. Submission: its features and function in the wolf and dog. *American Zoologist*, **7**, 319–329.

Siegel, S. & Castellan, N. Jr. 1988. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.

Stueckle, S. & Zinner, D. 2008. To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. *Animal Behaviour*, **75**, 1995–2004.

Vilà, C., Savolainen, P., Maldonado, J. E., Amorin, I. R., Rice, J. E., Honeycutt, R. L., Crendall, K. A., Lundeberg, J. & Wayne, R. K. 1997. Multiple and ancient origins of the domestic dog. *Science*, **276**, 1687–1689.

de Villiers, M. S., van Jaarsveld, A. S., Meltzer, D. G. A. & Richardson, P. R. K. 1997. Social dynamics and the cortisol response to immobilization stress of the African wild dog, *Lycaon pictus*. *Hormones and Behavior*, **31**, 3–14.

de Waal, F. B. M. 1986. The integration of dominance and social bonding in primates. *Quarterly Review of Biology*, **61**, 459–479.

de Waal, F. B. M. 1989. Dominance 'style' and primate social organisation. In: *Comparative Socioecology: the Behavioural Ecology of Humans and other Mammals* (Ed. by V. Staden & R. A. Foley), pp. 243–263. Oxford: Blackwell Scientific.

de Waal, F. B. M. & Luttrell, L. M. 1985. The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. *American Journal of Primatology*, **9**, 73–85.

Wittig, R. M. & Boesch, C. 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Taï National Park. *International Journal of Primatology*, **24**, 847–867.