Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (*Lycaon pictus*)

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Abstract

In many social species, relationships within groups seem to be non-random but related to variables such as rank, kinship or sexual attractiveness. The endangered African wild dog *Lycaon pictus* is a social carnivore that lives in large, stable packs, and intra-pack associations might be expected to display similar patterns. We investigated patterns of coalition formation (support during dominance interactions, and partnership interactions) and resting associations between members of a captive pack of 19 wild dogs. The social organization of the captive pack was similar to that of free-ranging packs in many respects. Polyadic (group) incidents of coalition support were also observed in a free-ranging pack. Patterns of coalition formation in the captive pack were related to rank. Most aggressive interactions involved high-ranking individuals (particularly the alpha, beta and third-ranking males) and coalitionary support tended to reinforce the existing hierarchy. However, there was at least one example of support influencing a successful rank challenge. Support was affected by potential risks and benefits, the latter including dominance through association and revolutionary alliances. An even stronger pattern overlaid associations between pack members: coalitions and resting associations were strongest between members of the same age–sex cohort, and may have enabled the eventual dominance of younger pack members over adults. Among adults, coalitionary associations were sometimes overridden by intersexual relationships. The results from this captive pack suggest that wild dogs are sensitive to differences in competitive ability. This information, in conjunction with strong affiliative bonds between littermates, is used to manoeuvre for position in the social hierarchy. It may also be important during dispersal, in encounters with other dispersing groups of the same sex. Although most features of the social structure of the captive pack were comparable to those of free-ranging packs, aspects such as the influence of relatedness on coalition formation still need to be explored.

Key words: coalitions, social systems, Carnivora, *Lycaon pictus*

INTRODUCTION

Primates that live in large, stable groups often exhibit a range of complex behaviours such as co-operation, manipulation and deception, indicating cognitive abilities that may have been shaped by natural selection for efficient functioning in a complex social environment (Humphrey, 1976). Group size and neocortex size are strongly correlated in primates, carnivores and cetaceans (Kudo & Dunbar, 2001), and several group-living non-primates share some of the cognitive abilities of primates. In particular, the formation of coalitions or alliances between group members has been recorded for bottlenose dolphins *Tursiops* sp. (Connor, Smolker & Richards, 1992; Connor, Heithaus & Barre, 1999), spotted hyenas *Crocuta crocuta* (Smale, Holekamp *et al*., 1995), wolves *Canis lupus* (Jenks, 1988) and coatis *Nasua narica* (Gompper, Gittleman & Wayne, 1997). Often, these co-operative relationships seem to be non-random, and may be based on rank (e.g. Silk, 1999), kinship (e.g. Mills, 1985; Zabel *et al*., 1992) or sexual attractiveness (e.g. Vasey, 1996). The strength of social bonds between group members may also be reflected by spatial associations; the latter may be the most useful measure of affiliative relationships (Hill & van Hooff, 1994). As for coalitions, association patterns within groups may also be related to rank and/or kinship (e.g. Holekamp *et al*., 1997).

The endangered African wild dog *Lycaon pictus*, like the wolf, is a social carnivore. Wild dogs live in packs of two to > 20 adults (Maddock & Mills, 1994). Within a pack there are separate, near-linear male and female hierarchies, headed by an alpha pair that usually monopolizes reproduction (Frame *et al*., 1979). New packs commonly form when dispersing male siblings join dispersing female siblings from another pack (McNutt,

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1996), and packs may later expand to include the offspring of the dominant pair (Girman *et al*., 1997). There have thus far been no published accounts of coalitionary relationships within wild dog packs. However, there is evidence that associations between pack members are not random but reflect the strength of social bonds (McCreery, 2000), as they do for wolves (Zimen, 1976; Schröpfer & Rhode, 1997). Given the social system of wild dogs, it seems probable that relationships between pack members might be based on rank, kinship, or sexual attractiveness.

Research on captive animals has inherent limitations, since conditions of captivity may cause aberrant behaviours (Erwin, Maple & Mitchell, 1979). Observations of social behaviour in captivity may be particularly misleading if group structure differs greatly from that which is the norm in the wild (Sadler & Ward, 1999). However, studies of captive animals may allow the observation of subtle social interactions that are overlooked in field studies because of limited visibility of the subjects, or a lack of continuity of observations.

The aims of the present study were threefold: (1) to determine whether pack members form coalitions and, if so, to investigate patterns of coalition formation; (2) to determine resting associations between pack members, and to compare these to coalitionary associations; (3) to compare features of the social organization of a study pack of captive wild dogs to that of free-ranging wild dogs, thereby highlighting any possible limitations of the present study.

METHODS

A captive pack of 19 wild dogs was maintained at the Hoedspruit Cheetah Centre, Northern Province, South Africa. At the outset of the study, the 9 females and 10 males ranged in age from 0.3 to 5.4 years. The pack comprised 3 age cohorts. Adults (defined as older than 2 years) belonged to cohort 1 and were all captive-bred siblings or half-siblings, born at the Johannesburg Zoological Gardens, South Africa, and transferred to the Hoedspruit Cheetah Centre in 1991. Only adults were ever observed to mate. Their offspring comprised cohort 2 (sub-adult littermates, 1.3 years old) and cohort 3 (juvenile littermates, 0.3 years old).

The pack was maintained in a 3-ha enclosure located in an area of natural bush, with excavated termite mounds providing denning sites for breeding. The animals were fed approximately every second day on eviscerated warthog carcasses or beef cuts, supplemented with minerals and vitamins. A cement dam provided a permanent water supply. The pack was observed from 5 to 100 m, from a vehicle to which it was habituated. Observations were made for 19 months (1992–94), for intermittent periods of no less than 5 days. The pack was observed from first light for 4 h in the morning and for 3 h in the afternoon until last light (total of 685 h), the dogs being extremely inactive outside that period.

Dominance and submissive behaviours were identified following Derix (1994) and J. R. Malcolm, K. Marten & L. H. Frame (pers. comm.), and recorded by means of focal and ad lib sampling. Rank hierarchies (separate for males and females) were constructed according to the direction of dyadic interactions (de Villiers, van Jaarsveld *et al*., 1997). These included agonistic interactions, which involved an expression of submission in response to aggression and could occur at any time, and also affiliative interactions, which were apparently unsolicited expressions of submission and were only observed during greeting ceremonies. Estes & Goddard (1967) described greeting ceremonies as ritualized ceremonies involving most or all pack members, which usually take place as the pack becomes active after a period of rest. Interactions used to construct dominance hierarchies involved no obvious competition for resources such as food or mates, the subordinate invariably deferred to the dominant individual, and relationships were constant over periods of 1 month or more. The interactions thus met the criteria listed by Lanctot & Best (2000) for the expression of dominance and were used to generate dominance rankings. Ordinal dominance ranks were assigned from rank hierarchies, with a rank of '1' assigned to the most dominant individual. Hierarchies were constructed according to the direction of dyadic interactions, so that the number of reversals was minimized. Hierarchies involving 6 or more individuals were tested for linearity according to Landau's index, as modified by Appleby (1983). For some statistical analyses, individual ranks were ignored and pack members were instead categorized as 'high', 'medium' or 'low' ranking. It was assumed that the rank of animals was consistent throughout an observation period and this assumption was almost always valid.

A separate hierarchy was constructed after each successful challenge for alpha position, resulting in 5 male (MH-5) and 3 female (FH1-3) hierarchies (Table 1). Two of the 4 changes in male hierarchies and 1 of 2 in female hierarchies were triggered by immobilizing alpha individuals as part of a broader study (de Villiers, van Jaarsveld *et al*., 1997), while all other hierarchy changes occurred spontaneously.

Intrasexual dominance interactions between members of a group, which did not involve competition for resources were recorded ad lib. These interactions involved a relatively large number of individuals (from 3 to 19) and were highly visible, thus we were confident that few such interactions were overlooked. A coalition was defined following Gompper *et al*. (1997) as an event when individuals combine forces; either 1 individual coming to the aid of the other(s), or 2 or more individuals directing aggression on the same target at the same time. Thus 2 types of coalitionary interactions were distinguished. The first of these were incidences of support during dominance interactions, and the identity and rank of the aggressor(s), target(s) and supporter(s) were recorded as well as whether the aggressor or target was supported. When determining the relative ranks of the supporter and the recipient of support, and when assessing support within and between age cohorts, only those interactions in which a single individual supported 1 other were considered.

Table 1. Description of five male (M) and three female (F) hierarchies recorded in a captive wild dog *Lycaon pictus* pack. Cohorts: 1, adults; 2, sub-adults; 3, juveniles. Significance of linearity (< 0.05) was only measured if the number of hierarchy members > six: S, significant; NS, not significant

Hierarchy code	Alpha (age in years)	Cohort of alpha	Duration (months)	Linearity	Number of hierarchy members
MH1	M4 (5.4)	1	> 1.5	S	8
MH2	M1 (5.5)	1	3	NS	8
	M7 (1.4)	2			
MH3	M2 (5.8)	1	2	S	10
MH4	M9 (1.0)	3	7	S	10
MH5	M10 (1.8)	3	> 1	NS	10
FH1	F1 (5.4)	1	> 6.5		4
FH2	F3 (2.2)	2	7	NS	8
FH3	F9 (1.4)	3	> 1	S	8

The second type of coalitionary interaction occurred when 2 or more aggressors acted in concert against another party. Such relationships were termed 'partnerships'. A 'partnership index' (PI) was calculated following the method used by Mitchell (1994) to quantify participation by male squirrel monkeys *Saimiri sciureus* in joint genital displays:

$$PI = X/(A + B - X),$$

where $X =$ the number of partnerships in which both individuals participated, $A =$ the number of partnerships in which individual A participated, $B =$ the number of partnerships in which individual B participated.

Associations between resting pack members were recorded after each disturbance that led to a disruption in the group composition, to avoid autocorrelation of samples. Samples were only included in the analysis if group composition was stable for > 10 min, and if all members of the group could be identified. Individuals separated by > 2 m (i.e. > 2 adult dog lengths; McCreery, 2000) were recorded as being in separate groups. An 'association index' (AI) was calculated following Ginsberg & Young (1992):

$$AI = Z/(N - D)$$

where $Z =$ the number of observations in which 2 individuals were in the same group, $N =$ the total number of observation periods, $D =$ the number of observation periods during which neither of the pair of individuals was observed.

Since partnership and resting associations were not strictly intrasexual, and since female hierarchies overlapped male hierarchies in time, these data were separated according to time periods corresponding to male hierarchies only. Dendrograms based on PI and AI values were constructed following Morgan *et al*. (1976). Estimates of PI and AI were arranged in separate square matrices. Mantel's (1967) matrix comparison method, as described by Schnell, Watt & Douglass (1985), was used to determine whether a statistical association existed between corresponding elements of the 2 matrices.

During the course of another study in the Kruger National Park, South Africa, ad lib observations were made of polyadic (group) interactions between members of a free-ranging pack of wild dogs. The pack of 38 wild dogs comprised 8 adults, 12 sub-adults and 18 juveniles, and was observed at a breeding den for 1 month after the alpha female had whelped. While these observations do not provide empirical support for the patterns of coalition formation observed in captivity, they do suggest that coalition formation occurs in the wild and are therefore included here.

RESULTS

Dynamics of the captive pack

For at least 2 years preceding this study, the two adult females in the pack (F1 and F2) competed for reproductive opportunities. Both females became pregnant each year but only F2 raised a litter in the first year and only F1 did so in the second year. During the present study, the mating season (corresponding to the middle of hierarchies FH1 and MH3) was accompanied by intense aggression by F1 towards F2. F1 became pregnant but died after a management-related handling procedure before hierarchy FH2.

During the first part of the study period (corresponding to hierarchies MH1–3 and FH1), adults of both sexes were dominant over most sub-adults. Successful challenges by younger animals for rank position followed so that during the latter part of the study period (hierarchies MH4, MH5, FH2 and FH3), some members of younger cohorts were dominant over some members of older ones (Table 1; de Villiers, van Jaarsveld *et al*., 1997).

Comparison of the social organization of the study pack with that of free-ranging packs

Most features of the social organization of the study pack fell well within the range recorded for free-ranging packs of wild dogs (Table 2). One exception was that in the captive pack, the alpha male and female were

Table 2. Comparison of aspects of the social organisation of the study pack of captive wild dogs *Lycaon pictus* with those of free-ranging packs. Differences are highlighted in bold

Feature of social organisation	Captive pack	Free-ranging packs
Pack size	19	2–> 50 (Mills, 1995)
Sex ratio (male : female)	1 : 0.9	1 : 1 (Maddock & Mills, 1994), or male-biased (Fuller *et al.*, 1992)
Maximum age of adults	7.4 years	> 8 years (Frame *et al.*, 1979)
Pack composition	**Related alpha pair**, related sub-dominants, offspring	**Unrelated alpha pair**, related sub-dominants, offspring (Girman *et al.*, 1997)
Dominance hierarchy	Near-linear	Near-linear
	Headed by an alpha pair	Headed by an alpha pair
	Separate for males and females	Separate for males and females (Frame *et al.*, 1979)
Dominance challenges	Alpha individual deposed by younger relatives	Alpha individual deposed by younger relatives (Frame *et al.*, 1979)
	Six challenges for alpha position over 19 months	**Ten challenges for alpha position over 11 years** (Frame *et al.*, 1979)
Reproduction	Alpha female monopolises breeding, but breeding attempts by sub-dominants	Alpha pair monopolise breeding, but breeding attempts by sub-dominants (Frame *et al.*, 1979)
	Seasonal breeding	Seasonal breeding
Care of offspring	Communal care by all pack members	Communal care by all pack members
	Pups have feeding priority (pers. obs.)	Pups have feeding priority (Malcolm & Marten, 1982)
Dispersal	**Not possible**	**Almost always before 3 years of age** (McNutt, 1996)

closely related. All pack members were thus far more closely related than would be expected in a free-ranging pack (Girman *et al.*, 1997) and the effects of kinship on patterns of coalition formation could not be investigated in the present study. The other major differences between the social dynamics of the captive and free-ranging packs were that no dispersal from the natal pack was allowed in captivity, and that the frequency of challenges for alpha position was far higher in the captive pack than seems to occur in free-ranging packs.

Observations of a free-ranging pack confirmed the occurrence of polyadic dominance interactions in wild dog society. Twenty interactions involved three or more individuals. Almost half of these interactions (nine) comprised aggression directed by several sub-adult littermates towards single adult females, and one involved a group of sub-adult littermates ganging up on a fellow littermate. Two interventions involved the alpha male separating single adult females from sub-adults towards whom the adult females had directed aggression. The alpha male also intervened once when a sub-adult approached an adult female, and once when one adult female approached another. Both the alpha female (four times) and the alpha male (twice, in the company of another adult female) intervened when sub-adults, together with an adult female, approached the pups at the den.

Patterns of coalition formation in the captive study pack

Distribution of aggression given and received

The incidence of dyadic (two individuals) and polyadic (many individuals) dominance interactions increased throughout the study period, peaking during the last male and female hierarchies. For males, high-ranking individuals contributed significantly more aggression than did members of other rank categories (ANOVA: $F_{2,45} = 23.82$, $P < 0.0001$; Tukey: high *vs* medium: $q = 7.35$, $P < 0.05$; high *vs* low: $q = 7.55$, $P < 0.05$). Medium-ranking males were the targets of most aggression (ANOVA: $F_{2,45} = 4.78$, $P < 0.05$; Tukey: high *vs* medium: $q = 5.92$, $P < 0.05$; medium *vs* low: $q = 5.71$, $P < 0.05$) (Fig. 1a). Sample sizes were smaller for females, so patterns were less clear; however, high- and medium-ranking females contributed significantly more aggression than low-ranking females (ANOVA: $F_{2,17} = 8.54$, $P < 0.005$; Tukey: high *vs* low: $q = 11.37$, $P < 0.05$; medium *vs* low: $q = 11.37$, $P < 0.05$) (Fig. 1b).

Support in dominance interactions

Incidents of intrasexual coalitionary support, corrected for the number of potentially interacting individuals, were 5.3 times as frequent as intersexual incidents. The total occurrence of intrasexual support was also significantly higher (binomial test: $X = 147$, $n = 173$, $P < 0.001$). In 93% of those support interactions in which there was no ambiguity regarding the relative ranks of aggressor(s) and target(s), aggressors outranked targets (binomial test: $X = 424$, $n = 456$, $P < 0.001$).

The number of incidents of support within and between cohorts was corrected for the number of combinations of potentially interacting individuals. Data from all male hierarchies were combined. For females, data from FH1 were excluded since interactions involving support during this period were rare ($n = 8$). Data from FH2 and FH3 were combined. For both sexes, members of each age cohort supported each other more often than they supported members of other cohorts (Table 3).

Rank-related patterns of support did not differ during the first and second parts of the study period. Supporters
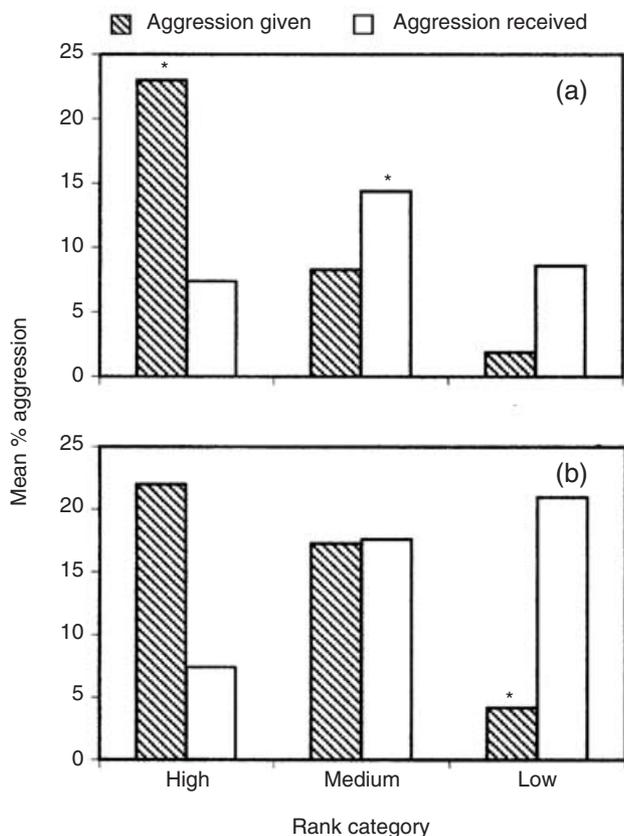
Fig. 1. Aggression given and received by wild dogs *Lycaon pictus* of three rank categories: high, medium and low. Values represent the means of the percentage of all aggression during a hierarchy that individuals of each rank category give or receive: (a) males (* categories, gave/received significantly more aggression than other categories; Tukey test, $P < 0.05$); (b) females (* category, gave significantly less aggression than the other categories; Tukey test, $P < 0.05$).

Table 3. Cohort patterns of help given and received by wild dog *Lycaon pictus* pack members. Helping frequencies were corrected for the potential number of combinations of interacting individuals, for each pair of cohorts. Figures for cohorts helped the most are in bold. Data for males are from all hierarchies combined ($n = 79$), while data for females (italics) are from hierarchies FH2 and FH3 ($n = 36$)

	Help given to		
Help given by	Cohort 1	Cohort 2	Cohort 3
Cohort 1	**1.7**	0.33	0.20
	N.A.	*0*	*0*
Cohort 2	0.67	**3.67**	1.00
	0.50	*4.00*	*0.30*
Cohort 3	0.20	2.50	**11.00**
	0.20	*0.40*	***2.30***

seemed to take the least risky options regarding which individual was supported against which other in dominance interactions (Fig. 2). Aggressors were supported significantly more often than targets of aggression

(binomial test: males: $X = 47, n = 93, P < 0.001$; females: $X = 31, n = 46, P < 0.05$). Aggressors were supported, regardless of their rank relative to the supporter (males: $X = 36, n = 70, P > 0.5$; females: $X = 17, n = 31, P > 0.5$). However, animals supported aggressors more often when they (the supporters) were dominant to the target (males: $X = 62, n = 70, P < 0.001$; females: $X = 26, n = 31, P < 0.001$). For males, if the target was dominant to the supporter, then supporters supported more often if the aggressor was also dominant to themselves ($X = 8, n = 8, P < 0.05$) (Fig. 2).

When targets were supported, the supporter tended to outrank the target (males: $X = 21, n = 23, P < 0.001$; females: $X = 12, n = 15, P < 0.05$). Additionally, males supported targets more often when the aggressors were their (the supporters') subordinates ($X = 22, n = 23, P < 0.001$) (Fig. 2). This pattern was largely influenced by support by the alpha male and female, who were responsible for a disproportionately high number of incidents of support of targets (12/23 for males and 7/15 for females).

The triad of (three) top-ranking males were involved in 70% of all incidents of coalitionary support. Over the study period, alpha males lent as much support as they received, beta males lent significantly more support than they received (binomial test: $X = 42, n = 58, P < 0.005$) and third-ranking males lent less support than they received, although this was not statistically significant (Fig. 3). Alpha males distributed the support that they lent fairly evenly among other hierarchy members but received most (91%) support from animals in the top half of the hierarchy ($X = 19, n = 22, P < 0.002$), particularly from beta males (Fig. 4a). Beta males lent most (81%) support to third-ranking and alpha males and received most (75%) support from males of those ranks, although support lent far exceeded support received ($X = 34, n = 47, P < 0.005$) (Fig. 4b). Third-ranking males lent most support to (50%) and received most support from (72%) beta individuals, although support received far exceeded support lent ($X = 24, n = 34, P < 0.05$) (Fig. 4c).

It was not possible to analyse female support interactions in such detail, owing to the smaller number of female hierarchies, the large differences in the number of females per hierarchy throughout the study period (from four to eight) and the smaller incidence of support observed for females. However, the three top-ranking females were involved in 64% of all dominance interactions involving support. As with males, alpha females lent as much support as they received (10 incidents of each).

Partnerships in dominance interactions

The general trend was that partnership associations were strongest between members of the same age cohort and, within cohorts, between members of the same sex (Fig. 5a,c,d,e).

The strongest association of the alpha male was with the beta male, when both individuals belonged to the same
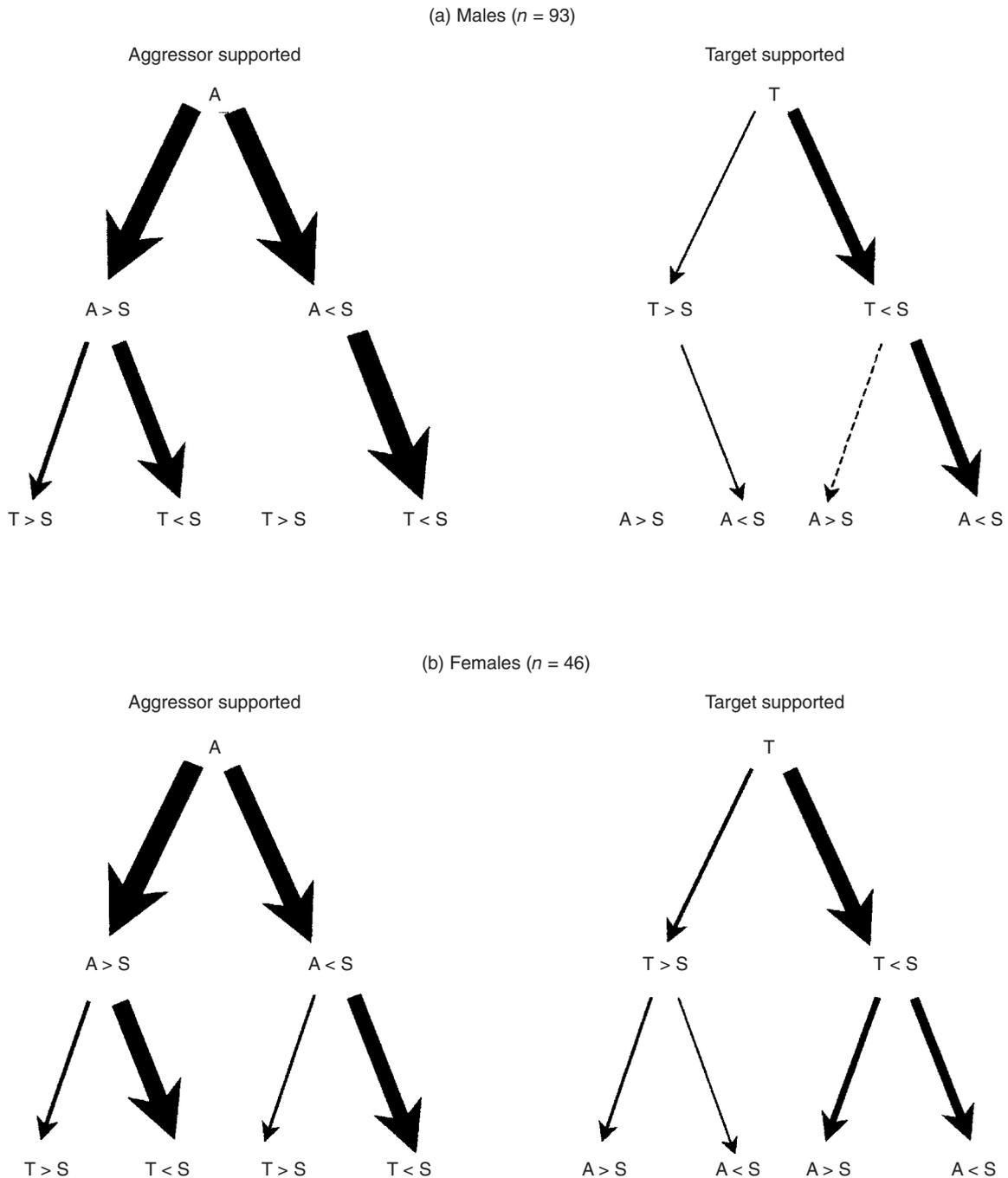
Fig. 2. Rank-related patterns of coalitionary support by wild dogs *Lycaon pictus* in triadic (three) dominance interactions. Interactants: S, supporter; A, aggressor; T, target of aggression. Arrow thickness, relative likelihood of a particular option being followed, dashed arrow indicating option least often observed; >, <, rank of supporter relative to aggressor or target.

age cohort (Fig. 5a,c,e). These partnerships sometimes broke up once an alpha male was deposed. For example, during hierarchy MH1, the alpha male (M4) had a strong partnership with the beta male (M1) (Fig. 5a), but after his loss of status, M4 formed no more partnerships until hierarchy MH4 (Fig. 5b–d). Similarly, the adult alpha male during MH2 (M1) lost the support of two younger males (M6 and M7) after his loss of status (Fig. 5b,c). A close partnership between M2 (rank 3) and M3 (rank 4.5) (Fig. 5b) may have allowed this pair to successfully

challenge and henceforth outrank the adult alpha male, M1 (Fig. 5c). Similarly, the partnership between the two youngest males (M9 and M10) increased in strength between hierarchies MH4 and MH5 and may have allowed them to eventually become the top-ranking males (Fig. 5d,e).

Of the three brothers of cohort 2 (M6, M7 and M8), M8 was the lowest ranking and the least closely partnered (Fig. 5a–d). This male eventually formed a partnership with his two younger brothers (M10 and M9, the alpha
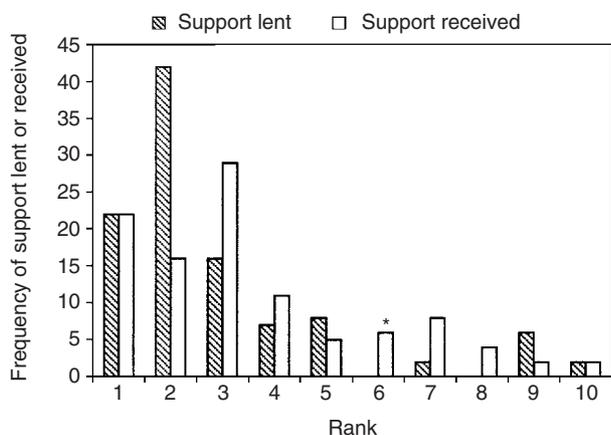
Fig. 3. Relative frequencies with which male wild dogs *Lycaon pictus* of different rank lent and received support in triadic interactions. *, statistical significance between support lent or received within a rank (binomial test, $P < 0.05$).
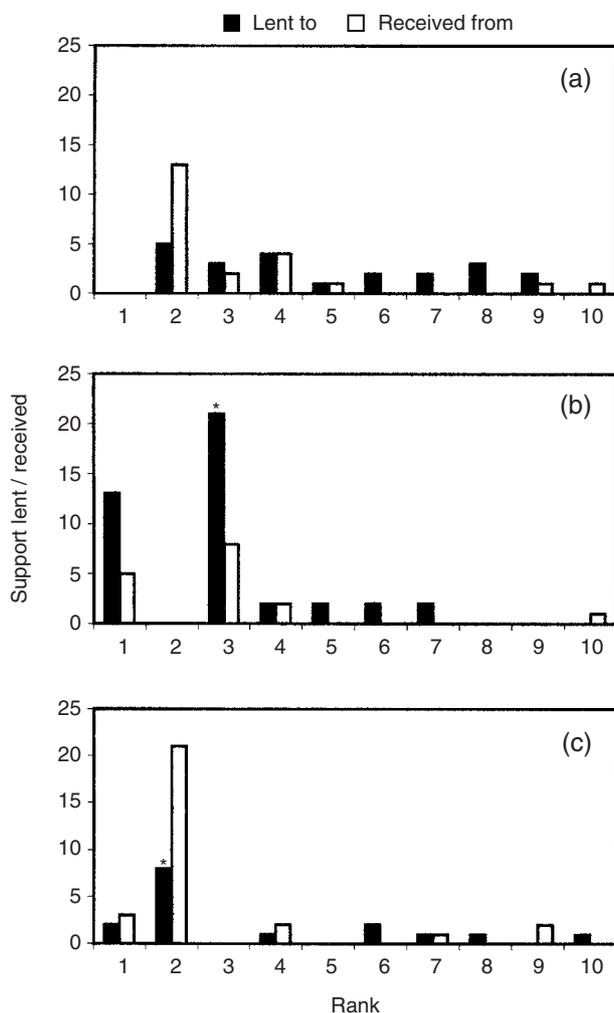

Fig. 4. Relative frequencies with which three top-ranking wild dogs *Lycaon pictus* lent support to and received support from males of other ranks in triadic dominance interactions: (a) alpha males (rank 1); (b) beta males (rank 2); (c) third-ranking males (rank 3). *, statistically significant difference in support lent and received (binomial test, $P < 0.05$).

and beta male at the time) and thereby surpassed his fellow cohort members in rank (Fig. 5e). During 6 h of observation on the first day of this coalition, 40 partnerships were observed between M8 and one or both of his younger brothers. M8 either supported the latter ($n = 4$), or was supported by them ($n = 22$), or acted in concert with them ($n = 14$). Of all recorded coalitions, this was the only one in which solicitation for support was evident to the observer. M8 paused and repeatedly looked back while approaching his targets, confirming the support of M9 and M10. Initially, if such support was lacking, M8 broke off his challenge of targets ($n = 3$). By the afternoon of the first day, M8 was able to dominate M6 and M7 alone, without the support of his coalition partners.

For females, competition between the two adult females (F1 and F2) during FH1 was intense and no partnership interactions were observed between them. As long as the alpha female (F1) was alive, F2 seemed to be an outcast from the pack (Fig. 5a–c). Only after the death of F1 did F2 form a partnership with another pack member (Fig. 5d). F1 did not form close partnerships with any other pack members. This could have been because she did not require a partner to protect her rank position, and/or because she perceived the only other member of her cohort as being her greatest competitor for reproductive opportunities. During the mating season (corresponding to MH3), F1's closest partnership was with M1, the third-ranking male. The sub-adult females of cohort 2 (F3 and F4) were always each other's closest partners and this may have allowed their dominance over F2 (Fig. 5a). Once the juvenile females began participating in dominance interactions, they formed their closest partnerships with one another (Fig. 5d,e).

Resting association patterns in the captive study pack

There was a significant ($P < 0.005$) positive association between the corresponding elements of partnership and resting association matrices for every hierarchy (MH1: $r = 0.574$; MH2: $r = 0.362$; MH3: $r = 0.697$; MH4: 0.792; MH5: $r = 0.830$). Initially, male and female littermates all associated equally closely (Fig. 6a–c), but once juveniles became involved in the adult hierarchy (a time period corresponding to MH4), segregation also occurred on the basis of sex. Then, as for partnership associations, resting associations were strongest between members of the same age cohort and, within cohorts, between members of the same sex (Fig. 6d,e).

Partnerships between adult males did not always correspond to resting associations and were sometimes overridden by resting associations of those males with adult females. During MH1, the alpha female (F1) rested most often with the alpha male (M4) and a subordinate male (M5) (Fig. 6a). During MH2, before the mating season, she was always in the company of the new alpha male (M1), and he remained her most constant companion during the breeding season (MH3), even though he was then the third-ranking male (Fig. 6b,c). The two males seen mating with her at this time were M1 and M5. Initially,
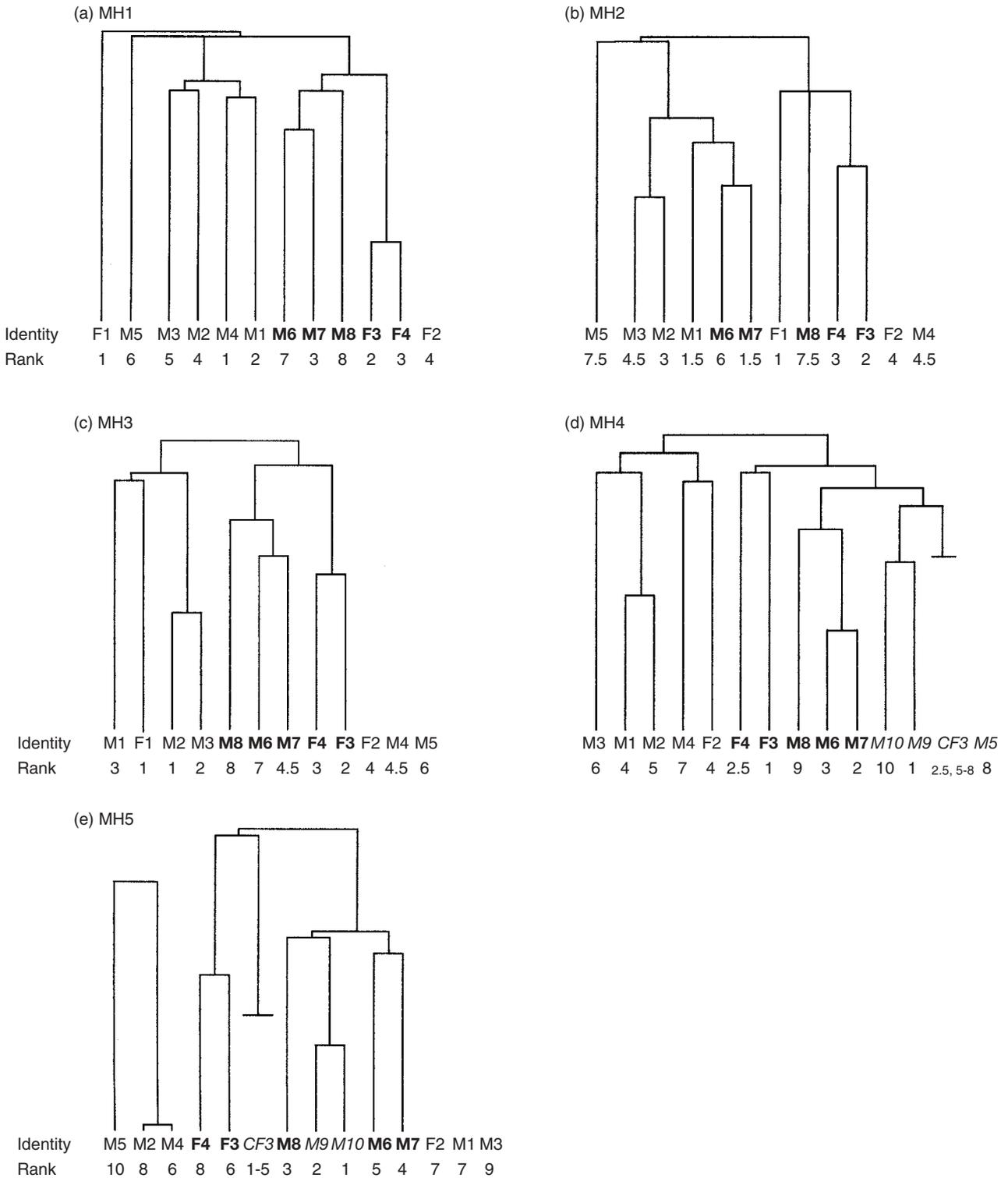
Fig. 5. Partnership associations between members of a wild dog *Lycaon pictus* pack during polyadic (group) dominance interactions: (a)–(e) partnerships during five male hierarchies (MH1–MH5). Indices of partnership between pairs or groups of individuals are indicated on dendrograms. *x*-axis: individual identity codes (M, male; F, female); ranks (1, highest rank). Cohorts: 1 (adults), normal font; 2 (sub-adults), bold font; 3 (juveniles), italic font. CF3, females of cohort 3, who all associated at the level indicated on the dendrogram. Individuals who did not form partnerships are listed next to each dendrogram.

the beta female (F2) was most often in the company of a subordinate male, M3 (Fig. 6a,b). From the mating season onwards, however, she associated most closely with M1

(Fig. 6c–e). Interestingly, neither adult female had a close association with the alpha male, M2, during the mating period.
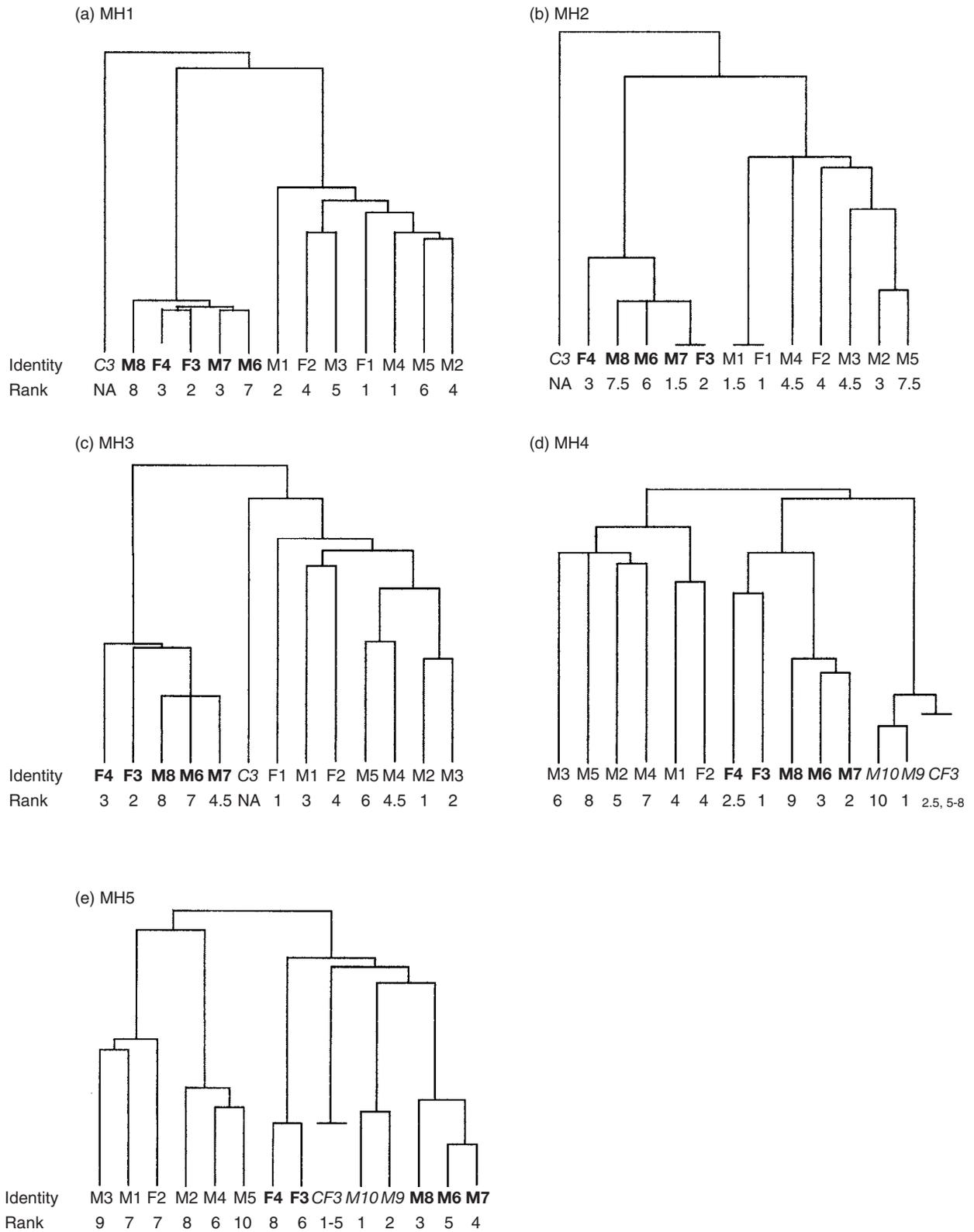
Fig. 6. Resting associations between members of a wild dog *Lycaon pictus* pack: (a)–(e) associations during five male hierarchies (MH1–MH5). Indices of association between pairs or groups of individuals are indicated on dendrograms. *x*-axis: individual identity codes (M, male; F, female); ranks (1, highest rank). Cohorts: 1 (adults), normal font; 2 (sub-adults), bold font; 3 (juveniles), italic font. C3, all members of cohort 3; CF3, all female members of cohort 3.

DISCUSSION

Our results indicate that within a wild dog pack, social bonds – as reflected by coalitions and resting associations – are not randomly formed but are influenced by the rank, age and sex of pack members. Conclusions drawn from captive animals regarding behaviour should be viewed critically, since conditions of captivity may cause aberrant behaviour patterns (Erwin *et al*., 1979). In the present study, the captive pack was held under semi-natural conditions, and most aspects of its social structure closely resembled that of free-ranging wild dog packs. Conditions of captivity did not seem to cause undue stress, since stress measurements (cortisol titres) were lower for the captive than for free-ranging wild dogs (de Villiers, Meltzer *et al*., 1995). Furthermore, coalitionary behaviour was also observed in a free-ranging pack. The number of observations was small but it seemed that partnerships in this pack often involved littermates, and interventions were by high-ranking individuals.

In the captive pack, however, successful dominance challenges by younger cohorts may have been triggered by the immobilization of alpha individuals. They may also have been influenced by the advanced age of the adult cohort; all members were > 5 years old at the outset of the study, and > 7 years old at the end. However, wild dogs can reach > 7 years old in the wild (Frame *et al*., 1979) and dominance challenges by younger relatives have been recorded in free-ranging packs. Frame *et al*. (1979) described three cases of a breeding male defeating challengers, but seven cases of such males losing status to younger relatives over an 11 year period. In another social canid, the wolf, Jenks (1988) recorded a subordinate male initiating a successful coalitionary attack against his dominant father. Note, however, that if dispersal had been possible in the captive pack of wild dogs, these challenges may have been avoided or resolved by the emigration of either the challengers or the challenged individuals. The escalation of aggression in the present study was probably related to an increase in social instability, associated with the recruitment of younger pack members into the hierarchy (as for captive dingoes *Canis familiaris dingo*; Corbett, 1988), and with the mating season (as for wolves; Zimen, 1982). In a free-ranging pack with a lower degree of inter-relatedness between members, even higher levels of aggression might be expected than were recorded in the captive pack. This is supported by sightings of free-ranging male wild dogs with severe bite wounds to the face and genitals, during the mating season in the Kruger National Park (pers. obs.).

For wild dogs, rank has associated reproductive advantages. While sub-dominant pack members may mate and produce offspring, these pups rarely survive to 1 year old. The alpha pair attains about 96% of their total reproductive success each year through their own offspring, compared to about 10% for sub-dominant pack members (Girman *et al*., 1997). Dominant individuals in a hierarchy thus potentially have the most to lose and should assert their status most often. This was true for captive dingoes (Corbett, 1988), sable antelope *Hippotragus niger* (Thomson, 1993) and spotted hyenas (Zabel *et al*., 1992). In the present study, wild dog males that were high-ranking initiated most aggression while medium-ranking males were the targets of most aggression. Top-ranking individuals might be expected to compete with one another, but they usually formed strong partnerships with each other (see below) and directed aggression towards their mutual rivals, middle-ranking males. Displacement aggression directed at the lowest-ranking hierarchy members occurs in some primates (e.g. Sapolsky, 1990) and in the present study, female wild dogs that were low-ranking received more aggression than they gave. However, low-ranking male wild dogs received relatively little aggression.

The stability of dominance hierarchies is tied to the alliance network of the individuals that make up their component parts (Vasey, 1996). By joining coalitions, animals can either challenge a dominance hierarchy (Zabel *et al*., 1992; Vasey, 1996) or reinforce it (Gust, 1995; Vasey, 1996). Triadic dominance interactions between wild dogs generally reinforced existing hierarchies, since the aggressor almost always outranked the target. The outcome of the interaction was thus unlikely to be affected by the assistance of a third party. Supporters usually aided aggressors rather than targets and thus further reinforced the existing hierarchy. One example was observed of a coalition being used to challenge for rank position, when the most weakly partnered male in cohort 2 solicited and received support from his two younger siblings. This support enabled him to later dominate the other two members of his own age cohort.

Primates minimize risk to themselves when they intervene in coalitions among kin (examples cited by Silk, 1999). If wild dogs use coalitions tactically, decisions to support should also be influenced by potential risks (such as retaliation by the target) and benefits (such as future reciprocal aid, and potential gain in status). If risks are taken into account, three predictions should hold true.

(1) Aggressors rather than targets should be supported, especially if aggressors outrank targets (supporters that are alpha individuals would prove the exception, putting themselves at little risk by supporting targets). This is borne out by observations of male rhesus macaques *Macaca mulatta* (Bernstein & Ehardt, 1985), male bonnet macaques *Macaca radiata* (Silk, 1993) and pre-pubertal spotted hyenas (Zabel *et al*., 1992).

(2) Aggressors should be supported more often when the supporter is dominant to the target than *vice versa*.

(3) Subordinates should rarely support other subordinates against a dominant target.

All three predictions held true in the present study.

Aggressors in dominance interactions usually outranked targets and, although their position may have been further strengthened by the support received, the support may not have been necessary to maintain their positions in the hierarchy. Indeed, solicitation for support by aggressors was rare (pers. obs.). However, even unsolicited support could strengthen an aggressor's position. The supporter, too, may benefit from lending support. Its

action may result in it receiving future reciprocal support from the individual it aided. Also, by joining a dominant animal in a challenge against a mutual subordinate, that subordinate may become even more wary of the supporter and less likely to challenge it later. This 'dominance through association' (Chapais, 1983) may have motivated coalitionary support in wild dogs, and may explain why beta males often supported alpha males.

The criterion for the selection of an ally should be the effectiveness of the support it can give, which is related to its rank. Individuals most likely to gain and/or lose through dominance interactions are those with higher ranks. (In this study, most coalitions involved the three top-ranking hierarchy members.) They should form coalitions to improve their own rank and/or to disrupt coalitions amongst their rivals. Alpha and beta animals should thus be each other's most powerful allies and in the present study, strong partnerships were formed between alpha and beta male wild dogs of the same age cohort. Evidence that beta males cultivated this relationship solely on the grounds of their partner's rank position is that deposed alpha individuals lost the support they had previously enjoyed. However, alpha individuals should avoid strengthening any other hierarchy member's position, particularly that of the beta individual, through the support which they provide. In the present study, the alpha male may have achieved this by distributing his support equally among other males and by lending significantly less support to the beta male than was received from him. By supporting targets that were attacked by high-ranking aggressors, the alpha male may even have weakened the positions of the latter in the hierarchy. While a beta individual may strengthen its position near the top of the hierarchy through a strong alliance with the alpha individual, the beta individual may also successfully challenge for alpha position by means of a revolutionary alliance (Chapais, 1992). The strongest ally for this purpose would be the third-ranking individual. In the present study, second and third ranking males exchanged most support, although third ranking males received more support than they lent. A revolutionary alliance during MH2 may have enabled the second and third ranking males to overthrow the alpha male. There is, however, the danger of confusing the influence of rank changes on the pattern of support and the influence of the pattern of support on rank changes (Silk, 1993).

These examples support the concept that high-ranking individuals are not necessarily the strongest, but the ones that can mobilize the most support (De Waal, 2000). However, while coalitionary support may be an important determinant of rank and while rank may usually influence mating opportunities, the importance of female choice should not be overlooked. Resting associations may serve to strengthen coalition bonds but may also be important in the establishment of friendly relationships with members of the opposite sex, as they are for male baboons *Papio anubis* (Packer, 1979). Mate preferences have been also been recorded in wolves (Derix *et al*., 1993), and were evident in the intersexual resting associations between the mature members of our study pack of wild dogs.

While high rank may be a trait that is attractive to the opposite sex, this is not necessarily always so, for example, both adult females seemed to prefer the company of the male, M1, regardless of his rank. For adults, therefore, mate preferences as well as partnership associations affected resting associations.

While rank-related patterns of coalition formation and resting association occurred, there was even stronger evidence that a combination of age and sex was important in relationships between wild dog pack members. Associations that are related to age and/or sex occur in several species. Male squirrel monkeys *Saimiri sciureus* of approximately the same age emigrate together from their natal group and support each other against other males (Mitchell, 1994). Young male bottlenose dolphins of similar age form bonds that may persist into adulthood (Wells, 1991). Among carnivores, young spotted hyena peers direct coalitionary attacks against older siblings (Holekamp & Smale, 1993) and certain adults (Smale, Frank & Holekamp, 1993), and there are high levels of intra-litter co-operation (Smale, Holekamp *et al*., 1995). Zimen (1982) referred to 'juvenile gangs' of wolves participating in joint attacks on pack emigrants, while Schröpfer & Rhode (1997) noticed that young wolves, newly introduced to an existing captive pack, reacted 'as a gang' to attacks on them. It has also been postulated that in lions *Panthera leo*, relationships formed early in life may be important in the development of larger coalitions between adults, since coalitions of four or more males are usually composed of members of the same natal cohort (summarized in Packer & Pusey, 1997).

It has been suggested that for hyenas, one of the advantages of co-operation with littermates may be the speeding up of the rank acquisition process (Smale, Holekamp *et al*., 1995). In this species, intra-cohort support is important in the acquisition and maintenance of rank positions, particularly by young, socially inexperienced clan members (Holekamp & Smale, 1993). In the study pack of wild dogs, triadic dominance interactions involved intra-cohort rather than inter-cohort support. This, together with the successful take-over of dominant rank positions by all members of cohort 2 and later, by all members of cohort 3, supports the hypothesis that littermates of the same sex may use coalitions to improve rank position. Unfortunately, the relative dominance positions of wild dog cohorts were almost always already established when observations began, so co-operative challenges leading to an improvement in the social status of all cohort members were not witnessed. Nevertheless, the occurrence of such challenges may be inferred from the simultaneous strengthening of intra-cohort coalitions between non-adults, and their achievement of dominant rank positions.

The origin of intra-cohort coalitions may lie in the close association that exists between young littermates before participation in dominance interactions. During aggressive encounters, male bonnet macaques tended to support individuals with whom they associated and interacted affiliatively (Silk, 1994). Similarly, association patterns between male bottlenose dolphins corresponded

to patterns of co-operation in the herding of females (Connor, Smolker *et al.*, 1992). In the present study, wild dog pack members rested in age-related groups and there was strong agreement between partnership and resting associations, supporting the hypothesis that spatial associations in social species may be a useful measure of affiliative relationships (Hill & van Hooff, 1994).

In a free-ranging pack, members of different cohorts are probably less closely related than in our study pack, and it is feasible that differences in the levels of co-operation between cohorts would be even more pronounced. Strong associations between siblings of the same age and sex bring to mind the dispersal pattern for the species. Wild dogs generally disperse from their natal pack before 3 years of age, and do so in groups of the same sex and more or less the same age (no male and female sibling groups have been recorded to disperse together) (McNutt, 1996). Only if the reproductive female dies or disappears, and unrelated females are recruited into the pack, do males remain in their natal home range. The motivation for dispersal seems primarily to be inbreeding avoidance, although competition for mating opportunities may also play a role (McNutt, 1996). Strong associations between dispersing littermates may influence competitive ability against other, unrelated groups of dispersers of the same sex. However, these associations may be so strong that they interfere with successful pack formation after contact with unrelated individuals of the opposite sex. McCreery (2000) found that social integration between the sexes was necessary for the formation of a stable pack, and that newly formed packs in which same-sex relationships were observed and maintained more often than opposite-sex relationships, eventually disintegrated.

In conclusion, the distribution of aggression and the patterns of coalition formation (both coalitionary support and partnership interactions) observed in the captive pack of wild dogs suggest that these animals are sensitive to differences in competitive ability of pack members. This information, in conjunction with strong affiliative bonds formed at an early age between littermates, and reflected in spatial associations between resting pack members, may be used to manoeuvre for position in the social hierarchy. During dispersal, it may be important in encounters with other unrelated packs. An awareness of intra-pack relationships in wild dogs could be a valuable tool in the captive management of this endangered species, e.g. in the timing of the introduction or removal of individuals from groups, and in the selection of such individuals. However, to confirm the broader implications of this study for intra-pack relationships in wild dogs, it is essential to obtain data from free-ranging packs or at least from captive packs which mimic the genetic relationships and dispersal opportunities available in the wild.

Acknowledgements

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