



## Alliances and reproductive success in Camargue stallions

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(Received 2 September 1996; initial acceptance 5 December 1996;  
final acceptance 19 October 1998; MS. number: 5330R)

A study of a herd of Camargue horses, *Equus caballus*, showed that while the majority of high-ranking stallions held single-male harems, some sons of low-ranking mares, being low ranking themselves, formed alliances that could last a lifetime. The two stallions were each other's closest associate and preferential grooming partner. Alliances were based on coalitions in which either both partners confronted an intruder synchronously or the dominant of the pair tended the female(s) while the subordinate simultaneously displayed towards the rival. Alliance partners were of similar age but were not more closely related to each other than to other stallions in the herd. Long-term paternity data revealed that subordinates sired close to a quarter of the foals born into the alliance group, and significantly more foals than low-ranking stallions in the herd adopting a 'sneak'-mating strategy. The dominant appeared to benefit from the presence of his subordinate partner. Fights occurred all year round, and the subordinate stallion of each alliance pair fought outside competitors more than twice as often as the dominant. Forming short-term alliances before defending mares on their own may enhance long-term reproductive success for both partners. Other benefits to both partners include higher survivorship of their foals and increased access to proven reproductive mares. These results suggest that the relationship between alliance partners is based on mutualism, but several conditions for reciprocity seem to be fulfilled: the benefit to the dominant (assistance in fights), and the benefit to the subordinate (access to reproduction), are both costly to the other partner and delayed in time.

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Alliances are long-term cooperative coalitions (de Waal & Harcourt 1992), cooperation often being provided in the form of support during competitive encounters (e.g. van Hooff & van Schaik 1992). Alliances between males are generally rare in mammals (Clutton-Brock 1989). As low-ranking males are disadvantaged over access to resources or reproduction (Dunbar 1988), they may be able partly to compensate by forming alliances based on coalitions. The value of male alliances with regard to mating success has been reported in a variety of primates (Smuts 1987), but seldom in nonprimate species, where they have been observed only in lions, *Panthera leo* (Packer et al. 1991), wild dogs, *Lycaon pictus* (Moehlman 1986), hyaenas, *Crocuta crocuta* (Zabel et al. 1992), dolphins, *Tursiops* sp. (Connor et al. 1992), captive plains zebras, *Equus burchelli* (Schilder 1990) and feral horses, *Equus caballus* (Berger 1986). Only the study on lions was able to measure individual reproductive success. Packer et al.'s (1991) results indicate not only that male lions form coalitions, but also that paternity in coalitions of unrelated males is more evenly shared than in coalitions of related males. Therefore, whereas the immediate benefits of cooperative

behaviour have been widely demonstrated (e.g. Smuts 1987), few studies have been able to show the effect of alliances on survival or reproduction (Harcourt & de Waal 1992) or to measure trade-offs between the partners.

Horses and plains zebras provide an unusual opportunity to investigate the effects of alliances on male reproductive success. Adults form small, long-term groups, usually consisting of one stallion, one to two mares and their offspring. As is typical for a species in which males have long tenure of a group, both sexes disperse from their natal family (Clutton-Brock 1989). Young mares usually join reproductive units directly (Monard & Duncan 1996), whereas young males first spend 1–2 years in a stallion group before forming their own family (this study). Apart from the typical one-male family, groups with more than one adult stallion have been reported by all authors who have studied free-living horses. Berger (1986) noted that 12% of the families that persisted longer than 7 months had two or more stallions, and Stevens (1990) reported that half of the 12 groups she watched for 2 years were multimale. With regard to these different types of groups in horse societies (one-male, multimale and all-male), the following mating strategies are observed in stallions: exclusive access to females in one-male families; shared reproduction in multimale

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groups, including preferential male–female relationships in terms of proximity and exchanged interactions over several years (Feh 1987); and sneak matings by stallions living in all-male groups, these matings mainly occurring at night and without a social bond between partners (personal observation).

Individual reproductive success in Camargue stallions is positively correlated with their mother's rank and their adult rank, but not with their weight (Feh 1990). Stallions may therefore vary in 'quality' (e.g. rank), and the high-ranking individuals may be better able to hold groups on their own than others. The alternative for low-ranking individuals might be to team up in alliances in order to be able to defend females.

In this paper, I describe alliance behaviour based on coalitions between Camargue stallions living under semi-natural conditions. I then investigate the influence of genetic relatedness, rank and age on alliance formation and describe costs and benefits to the two partners with regard to fighting and reproductive success, based on paternity analyses. I finally examine mutual benefits to both alliance partners in terms of overall reproductive success, foal survival and access to specific females.

## METHODS

### Study Animals

The study herd started in 1974 with 14 horses of known genetic relatedness. They were released in a Camargue pasture of 300 ha composed of freshwater marshes, salt steppes and halophyte grassland. The number of horses peaked at 94 in 1981, with 11 family groups and one bachelor group. From 1980 on, horses were removed regularly to avoid overgrazing. No supplementary food or veterinary care was given. From 1979 on, all individuals were weighed twice a week. At the same time, blood samples were taken for paternity tests. All individuals were easily approached and identified and their exact dates of birth are known. From 1977 on, several family groups existed and from 1978, these family groups lived together in one herd. This meant that the horses were in sight of each other most of the time, so interactions between stallions were relatively frequent. This analysis considers 13 stallions, for which long-term reproductive success and social behaviour from birth to the respective ages of 11–14 years were known. These ages are beyond the peak of reproductive success in stallions (Berger 1986; Feh 1990).

### Paternity, Relatedness and Foal Survival

Paternity exclusion tests were based on electrophoresis on a number of proteins at 28 loci (for further procedural details see Scott 1978). The combined reproductive success was calculated up to 11 years, when the paternity analyses stopped. A total of 154 foals were born to the groups under consideration; 10 foals were found dead shortly after birth (<48 h) and therefore were not analysed for paternity as the analyses needed fresh blood

samples. As the adult sex ratio of the herd changed over the study years, stallions of different ages did not have the same opportunity for siring foals in each year. To standardize data for each stallion, I calculated the number of 'available' mares for each stallion at each age in the following way. Nearly all the mares had a foal every year and gestation lasts 11 months. The age at first breeding is taken as 2 for the mares and 4 for the stallions. The number of 'available' breeding mares was thus the ratio of the number of mares 2 or more years old divided by the number of stallions 4 or more years old. So the relative reproductive success of a stallion at a given age was the number of foals produced at that age divided by the number of available breeding mares the year before.

I calculated the relatedness of each pair of horses (e.g. H1 × K6) in the herd measured as the additive relationship ( $a$ ) as follows:

$$a_{H1 \times K6} = 0.5(a_{H1 \times G3} + a_{H1 \times G4})$$

where G3 and G4 are, respectively, the mother and father of K6. For the full description of the method, see Evans et al. (1977).

For the comparison of foal survival between one-male and alliance families, I considered all 154 foals found shortly after birth (<48 h). Under such circumstances, identification of the mother, and therefore of the group into which the foal was born, was easy even for dead foals.

### Assessment of Ranks

From 1976 to 1987, I established the dominance hierarchy in the field using observations of headthreats and bites, followed by a clear avoidance reaction by the recipient (Wells & von Goldschmidt-Rothschild 1979). Both focal animal and all-occurrences sampling were used. Observation hours varied from 564 to 1872 per stallion. Contexts were food, water or wind shelter. The horses were then ranked according to the classical method (Martin & Bateson 1993), where the individual that is never supplanted is at the top and the one that is always supplanted is at the bottom. As it was sometimes difficult to observe a resource-based hierarchy in the field, the herd was brought to a 1-ha enclosure where access to water could be controlled. Every 48 h, I stopped their otherwise free water supply for 24 h, so the horses were induced to show agonistic behaviour at a measurable rate (1.4 headthreats and 0.17 bites per horse in the first hour after having access to water). I repeated the experiment 10 times over a 3-week period in 1988 and 1989, and compared the results with data obtained in the field. There was no difference between the two data sets, and a stable linear dominance hierarchy could thus be determined among the stallions.

### Relationships, Confrontations and Fights

Observation hours were evenly distributed over day-light hours in all seasons. The nearest horse to any other

horse of the herd was determined every 15 min. Single linkage cluster analysis based on these data was used to define groups and establish preferential individual relationships (Duncan 1992). For the same purpose, I used focal animal sampling, following each stallion for 60 min per day, 200 days per year from 1976 to 1980. I recorded 30 different types of interaction with the aid of a tape recorder and used them to calculate frequencies per h of 11 behavioural categories. A detailed description of observational methods is given in Feh (1987). For 2 years, the herd was observed for 48 h consecutively every 2 weeks in order to establish activity budgets. These observations also allowed sneak matings to be detected, although not quantitatively for all stallions. As all the families stayed close together during the study period and fights are conspicuous, I used all occurrence sampling to calculate the fighting frequency for each stallion. Fights in equids typically consist of rearings, attempts to bite or bites, and kicks with the fore or hind legs (Feist & McCullough, 1976; Berger 1986). Before the stallions start to fight, they usually go through a confrontation (Tschanz 1985; Berger 1986), where one stallion defecates on a dung pile while the other approaches. They then smell the dung together, and most often raise their heads rapidly while squealing. These actions are typically followed by kicks with the forelegs, and the dominant stallion of the pair then defecates over the dung while the subordinate leaves (Feh 1987). If the subordinate stallion is reluctant to leave, the confrontation usually ends in a fight.

### Statistical Analysis

The statistical analysis is based on two categories of stallions. The first takes into account the stallions that adopted only one reproductive strategy during their life. They were treated as independent samples and compared with the Wilcoxon test (Siegel & Castellan 1988). For stallions that changed reproductive strategies during their life, I compared these using the Wilcoxon signed-ranks test or the permutation test for paired replicates (Siegel & Castellan 1988). For comparisons between alliance partners, these same pairwise tests were used.

## RESULTS

### Proportion, Duration and Stability of Two-male Groups

Detailed descriptions of the herd history, including group composition, genealogy and births are given in Duncan et al. (1984) and in Duncan (1992).

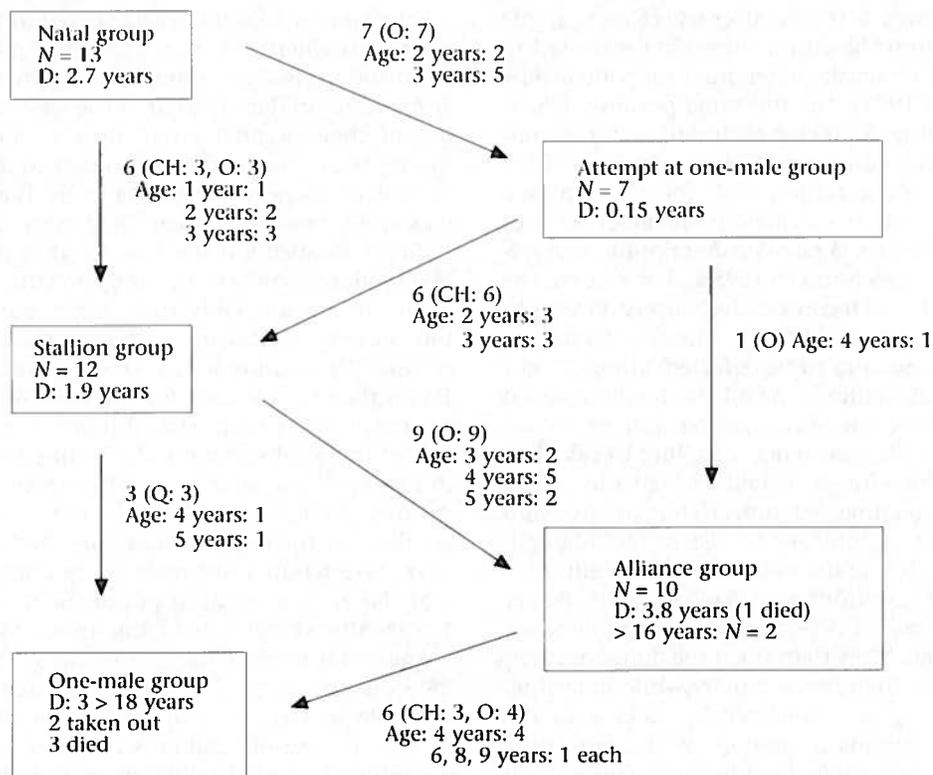
The majority of stallions first tried to monopolize mares on their own, but few succeeded at the first attempt. Stallions that failed to do so seem to have had two options: either they joined another stallion in a two-male group or they stayed in a bachelor group and tried to mate mares as 'sneaks'. Forming a two-male group with another stallion was a temporary situation for the majority of individuals but permanent for four out of 10 males that formed a two-male group.

Seven out of 13 stallions attempted to form a family on their own when 2–3 years old (corresponding to sexual maturity in males), whereas the other six joined an all-male group (Fig. 1). Half of the latter had been chased out of their original group by the dominant stallion. Attempts by young stallions to defend at least one mare against rivals never lasted for more than one breeding season (2 months), when they were forced by other stallions to abandon the mare(s) after numerous fights. The stallions then became integrated into a stallion group for up to 2 years. Only three males out of the 13 were subsequently successful in forming a one-male family group with a tenure length of up to 18 years. The other 10, on their own accord, formed a two-male group with a partner. Four of them stayed together over many years: one of these subsequently died while two stallions were still living in the same group after 16 years at the time of writing. Six left their partners after 2–3 years to form families on their own. Once they had succeeded, they never reverted to a two-male group until they died (9–17 years later) or were taken out of the herd (two stallions, 4 years after they formed a one-male group).

Anecdotal evidence suggests that from a certain age, the strategies adopted by stallions are fixed. In one case, I was able to test the stability of reproductive strategies in four 13-year-old stallions followed since birth. Each stallion had adopted a different strategy between the ages of 4 and 6 years. The dominant had gained control over three mares, the second-ranking stallion was a bachelor, and the third- and fourth-ranking stallions had formed a two-male group. The four stallions were separated from their mares and kept together on a different pasture for 2 months. They were then introduced to a group of six mares unknown to them. Initial fights ( $N=16$  for all stallions) after the release lasted for 21 min in total. By the end of this period, the dominant stallion had monopolized three mares on his own, the second-ranking was a bachelor, and the two last-ranking stallions had teamed up in a two-male group and controlled the other three mares. The group composition remained stable over the next 3 months. Therefore, 7–9 years after initially forming their families with different mares, the stallions had adopted the same reproductive strategy and kept the same rank position. Three months later, when the stallions were reintegrated into the herd together with their old mares, there was again no change detectable in their strategies.

### Relationship between Partners of Two-male Groups

Apart from the low-intensity agonistic interactions (bites and headthreats) maintaining the relative rank position seen in all pairs (Table 1), stallion partners in two-male groups were each other's closest associate. Proximity between the partners was maintained by the subordinate. Their relationship was further based on a high frequency of mutual groomings mainly initiated by the subordinate, smellings or body contacts as well as lightly agonistic rank displays that caused no physical harm (Tschanz 1985). The relationship with the mare(s)



**Figure 1.** Succession of group changes showing alternative reproductive strategies adopted by the different stallions over their lifetime. D: mean duration of stay in the respective group. Age: respective age when the stallions changed groups or reproductive strategies. Of the 13 stallions studied, seven were still alive at the time of writing and in the herd. Four died and two were removed; all were more than 11 years old so were still included in the analysis. CH: number of stallions changing groups or reproductive strategies after being aggressively chased by a dominant stallion or subsequent to losing a fight. O: number of stallions changing groups or reproductive strategies on their own accord, that is, without being chased or attacked by other stallions.

differed between the dominant and the subordinate, the former being closer, engaging in more mutual grooming, and driving her (them) more often than the latter. The relationships of dominants and subordinates with both foals and yearlings of their group were similar, characterized by an exchange of mutual groomings, and submissive behaviour from the young horses towards the adults.

### Alliance Behaviour Based on Coalitions

When an outside stallion approached the two-male group, the partners took one of two options. They either confronted their rival together, with aggression mostly initiated by the subordinate (20 times versus 4 times by the dominant; binomial test:  $N=24$ ,  $P=0.002$ , two-tailed; in 10 cases initiator not determined), or the subordinate usually displayed to the rival stallion while the dominant drove away the mares (Fisher's exact test:  $P=0.001$ ; Table 2).

### Identity of Alliance Partners

Partners teaming up for alliances were low-ranking unrelated stallions of the same or similar age who had developed strong bonds during the time they lived together in a stallion group.

Of the individuals that formed alliances at some stage in their lives, seven out of 10 were part of the low-ranking half of the male dominance hierarchy (Table 3), and were sons of mares in the lower-ranking half of the female dominance hierarchy, whereas the three one-male family holders that never participated in alliances were sons of the higher-ranking mothers (Fisher's exact test:  $P=0.035$ ) and were themselves in the high-ranking half of the dominance hierarchy (Fisher's exact test:  $P=0.02$ ).

There was no consistent tendency for stallions to form alliances with close relatives. Thus, there was no significant difference between the genetic relatedness (additive relationship) of an alliance member with its partner and the relatedness of the same individual with any other stallion of the herd (paired  $t$  test:  $t_9=1.91$ , NS) or with another member of the same stallion group (Fig. 1) before the pair formed an alliance (paired  $t$  test:  $t_9=1.85$ , NS), although the mean additive relatedness between low-ranking mothers was higher ( $X=0.239$ ,  $N=4$ ) than that between dominant mothers (0.083,  $N=3$ ). It cannot therefore be concluded that close genetic relatedness was at the origin of alliances. Moreover, six pairs of maternal half-siblings (same mother, different fathers) from five different mothers knew each other well, having spent up to 2 years in the same group during their youth. None of these formed an alliance pair. The effect of paternal half-siblings could not be investigated. The fathers of six

Table 1. Spatial relationships and interactions exchanged between alliance partners and between alliance partners and all other herd members

Partners	Approach	Smell	Light agonistic	Strong agonistic	Mutual grooming	Stallion display	Greeting	Driving	Submissive gesture	Play	Interposition	Nearest neighbour	All interactions
Dom-Sub	0.46	0.29	0.22	0.04	0.15	0.38	0	0	0	0.02	0.04	168	1.58
Sub-Dom	1.82	0.35	0.01	0	0.21	0.34	0	0	0	0.01	0	122	2.74
Dom-mare													
Initiated	2.29	0.17	0.13	0	0.67	0	0.04	0.57	0	0	0.14	107	3.99
Received	0.21	0	0.23	0	0.12	0	0	0	0	0	0.03		0.59
Sub-mare													
Initiated	1.15	0.16	0	0	0.07	0	0.1	0.07	0	0	0.12	46	1.66
Received	0.12	0	0.23	0	0.05	0	0	0	0	0	0		0.39
Dom-yearling													
Initiated	0.13	0.12	0.05	0.03	0.24	0	0	0.01	0.12	0	0	16	0.67
Received	0.09	0.09	0	0	0.09	0	0	0	0.07	0	0		0.34
Sub-yearling													
Initiated	0.18	0.08	0	0.03	0.32	0	0	0	0.06	0	0	9	0.66
Received	0.08	0.03	0	0	0.09	0	0	0	0.03	0	0		0.22
Dom-foal													
Initiated	0.09	0.06	0.06	0	0.05	0	0	0.04	0	0	0	23	0.28
Received	0.01	0.04	0	0	0	0	0	0	0.03	0	0		0.07
Sub-foal													
Initiated	0.06	0.05	0	0	0.03	0	0	0	0	0	0	28	0.13
Received	0.08	0	0	0	0	0	0	0	0	0	0		0.08
Dom-rival													
Initiated	0	0.01	0.01	0.003	0.003	0.06	0	0	0	0.003	0	0	0.09
Received	0.01	0.04	0.14	0.02	0.003	0.09	0	0	0	0.01	0		0.32
Sub-rival													
Initiated	0.003	0.02	0.02	0	0.003	0.23	0	0	0	0	0	2	0.36
Received	0.01	0.03	0.09	0.01	0.01	0.30	0	0	0	0.01	0		0.46

Dom: dominant stallion in an alliance; Sub: subdominant stallion in an alliance. The mean frequencies of interactions per h for four pairs of alliance partners observed during 44 h each over 6 months are shown. Light agonistic: headthreats and bites. Strong agonistic: attacks and chases. Interposition: one horse moves in between two interacting horses. The nearest neighbour data were recorded every 15 min at the same time as the interactions. The frequency indicates how many times the second of the 'partners' was seen closest to one of the alliance partners, e.g. 'Sub was closest to Dom 168 times'.

**Table 2.** Number of occurrences of display by one alliance partner to a rival while the other drives away their mare(s)

Actor	Display	Driving mare(s)	Total
Dominant alliance partner	2	33	35
Subordinate alliance partner	32	3	35
Total	34	36	70

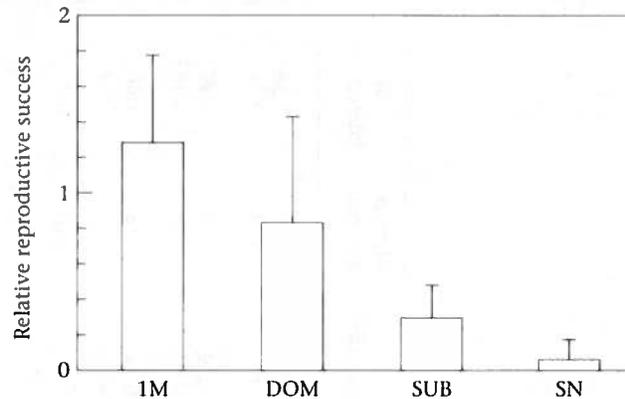
See text for test. The total number of observation hours: 564 for each of the five alliance pairs.

of the stallions were absent from the herd, having sired their sons before the start of the study. The fathers of the other four were present, but the sons did not grow up in the same group as their fathers.

Stallions usually formed alliances with partners of the same age. Six stallions formed alliances with partners born in the same year, the difference in age for the other two pairs being 1 and 2 years, respectively. All but one of the pairs formed while they were together in a stallion group. Two such groups existed during the study, and all stallions forming alliances after leaving the stallion group had preferred social relationships with their future partner during their time together in this group. Future alliance partners were always the most frequent nearest neighbours and exchanged more interactions than with all other members of the herd (Wilcoxon signed-ranks test:  $T=55$ ,  $N=10$ ,  $P=0.002$ , two-tailed, for both nearest neighbours and interactions).

### Benefit of Alliance to Subordinate Stallion

Subordinate alliance stallions had a higher relative reproductive success than sneaks (Table 3, Fig. 2). The sneak strategy was the least successful reproductive strategy (sneak strategy versus subordinate alliance strategy: permutation test for paired replicates:  $N=5$ ,  $P=0.02$ , two-tailed; sneak strategy versus dominant alliance strategy: permutation test



**Figure 2.** Relative reproductive success in relation to the four reproductive strategies (mean number of foals per year+SD). Data cover the stallions' relative reproductive success up to 11 years of age and correspond to the 10 years of analysis on fighting frequency. The data for this figure are pooled, but the statistical tests are based on independent samples or pairwise comparisons (see text). 1M: one-male family holders,  $N=8$ ; DOM: dominant alliance stallions,  $N=5$ ; SUB: subordinate alliance stallions,  $N=5$ ; SN: sneaks (bachelors),  $N=12$ .

for paired replicates:  $N=5$ ,  $P=0.02$ , two-tailed; sneak strategy versus one-male family holders: permutation test for paired replicates:  $N=8$ ,  $P=0.01$ , two-tailed). Although in all of the five alliance pairs, dominants sired more foals than subordinates (permutation test for paired replicates:  $N=5$ ,  $P=0.02$ , two-tailed) and dominants had a higher relative reproductive success than subordinates in individuals that never changed strategies (Wilcoxon test:  $W_x=15$ ,  $N_1=N_2=3$ ,  $P=0.05$ , one-tailed), stallions adopting a subordinate alliance strategy had a higher relative reproductive success than when remaining as sneaks (see tests above).

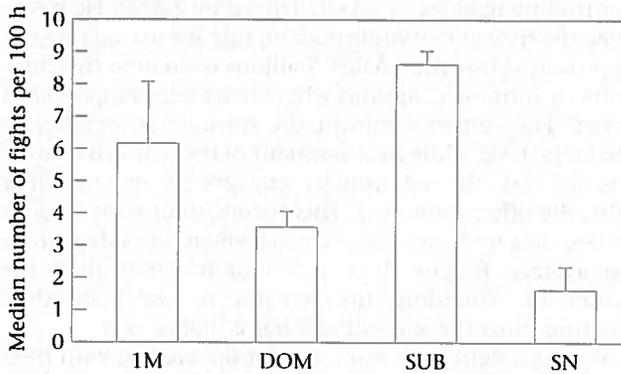
### Cost of Alliance to Dominant Stallion

Apparently as a result of conceding foals to the subordinate, dominant stallions in alliances had a lower

**Table 3.** Relative individual reproductive success\* and rank for the different reproductive strategies

Individuals	Rank	One-male harem	Dominant alliance	Subordinate alliance	Bachelor	Combined over all years
G4	1	1.89±0.27	1.88±0.59		0.29±0.40	0.99
H1	7	1.36±0.42	0.50±0.71		0	0.72
H4	8	0.57±0.17		0.56±0.42	0	0.37
I3	3	0.77±0.18		0.25	0.30	0.56
I4	2	1.66±0.77			0	0.92
I5	5	1.85±0.48		0.38±0.54	0	0.97
I6	11			0.17±0.71	0	0.10
J1	9		0.67±0.52		0	0.50
J7	6	1.07±1.05			0	0.63
K3	12		0.58±0.59		0	0.42
K6	13			0.10±0.28	0	0.08
K8	4	1.04±0.64			0	0.76
O11	10		0.50±0.29		0	0.50
N=13	13	8	5	5	12	13

\*Mean±SE number of foals fathered per year from birth to 11 years, corrected for the number of available mares in the herd the year before.



**Figure 3.** The stallions' fighting frequency with outside competitors in relation to the four reproductive strategies (number of fights per 100 h, median and interquartile range for all stallions). Data were collected from 1977 to 1986, at the same time as the paternity analyses. Observation hours for each stallion varied from 1240 to 1872, distributed over the 10 years. The data for the figure are pooled, but the statistical tests are based on pairwise comparisons (see text). 1M: one-male family holders,  $N=8$ ; DOM: dominant alliance stallions,  $N=5$ ; SUB: subordinate alliance stallions,  $N=5$ ; SN: sneaks (bachelors),  $N=12$ .

relative reproductive success than males controlling mares on their own. Excluding individuals that changed strategies (Table 3, Fig. 2), stallions in one-male groups were more successful than dominant alliance stallions (Wilcoxon test:  $W_x=15$ ,  $N_1=N_2=3$ ,  $P=0.05$ , one-tailed). Stallions changing from alliances to one-male family holders improved their relative reproductive success (permutation test for paired replicates:  $N=5$ ,  $P=0.02$ , two-tailed). As they changed strategies after the age of 4, fertility linked to age could not act as a confounding factor (Evans et al. 1977).

### Cost of Alliance to Subordinate Stallion

Subordinate stallions took more risks and probably expended more energy because they fought more often than dominants and sneaks (Fig. 3). In all pairs, the fighting frequency of subordinate alliance stallions with other stallions of the herd was significantly higher than that of the dominants (permutation test for paired replicates:  $N=5$ ,  $P=0.02$ , two-tailed). Comparisons between reproductive strategies show that subordinate stallions fought more often than sneaks (permutation test for paired replicates:  $N=5$ ,  $P=0.02$ ). There was no significant difference between the frequency of fights for the other categories.

### Benefit of Alliance to Dominant Stallion

Dominant alliance stallions benefited from the presence of the subordinate because he assisted in fights against outside rivals. Excluding stallions that changed reproductive strategies, the total fighting frequency for both alliance stallions combined was significantly higher (Wilcoxon test:  $W_x=15$ ,  $N_1=N_2=3$ ,  $P=0.05$ , one-tailed) than the frequency for one-male strategists, probably

because alliance stallions were lower ranking so had to defend their mares more often. The sample size was inadequate to test for tenure length and/or survival in order to see whether there was a long-term benefit to the dominant from the presence of his subordinate ally. Again, only anecdotal evidence suggests that this may be the case. At the time of writing, of the same four stallions tested for the stability of reproductive strategies, the bachelor stallion died 3 years ago, the one-male family holder now controls two mares whereas the two alliance partners share five mares between them.

### Mutual Benefits to Alliance Partners

Short-term alliance partners, dominants and subordinates alike may have the same long-term reproductive success as one-male group holders that never formed alliances. The stallions that lived in alliances for 2–3 years only and later changed to form a one-male group did not have a lower overall reproductive success than stallions adopting a one-male strategy from the start: when comparing the combined reproductive success up to 11 years (Table 3), there was no significant difference between stallions that had never formed an alliance and those that were temporarily dominant (Wilcoxon test:  $W_x=8$ ,  $N_1=N_2=3$ ,  $P>0.90$ ) or even temporarily subordinate in an alliance (Wilcoxon test:  $W_x=12$ ,  $N_1=N_2=3$ ,  $P=0.35$ ) that had later changed to a one-male group strategy.

Stallions in alliances were more successful than those in one-male groups in rearing their foals to weaning. There was significantly less neonatal (0–1 week) mortality in foals born into alliance families than in foals born into one-male groups. Only one foal out of 31 (3.2%) died in a family with two stallions, whereas 27 out of 123 (22%) were found dead in families with only one male (Fisher's exact test:  $P=0.02$ ). As the overall foal mortality in this herd was highest during the first week and close to zero thereafter (Duncan 1992), foals born into alliance groups had a higher chance of survival.

Alliance stallions had increased access to proven reproductive mares. All young females of breeding age leave their natal family to integrate into a reproductive unit (Monard & Duncan 1996). They therefore become 'available' to stallions outside their natal group. The majority of mares (72.5%, Monard & Duncan 1996) leave at puberty before having a foal (gestation length is 11 months), but some mares wait until shortly after the birth of their first foal before they change groups. When two allies start their group, or integrate a new female into their already existing group, they associate preferentially with mares with very young foals of less than 1 week of age. Nine (50%) out of 18 available mares with very young foals were acquired subsequent to fights by allied partners compared to only four (16%) out of 25 taken over by single males (chi-square test:  $\chi^2_1=4.24$ ,  $P<0.05$ ).

### DISCUSSION

In this herd of horses, low-ranking unrelated stallions of similar age formed alliances based on coalitions where

both partners participated in defending their mares against rivals. Why should some stallions engage in alliances at all? As Dunbar (1988) stated, low-ranking males in general are at a disadvantage with regard to access to females. Alliance stallions both gained substantial benefits from their cooperation. Some individuals seemed to engage in short-term alliances in order to enhance their long-term reproductive success so as to catch up, in the long term, with the most successful strategy, holding mares alone, but the mechanisms are unclear. Other stallions seemingly engaged in long-term alliances because this represented the best option or because they might have had an advantage in controlling more mares in the distant future, but only anecdotal evidence suggests the latter. Another benefit was higher foal survival in alliance groups than in one-male groups. Again, the reason is not entirely clear, but a number of newborn foals were wounded accidentally during fights between adults shortly after birth, although we never observed infanticide. The young foals during their first critical hours after birth may benefit from the protection of two stallions against harassment from other horses. The third advantage of alliances was increased access to proven reproductive females that already had a foal. Mares are usually on heat from 7 to 10 days after the birth of their foal. However, since the majority of young mares, most of them without foals, change groups when they are on heat anyway (Monard & Duncan 1996), this may well indicate that oestrus alone was not the key factor in the alliance stallions' preference for proven breeding mares. Ninety-five per cent of the mares from the herd had a foal every year (Duncan 1992), so it was not possible to investigate the long-term consequences for this preference of stallions in alliances.

In conclusion, the benefits for both alliance partners seem to be straightforward. Mutual benefits to male alliances have been widely reported in mammals, although nonprimate species are poorly represented (for a review, see Clutton-Brock 1989), and benefits are usually discussed in terms of access to resources or enhancement of the common rank position rather than direct measurements of the consequences for an individual or its offspring (Harcourt & de Waal 1992). Nevertheless, mutualism or its synonym by-product mutualism (Mesterton-Gibbons & Dugatkin 1997) is defined as 'cooperation regardless of the opponent's behaviour, cooperation being merely a by-product of following the best strategy' (West-Eberhard 1989). My results suggest that alliance stallions both benefit from their association and follow the best strategy for both of them but not without costs to each of the partners.

Two main conditions are required for a cooperative behaviour to be reciprocal, first that the initiator behaves altruistically, which implies at a cost to him, and second that his reward, costly to the recipient, is delayed in time (Axelrod & Hamilton 1981). Moreover, if reciprocal altruism exists not only to enhance inclusive fitness, it should be observed between unrelated individuals and not just between kin. This seems to be the case in stallions. In a herd with many groups and multiple reproductive males, there is a dilemma for any stallion

controlling females when challenged by a rival. He has to keep the rival at bay while making sure his mare(s) are not approached by other males. Stallions overcome this difficulty by forming coalitions where two males support each other. They either confront the intruder(s) together or share the task: while the dominant of the pair drives away the mare(s), the subordinate engages in an encounter with the other stallion(s). This is consistent with Berger's (1986) data on three alliance pairs, where the subordinate on average fought three times more often than the dominant. Guarding the females is less risky than fighting, thus the subordinate has a higher cost.

During a fight both stallions rear up, kicking with their forelegs or trying to bite each other at the throat, neck or legs. The risks incurred during these fights are infected wounds or damage to the legs which may lead to severe limping and can incapacitate a stallion to the point of his not being able to follow his group and permanently losing it as a consequence (Berger 1986; this study). During Berger's 5-year study, he estimated that 3% of all stallions died as a result of fighting. In our herd, no stallion was killed or mortally wounded, but fights clearly are risky and costly in terms of an individual's fitness. Two stallions, a one-male family holder and a subordinate alliance stallion, had reverse melanism (their usually white coat-hair grew black on scars); at the age of 20 in May 1996, the first had 35 permanent scars whereas the second had 146. Besides the risks, fights and displays are energetically costly. I do not have data on direct energy expenditure stemming from the higher frequency of displays or fights for subordinates, but Berger (1986) calculated that one of his dominant alliance stallions spent 7.1 MJ/day less than the subordinate. In domestic horses, the basal rate (digestible energy without work) is 65 MJ/day (National Research Council 1978), so the difference is considerable.

In exchange for his investment in defending their mares, the subordinate stallion gains paternity. Alliance stallions of one family almost never lose sight of each other. Mating needs a minimum of 3 min if the mare is receptive. The position of the stallion during mating is unbalanced, and therefore makes it easy for another stallion to intervene and prevent it. For example, a one-male family holder immediately interferes when another stallion tries to make body contact with one of his mares. The benefit granted by the dominant alliance partner to the subordinate is thus a passive one.

Finally, fights are not immediately related to matings. Although fights are most frequent during the reproductive season, they occur all year round (Feh 1987), whereas the majority of mares are on heat for only a few days per year (Duncan 1992). The reward to the subordinate partner, siring foals, is therefore delayed in time.

These results suggest that the relationship between the two allies contains elements of reciprocity. Although I could not test the Prisoner's Dilemma model or any strategy such as 'Tit for Tat' experimentally, in one case I was able to observe a dominant alliance male punishing noncooperation by the subordinate. In the experiment on the stability of reproductive strategies (see above), the four stallions were filmed individually and continuously

after their release with the new mares. For the first 15 min, the subordinate alliance stallion tried to monopolize a mare on his own without participating in the defence of the dominant's mares against the other stallions. In the 16th minute, the dominant attacked the subordinate repeatedly, tearing out part of his lip. From that moment on, the subordinate cooperated in the defence of the mares. This may imply that in some situations, the dominant may coerce the subordinate into cooperation (Clutton-Brock & Parker 1995).

Authors mostly agree that reciprocal altruism between unrelated mammals is difficult to measure and examples are rare (Harcourt & de Waal 1992; Slater 1994). This study, like Packer et al.'s (1991) on lions, and Connor et al.'s (1992) on dolphins, shows the existence of male alliances in a nonprimate species, the alliance being based on coalitions against rivals with reproductive benefits to both partners.

### Acknowledgments

All my thanks to S. Faraman for teaching me alliances in horses. The long-term study was initiated and supported by the Foundation Tour du Valat. I thank its president, Dr L. Hoffmann and director general, J.-P. Taris. Part of the analysis and writing up was done at LARG, Cambridge University. Many thanks to Professor T. Clutton-Brock and the whole team for stimulating discussions and corrections. Several persons were involved in the data collection, especially Ph. Malkas and J.-C. Gleize. Dr M. Scott from the Animal Health Trust in Newmarket performed all paternity analyses without charge to the project. Long-term financial aid was provided by the Basler Stiftung für Biologische Forschung and the Fondation Tour du Valat.

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