Aggression, dominance, and mating success among capybara males (Hydrochaeris hydrochaeris)

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Aggression, dominance, and mating success among capybara males (*Hydrochaeris hydrochaeris*)

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Social groups of capybaras, *Hydrochaeris hydrochaeris*, averaging 10 adults contained a mean of 3.6 adult males. Of 2911 interactions observed within social groups of capybaras, 34% were among adult males, and these were invariably aggressive. Males were organized in stable, linear hierarchies. The dominant male in each group was significantly heavier than any of the subordinates, but among subordinates, status was not correlated with weight. The dominant male maintained a central position at the core of the group, and time spent in the group by males was correlated with their social status. Each dominant male secured significantly more matings than did each subordinate, but subordinate males, as a class, were responsible for more matings than was each dominant male. Regarding alarm calls, although each subordinate male called less on average than the dominant, subordinates were responsible for the majority of alarm calls in a group. The stability of these hierarchies, in one case over 3 years, and the tendency for males to move up the social ladder in an orderly queue, suggest that many males are unlikely ever to secure dominant status. *Key words:* capybara, dominance, hierarchy, reproductive success. *[Behav Ecol 4:114–119 (1993)]*

Dominance hierarchies are common in group-living species; they may be confined to males (e.g., Appleby, 1980; Dewsbury, 1984; Huck and Banks, 1982), or they may structure the relationship of both sexes as in some primates (e.g., Dunbar, 1984; Hrdy, 1977). Dominance hierarchies can be viewed as a way of limiting aggression within social groups so that both dominant and subordinate animals benefit by reducing costs associated with it (Slobodchikoff and Schulz, 1988; Tinbergen, 1951). Alternatively, "dominant" and "subordinate" may be separate strategies adopted by different individuals and, as such, they may be viewed as the evolutionary resolution of a conflict through a mixed evolutionarily stable strategy (Maynard Smith, 1982). An extreme case of this is exemplified by the two morphs of Coho salmon described by Gross (1985). Despite the fact that the study of dominance has pervaded the ethological literature since its inception, its significance has been questioned (Appleby, 1983; Rowell, 1974).

Capybaras, *Hydrochaeris hydrochaeris*, weigh about 50 kg and are grazing rodents common in the seasonally flooded savannas (Llanos) of the northern Neotropics. They live along the shores of ponds and rivers in stable groups, typically comprising two to five adults of each sex, together with young of the year, which disperse as yearlings (Herrera and Macdonald, 1987). In the Venezuelan Llanos, groups defend territories of some 10 ha, whose borders remain rather stable for 3 years and possibly longer (Herrera and Macdonald, 1989).

Signs of a dominance hierarchy among the males in capybara groups have been mentioned (Azcarate, 1980; Macdonald, 1981a; Schaller and Crawshaw, 1981), but not studied in detail. Here we describe aggressive encounters among male capybaras and how they lead to a dominance hierarchy.

Then we investigate costs and benefits associated with dominance rank, with special reference to mating success. We then analyze the hierarchy's stability and how this relates to fitness among dominant and subordinate males.

STUDY AREA AND METHODS

Capybaras were observed between March and October 1982–1984 around scattered, shallow pools on a ranch, Hato El Frio (7°46′ N, 68°57′ W), in the Venezuelan low Llanos (state of Apure). Here, flat tropical savannas are flooded between May and October and endure drought in February and March, when capybaras suffer a high, density-dependent mortality (Ojasti, 1978).

We marked individuals with expanding plastic collars (similar to those used by Clutton-Brock et al., 1982), painted with unique two-letter codes. We captured individuals each February either by lassoing them from horseback or using a "dog-catcher" noose to "fish" them from thorny thickets of *Cassia aculeata*. Hind-foot length was measured and weight was estimated from a measure of girth (Herrera, 1986).

We selected groups for intensive study on the basis of accessibility and numbers of marked animals. Each group was individually observed in turn for sessions of 2–12 h. Observations were evenly spread throughout the daylight hours for each group. We monitored the size, composition, and movements of other groups regularly but less frequently. Of the groups intensively watched in 1982, only one was recognized in subsequent years, whereas all four groups studied in 1983 (including the one known from 1982) were studied in 1984. Groups are referred to by two-letter mnemonics.

We identified behavior patterns on the basis of

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previous studies (Azcarate, 1980; Macdonald, 1981a). Aggression consists mainly of simple chases in which one animal walks toward another that walks away, and individuals may be classified in terms of a "winner" and "loser" for each dyadic interaction. Retaliation was rare and involved the pursued animal facing its opponent, both individuals rushing toward each other, rearing on their hind legs, and grappling briefly before the loser broke free and fled. We also recorded sexual pursuit and mounting; these behavior patterns were treated as instantaneous events (sensu Altmann, 1974). When alarmed, a capybara usually emits a loud bark, at which its companions stand alert or plunge into the nearest water (Macdonald, 1981a). Alarm calling was also recorded as an event.

State behaviors such as grazing, resting, and wallowing were recorded during scans of the group every 10 min (Altmann, 1974). The rates at which individuals performed event-type behaviors depended on the length of time each animal was in sight, which varied between animals. Therefore, we used the proportion of time each animal was present, calculated from scan data, as a correction factor for behavioral rates. During scan sampling, the position of each animal within the group with respect to three imaginary concentric circles (zones) was recorded, each annulus being of approximately equal width (Macdonald, 1981a). The size of zones did vary, however, depending on how scattered the group was. Thus, animals were recorded as in the core (zone 1), the intermediate zone (zone 2), and the periphery (zone 3). Animals outside the group were assigned to zone 4.

RESULTS

Aggressive interactions accounted for 71.6% of all interactions recorded in all groups during the 3 years (2911 interactions in 729 h of systematic observation). The rest of the interactions were other event-type behaviors, which included social interactions such as sniffing another individual, a type of grooming, and alarm calling. Scent marking is not included in this sample. At least one male was involved in 81.3% of all aggressive interactions, and 58% occurred between two males. Thus, aggression between males made up 34% of all observed social interactions. Aggression between females was much less frequent (8.3%).

We then constructed the dominance matrices (one for each group–season) following Brown (1975) and Martin and Bateson (1986). In a dominance matrix, entries indicate the number of times each animal in a row beats each animal in a column. Individuals are then ranked so that the lowest numbers appear on the lowest half of the matrix. Table 1 shows examples of hierarchies. In one case, scores were balanced in a draw, and the animal winning the greater proportion of his aggressive interactions (including those against unidentified males) was assigned the higher rank.

In each group, dominance relations among males were clear-cut: in the majority of dyads one individual invariably won. There was only one case of a reversal, indicating that the hierarchies were strongly linear. However, according to critics of earlier studies (e.g., Appleby, 1983; Rowell, 1974), two conditions are necessary if a hierarchy is to be

Table 1

**Dominance matrices for identified males in the groups of capybaras studied**

Winner	Loser			
	WSC	WTC	OJX	Unknown
Group C1, 1983				
WSC	—	0	24	14
WTC	0	—	1	1
OJX	1	0	—	4
Unknown	0	1	1	(3)

	R15	WTE	WNA	1DG	Unknown
Group NC, 1983					
R15	—	15	9	3	39
WTE	0	—	8	0	8
WNA	0	0	—	1	3
1DG	0	0	0	—	0
Unknown	0	1	16	12	(18)

	I65	G14	WW7	W14	Unknown
Group P5, 1984					
I65	—	4	5	4	16
G14	0	—	1	4	11
WW7	0	0	—	3	4
W14	0	0	0	—	1
Unknown	1	0	4	18	(13)

	1BY	WJU	DII	Unknown
Group VQ, 1984				
1BY	—	16	5	8
WJU	0	—	1	6
DII	0	0	—	0
Unknown	0	0	0	(3)

Row animals are winners and column animals are losers. Entries are total numbers of interactions in each dyad. The last column and the bottom row are outcomes against unidentified males. The numbers in parentheses at the bottom right corner of each matrix correspond to the total number of interactions seen between unidentified males and do not indicate which animal won. They are shown in parentheses because they are not the sum of their respective columns or rows, nor the total number of interactions in the group.

considered linear: (1) Dominant–subordinate relationships must be statistically significant and long-lasting, and (2) all dyadic relationships must be asymmetrical and all possible triadic relationships must be transitive, i.e., if A dominates B and B dominates C, then A should also dominate C. In the present study, the top dominant position in each group was invariably clear, so the problem of linearity lies within relationships among subordinates.

Using the binomial test (Siegel and Castellan, 1988) for those cases with five interactions or more ($n = 19$), we found that all asymmetries in dyadic relationships were significant (4 at $p < .05$ and 15 at $p < .01$). The rarity of aggression led us to define a permanent relationship as one in which at least two interactions were recorded. Of 16 such cases among the subordinates, one was a 1–1 draw, another was 24–1, and the rest were all n–0 wins.

Figure 1
The relationship between body weight and dominance rank of male capybaras in study group CZ during the 1982 field season in the savannas of Venezuela.
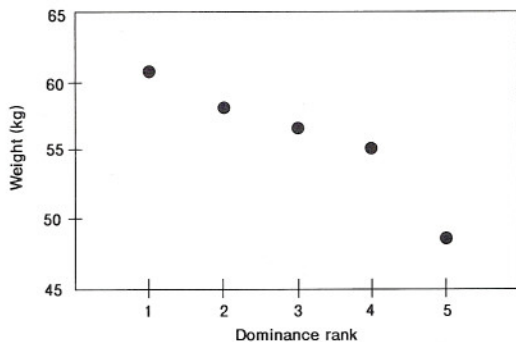
Therefore, with one possible exception, all dominance relationships among capybara males were permanent.

Considering 17 triads in which each of the three pairs had interacted aggressively at least twice, all of 13 such triads that included the dominant male, and all of four that were among subordinates, were transitive. The dominance hierarchy among marked adult males in groups of capybaras of the Venezuelan Llanos is, therefore, strongly linear.

Correlates of rank: benefits and costs

Weight was significantly correlated with rank (pooling all group–seasons, Spearman rank correlation coefficient $r_s = -.457$, $n = 37$, $p < .01$). Although it would have been more appropriate to calculate a correlation coefficient for each group, low numbers of identified males precluded this. Figure 1 illustrates the hierarchy in the group for which the most complete data were available.

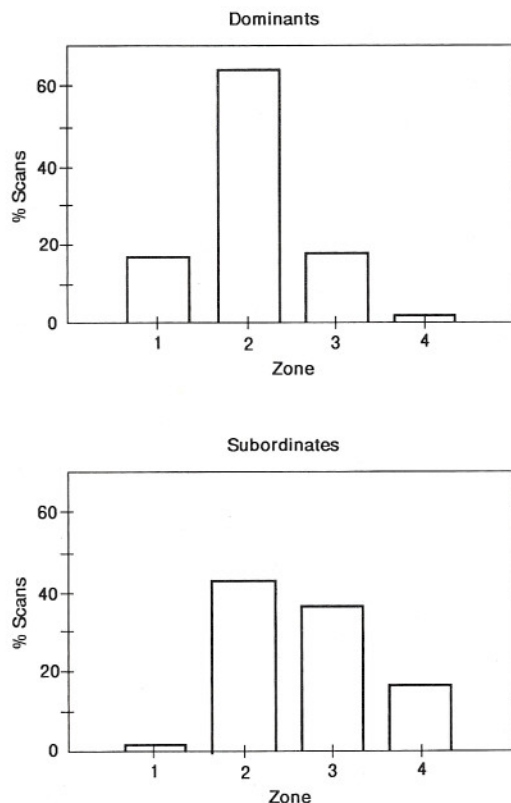In four of five cases, the heaviest male was the

Figure 2
Histogram of the percentage of observation scans that dominant and subordinate capybara males spent in four concentric zones away from the center of the group. Zone 1, innermost; zone 4, outermost.

highest ranking. Among subordinates the weight–status relationship was less clear, and, if dominant males are excluded from the pooled data, the correlation between weight and rank is lost ($r_s = -.292$, $n = 26$, ns).

Dominant males were found near the core zone of the group significantly more often than were subordinates (using a subsample of independent scans: $\chi^2 = 299.03$, df = 3, $p < .001$; Figure 2; independent scans were obtained by using only those contiguous scans in which at least 50% of the animals had changed behavior or else used scans at least 3 h apart). No animal was present 100% of the time, so the presence of each was analyzed as a proportion of the total time the group was watched. Time spent in the group by males was significantly correlated with rank ($r_s = -.633$, $n = 53$, $p < .01$), although not if dominant males are excluded ($r_s = -.145$, $n = 38$, ns). Thus, to the extent that presence in the group is advantageous, and despite a linear hierarchy among all males, it seems that the important distinction lies between the dominant males and all other males.

Rank did not affect the percentage of time spent feeding in good-quality feeding habitat (as ranked by Herrera and Macdonald, 1989; $r_s = -.122$, $n = 53$, ns). Nonetheless, field observations indicated that dominant individuals had priority of access to food: Characteristically, a subordinate grazing on a particular patch of grass would move if a higher-ranking animal arrived to feed there. Similarly, dominant males commonly displaced subordinates from wallowing sites. One interesting example of resource monopolization by a dominant individual was observed in group CZ on 29 June 1982. A yellow-headed caracara (*Milvago chimachima*) was gleaning for ticks on a subordinate (a symbiosis described by Macdonald, 1981b). The dominant male approached, ousted the subordinate, and thus usurped the attentions of the bird.

We have investigated three costs to which dominants might be subject: (1) energy expended while chasing other males, (2) risk of injury from retaliation, and (3) shortage of time for feeding, etc., due to preoccupation with shepherding subordinate males. Capybaras are subject to predation, principally by feral dogs and caiman. Although it is conceivable that the dominant male is more at risk while preoccupied with chasing subordinates, we have no evidence for this.

With respect to energetic demands, the number of aggressive interactions initiated per unit time correlates significantly with rank ($r_s = -.777$, $n = 53$, $p < .01$). However, the number of aggressive interactions received per unit time correlates with decreasing rank ($r_s = .595$, $n = 53$, $p < .01$). Because winning and losing appear equally costly (both animals cover the same distance at the same speed), the costs of aggression for animals of all ranks are approximately the same. We do not know whether there is a stress-related cost associated with being chased. The risk of injury seems to be small because subordinate males rarely retaliated. On the other hand, subordinates sometimes suffered serious gashes to their rumps as they fled, although these wounds were generally confined to males that lived on the periphery of the group to the extent of being solitary.

There was no correlation between rank and feed-

Table 2
Alarm-calling bouts recorded for each age–sex status class

Class	N	%	Expected[a]	Observed	χ^{2b}
Dominant male	7	11.9	4.4	7	1.54
Subordinate male	23	39.0	16.9	23	2.20
Female	14	23.7	22.7	14	3.33

[a] Expected values are calculated from the average ratio of dominant:subordinate:female of 1:3.8:5.1.
[b] Total $\chi^2 = 7.07$, df = 2, $p < .05$.

ing rate ($r_s = -.121$, $n = 53$, ns), nor any difference in feeding rates between dominant males as a whole and subordinates (Mann-Whitney U test, $p = .542$, $n_1 = 15$, $n_2 = 36$). Thus, there is no indication that subordinate males had more time for feeding than dominants.

Rank and mating success

Capybaras invariably mate in water. During the mating season dominant males conspicuously patrol their females. When a female is in estrus, the dominant will follow her avidly, frequently sniffing her vulva. The consorting pair enter the water and swim around for several minutes, the male continuing to follow the female closely. The female may lead the male out of the pond for a wide detour on land and then lead him again into the same or another pond. Swimming in her wake, the male will try repeatedly to mate the female, during which she is forced under water by his weight. In general it seems that while in the water the female can control mating by swimming down beneath the male's grasp when he tries to copulate. By prolonging the mating ritual, the female allows a more dominant male to chase the consorting one, indirectly exerting mate choice. Sometimes subordinate males will enter the pond with the mating pair and watch them intently, occasionally trying to mount the female while the dominant male is distracted.

In the absence of genetic data with which to assess paternity, we estimated reproductive success from observations of sexual behavior. The data used were the numbers of matings by identified males that achieved intromission. Of these, during 3 years, 15 successful matings were performed by dominants and five by identified subordinates. Taking into account that there are 15 dominants (15 group–seasons) and 38 identified subordinates (0.39:1, dominants: identified subordinates), the expected numbers of matings by each class differed significantly from the numbers observed ($\chi^2 = 21.2$, df $= 1$, $p < .005$). It is noteworthy that subordinate males did secure copulations; in a separate sample the total number of females that mated (12) with all subordinate males exceeds that with all dominants (8).

Males commonly interfered with sexual pursuits initiated by other males. Of sexual pursuits initiated by subordinates, 53 (29%) were interrupted by the dominant male and 11% by other, higher-ranking subordinates. Most of the remainder failed because the female evaded the subordinate, and none was interrupted by lower-ranking males. Dominant males had to stop their mating pursuits seven times (11% of all pursuits started) to prevent a subordinate from mating with another female.

Alarm calling and rank

Table 2 summarizes the frequency of alarm calling by age, sex, and status. Using the proportion of each age–sex class, the expected frequencies of alarm calling for each were calculated. Females called less frequently than expected, whereas dominant and subordinate males called slightly more often than expected ($\chi^2 = 7.07$, df = 2, $p < .05$). Overall, a group received most warnings from subordinate males, the category that was most populous and that predominated, perforce, at the periphery of the group.

Stability of the hierarchies

The dominant position in hierarchies appeared to be very stable. For instance, male I65 of group P5 was dominant for all 3 years of the study, and during 126 h of observation and 88 interactions, he was challenged only three times. Groups VQ, C1, and C2 each had the same dominant males in 1983 and 1984.

Two takeovers were documented. Between 23 March and 30 April 1982, male D02 was dominant in group CZ. In the morning of 30 April, group C2 rested alongside another group (as is often the case in the dry season; Herrera and Macdonald, 1987), and an unidentified male chased D02. This protracted interaction led the combatants to walk past male D86, whose group affiliation was unknown. Male D86 attempted to bite D02, who immediately withdrew. D86 then chased the unidentified male, who had initiated the attack on D02, but this male retaliated and no winner emerged. For the next 2 h, D02 sat alone about 30 m from group CZ. When CZ was next seen, 1 week later, male D02 had disappeared and D86 was clearly dominant. Male D02 was never seen again in the CZ group territory; D86 remained unchallenged throughout 1982. D02 was seen subsequently some 800 m (about twice the average range width) northwest of his former territory, in a group of six obviously younger animals. He won all nine interactions in which he was involved that year, and was seen throughout the following year in the same area and probably in the same company. In 1983, male R15 was dominant in group NC, and when challenged once by WTE (number 2 in the hierarchy), R15 retaliated and wounded his opponent's face. By 1984, R15 had disappeared, WTE was dominant, and WNA, previously number 3, was number 2.

DISCUSSION

The existence of dominance hierarchies has been known for centuries, and they have been a peren-

nial topic for ethologists since Schjelderupp-Ebbe (1922) formalized the idea of a pecking order among chickens. Nonetheless, studies demonstrating the existence of clear-cut linear dominance hierarchies in wild mammals under natural conditions with an effect on mating success are few, and none concern caviomorphs. Dominance hierarchies have frequently been dismissed as artifacts of captivity (Rowell, 1974). Many studies of dominance in nonprimate mammals have been carried out in captivity (e.g., Dewsbury, 1984; Reinhardt, 1985; Shapiro and Dewsbury, 1986), and work on rats (*Rattus norvegicus*) demonstrates the importance of studying dominance under natural conditions (Berdoy M, Macdonald DW, and Smith P, in preparation). Our findings indicate that, in the case of the capybara, dominance relationships are extremely clearcut: only in 2 cases out of 50 dyads (4%) did any rank reversal occur (and this occurred only once in each case). Most dominance hierarchies reported in the literature have been based on less incisive asymmetries (Appleby, 1983). What, then, has favored the development of such a clear-cut linear hierarchy among male capybaras?

For any male, being a member of a group is crucial to survival because outside of groups the probability of survival and reproduction may be negligible. In the Llanos, group living is important for capybaras' survival and reproduction. Groups monopolize access to essential resources such as water and grass (Herrera and Macdonald, 1989), and members of larger groups probably benefit in antipredator terms (Herrera, 1986; Macdonald, 1981a) and certainly benefit through increased reproductive success (Herrera and Macdonald, 1987). Indeed, groups smaller than four adults failed to rear any young (Herrera and Macdonald, 1987). Some adult capybaras spend much of their time alone, and these are invariably male (Macdonald, 1981a), but even these solitary males try, at least intermittently, to insinuate themselves into a group (Herrera and Macdonald, 1987). Outsiders enjoy none of the antipredator advantages of group membership. They are harassed by territorial groups, probably have limited access to critical resources (Herrera and Macdonald, 1989), and certainly have no access to females. For such solitary males, group membership under almost any terms would seem preferable. Whitehead (1990) devised models to predict the conditions under which a male should join a group of females or move between groups of females, with special reference to large mammals. He found that when females are grouped, being resident was an evolutionarily stable strategy for males.

The alternatives are, thus, to form bachelor groups or to be a member of a mixed-sex group and thus tolerate subservience to and harassment from a dominant male. We have demonstrated that the latter option has the major advantage of allowing the possibility of mating. Indeed, bachelor groups of capybaras have not been recorded. There are no hormonal studies of male capybaras, but Sachser and Prove (1986, 1988) demonstrate a correlation between social status and concentration of testosterone in the blood in the capybara's closest relative, *Cavia aperea*.

Why do dominant males tolerate subordinates? It seems likely that subordinate males bring several advantages to dominant males: first, they participate in territorial defense (Herrera and Macdonald, 1987; see also Davies and Houston, 1984), and second, as a class, they give off more warnings as alarm calls than other group members. Although the subordinates' alarms benefit dominant males, they may also benefit the subordinates (see Sherman, 1985). If McNaughton's (1984) suggestion that group grazing increases primary productivity is correct, the presence of subordinates may bring foraging advantages during the growing season.

In terms of cost to the dominant male, the greatest is probably the matings lost to subordinates. As females come into estrus synchronously, it is inevitable that the dominant male will lose some matings to subordinates (see Ridley, 1986). Females cycle every 7 days unless pregnant, and receptivity lasts possibly only 8 h (Lopez-Barbella, 1982, personal communication). The loosely knit cohesion of capybara groups and the lumbering morphology of the species combine to make it very difficult for a single male to keep at bay even one, far less several, persistent interlopers. This is evidenced by the plodding persistence with which dominant males chivvy their rivals to the periphery of resting groups (described in Macdonald, 1981a), by the fact that larger groups have a retinue of more or less closely affiliated "hangers-on" (Herrera and Macdonald, 1987), and by the very protracted efforts involved when attempts are made to drive off an intruder (detailed descriptions in Herrera, 1986; Macdonald, 1981a). The cost of excluding interlopers may be heightened because capybaras, by virtue of their body size and paucity of sweat glands (Pereira et al., 1980) may live on the threshold of thermal stress.

These arguments explain the presence of more than one male in groups, both from the dominant's and the subordinate's points of view. But the formation of a hierarchy remains unexplained. Using game theory, Maynard Smith (1982) has shown that subordinates and dominants may be the two alternatives in a mixed evolutionarily stable strategy (ESS) for competing animals living in groups. In his model, other alternatives lead to disadvantages on both sides and thus reversion to the hierarchy. Slobodchikoff and Schulz (1988) also found, in a theoretical analysis, that when resources are abundant, both dominant and subordinates benefit from sharing.

Clearly, avoiding injury while obtaining some benefits and perhaps securing a chance to succeed eventually to a higher status seems a favorable compromise when compared to a solitary life or fighting. The ESS model does not incorporate the possibility that male capybaras in a hierarchy are queuing to inherit the dominant position, and thus that both subdominance and dominance are a continuum and therefore part of the same strategy, being stages through which each individual graduates as it ages (as in male rats; Berdoy et al., in preparation). Age and size are correlated in male capybaras only up to about 2 years or 40 kg (Ojasti, 1973). The predictions of both the ESS model and the queue model are compatible with our observation that where a dominant disappeared, the second and third subordinates became numbers one and two. The question is whether most individuals get a chance at both roles.

Our evidence suggests that most individuals do not get a chance at both roles and that once attained, dominance is retained for the long term. One male, already dominant at the start of our study in February 1982, was still dominant at the end in October 1984. Four other males retained dominant status from 1983 to 1984. In two cases where at least two subordinates were known for 2 years, their relative positions remained the same. Thus, the hierarchies seem to be quite stable over relatively long periods of time. Because capybaras in the llanos have a life span of 6–7 years (Ojasti, 1973) and a typical group may contain three to four adult male subordinates, it seems highly improbable that all subordinates can reach dominant status within their lifetimes. Therefore, it seems likely that at least in some cases, and possibly most, a dominant male remains such for much of his adult life, while others remain subordinates. To have any chance of becoming dominant, it is in the interest of each animal to be as close to the top as possible and therefore to maintain its relative position. Because this is occurring at all levels and in all dyads, the overall result is a linear hierarchy.

There is evidence indicating that some subordinate males accompany yearlings as they disperse in groups (Herrera and Macdonald, 1987), presumably to become dominant in these incipient social units. In the only case (out of 10) where the rank of the recruiting male was known, he was lowest (third). Perhaps low-ranking males, whose chances of reaching the top within their natal group are low, may opt for this alternative, which is doubtless a risky one because successful establishment of a new group in good habitat is rare (Herrera and Macdonald, 1987, 1989).

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