

A new model of fission in primate troops

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Consider a group of animals, with a fixed linear hierarchy, which is forced to split, owing to ecological or other factors. If rank promotion is the main consideration of individuals in choosing which of the two daughter groups to join, they should adopt the simple splitting strategy we describe here. This strategy, which we term Abandon Your immediate Superior (AYS), instructs its holders to join whichever new group has not been joined by their immediate superior in the hierarchy. We show here that this strategy was indeed adopted by the females of a troop of chacma baboons, *Papio cynocephalus ursinus*.

The AYS strategy has some desirable properties which tend to make it stable. If it is adopted by all individuals, then each one, except of course the top ranking member of the original troop, enjoys a rank promotion. Moreover, no individual adopting a different strategy can do better, in terms of rank improvement.

As an illustrative example, consider an original troop of six females (denoted, according to their ranks, by 1, 2, 3, 4, 5 and 6). Under the AYS strategy, a split results in the new groups {1, 3, 5} and {2, 4, 6}. If, on the other hand, these females split horizontally in terms of dominance rank, resulting in {1, 2, 3} and {4, 5, 6}, such a split, although it is more advantageous to certain females (e.g. 4 and 5), would be unstable: there is an advantage to 2 and 3 to move to the other group, and as a consequence, to 4 and 5 not to remain in that group, and so on.

Although the AYS strategy is similar to an evolutionarily stable strategy (Maynard Smith & Price 1973), it is not identical because it does not fulfil the second requirement of its definition. While no mutant strategy can do better, there are strategies

that can do just as well. These are the strategies that instruct their holders to depart from their immediate superior if their rank in the original group was an even number (i.e. rank position 2, 4, etc.), whereas if their rank was an odd number (position 3, 5, etc.), they are free to join either group. Thus, AYS is only collectively stable (Axelrod 1984): it is a strategy that is in Nash equilibrium with itself. Nevertheless, AYS is both simpler and more robust than any equally valid alternative, since it does not require an individual to know its numerical place in the hierarchy. It is interesting to note that the AYS strategy is somewhat analogous to Fretwell & Lucas' (1970) concept of an ideal free distribution, with dominance hierarchy as the spatially distributed 'resource'.

We saw an apparent case of AYS in a troop of chacma baboons (Mtshopi Troop) at Mkuzi Game Reserve, Zululand, South Africa, which we observed for over 1200 h during 18 months between January 1989 and November 1991. The troop grew from about 44 individuals in June 1986 to about 76 in March 1990, including eight adult males, 17 adult females, six subadult females and about 45 immature individuals. All adults were individually identified, but relatedness between females was unknown. Dominance rank was established through win-loss matrices of the outcomes of all recorded agonistic encounters. By May 1990, following a long phase of social instability, the troop divided into two: about 43 members in Darth's Troop and 33 in Flash's Troop.

Most of the females of Mtshopi Troop adopted the AYS strategy (Table I). Of the 22 females (excluding Peri, the top-ranking female), 18 abandoned their immediate superior in rank, and only four joined the same new troop as their superior. Under the assumption of random splitting for example, the number of abandonments should follow a binomial distribution, with parameters

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Table 1. The splitting pattern of the Mtshopi Troop females

Female	Original rank	New troop	New rank	Female associates	New troop	Male associates	New troop
Peri	1	D	1	Mel Jes Mod	D D D	Flash	F
Bonni	2	F	1	Lucy Tina	F D	John	F
Doris	3	D	2	Tina	D	Darth Flash	D F
Suzy	4	F	2	Alice Flaggy Lucy	F F F	Flash	F
Joan	5	D	3	Lucy	F	Ringo Flash	D F
Jes	6	D	4	Mel Peri Pitzi	D D D	Ter	D
Katy	7	F	3	Mel Honey Doda	D F D	Ter Darth	D D
Mel	8	D	5	Peri Jes Katy Extra	D D F D	Ter Darth	D D
Alice	9	F	4	Honey Suzy Lucy	F F F	Flash	F
Mod*	10	D	6	Peri Tina	D D	SAM Darth	D D
Flaggy	11	F	5	Suzy Esti	F D	Flash John	F F
Doda	12	D	7	Katy Honey	F F	Flash	F
Tiki	13	F	6	Honey	F	Flash Ringo	F D
Esti	14	D	8	Flaggy Crabs Gili	F F F	Darth John	D F
Lucy	15	F	7	Bonni Alice Suzy Joan	F F F D	John	F
Tombi*	16	F	8	Grazia	F	Darth	D
Extra	17	D	9	Mel	D	Goose	F
Gili	18	F	9	Esti	D	John	F
Honey	19	F	10	Alice Katy Doda Tiki	F F D F	Flash	F

Table I. Continued

Female	Original rank	New troop	New rank	Female associates	New troop	Male associates	New troop
Tina*	20	D	10	Doris Bonni Grazia Mod	D F F D	SAM Darth	D D
Grazia*	21	F	11	Tombi Tina	F D	SAM SAM Ringo	D F D
Crabs*	22	F	12	Esti Pitzi	D D	Darth SAM SAM	D F D
Pitzi*	23	D	11	Jes Crabs	D F	SAM Arc	D D

*Subadult females; SAM = Subadult males. The original rank order of females in March 1990 is given; a new troop affiliation (D = Darth's Troop; F = Flash's Troop) and new rank of each female, after fission, in May 1990; female associates with whom each female spent over 15% of her socializing time with females, prior to fission, and their new troop affiliation; and male associates with whom she spent over 25% of her socializing time with males, prior to fission, and their new troop affiliation.

$N = 22$ and $P = 0.5$, and the probability of obtaining at least 18 such abandonments (given that a split actually occurred) is only 2.17×10^{-3} . As predicted by the AYS strategy, the Mtshopi Troop divided into two daughter troops with an almost equal number of females (11 and 12).

Only two of the four females who did join their immediate superior, Jes and Crabs, could improve their new rank by choosing the other troop. Tombi's choice of the same troop as her superior improved her own rank by correcting the deviation created by Jes. Honey, who occupied an odd rank position, could do just as well by joining either troop. Jes was a very old female and had all of her female and male associates in Darth's Troop, which she chose to join in spite of the consequent loss of one rank position. Crabs' choice of Flash's Troop was only temporary and she later moved to Darth's Troop, where she improved her rank (and joined her associates).

Female baboons and macaques tend to form linear and stable dominance hierarchies, where they associate closely with their kin, who also occupy adjacent ranks (Hausfater et al. 1982; Dunbar 1988). These dominance hierarchies are stabilized through support coalitions within and between dominant matrilineal groups against lower ranking ones (Samuels et al. 1987; Dunbar 1988; Chapais

et al. 1991; de Waal 1991). Troop fission usually occurs when lower ranking matrilineal groups withdraw from the original group, and is therefore horizontal in terms of female rank (Chepko-Sade & Sade 1979; Dunbar 1988; Prud'Homme 1991; A. Whiten, personal communication). The significance of this is assumed to be in retaining the social alliances necessary for successful social functioning (Dunbar 1988; de Waal 1991). Some data suggest that females join the same troop as their male allies (Prud'Homme 1991; Hamilton & Bulger 1993).

Females at Mkuzi did not necessarily choose to retain their social associations. Any splitting of the original group into two distinct new groups would have resulted in breaking some of the 27 female associations that existed prior to fission. If we consider only splits into groups of 11 and 12 females, some would have retained 24 pair-wise associations. The actual split of the group disconnected 10 and retained 17. However, under the assumption of random splitting, the estimated probability of retaining at least 17 associations is 0.1216. (This estimate was obtained by randomly drawing 10 000 splits, out of the $2^{22} - 1 = 4194303$ possible splits, and calculating the proportion of splits that retained at least 17 associations.) The apparently large number of associations that were retained is, therefore, not significantly larger than that one

would expect under the assumption of random splitting.

Eighteen of the females joined a troop where they had at least one male associate, and only five joined a troop where they had none. This seems to indicate the importance of keeping associations with males in deciding which troop to join. However, 17 of the females who kept any of their male associations also used the AYS strategy. Of the six females for whom there was a choice between choosing the AYS and keeping male associates, five adhered to the AYS strategy and abandoned their male associates, while only a single female (Jes) favoured joining her male associate rather than rank promotion. This suggests that females preferred the AYS to keeping male associates.

Thus, improving individual rank seemed to be the major consideration for the Mtshopi Troop females in choosing a new group. This may be explained by the fact that, although high rates of female aggression were recorded at Mkuzi, almost no support coalitions were observed.

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