

Ruths amid the alien corn: males and the translocation of female Chacma baboons

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Among the primates, Old World monkeys (superfamily Cercopithecoidea) are distinguished by social systems in which females are philopatric¹ and males emigrate at sexual maturity. Females therefore spend their lives among same-sex kin, and have evolved a suite of strategies, in which kin associations feature prominently,² to deal with the conflicts of reproductive interest that must result from the need for such groups to cohere in the face of predation.³ It has been argued, both generally⁴ and for baboons (*Papio cynocephalus*) in particular,³ that troop fission is the one way that females can respond to an unacceptable increase in resource competition as group size increases; lower-ranking females can simply depart in the company of kin⁵ and, by living in a smaller group, re-set the activity budget schedule to their advantage.³ One thing that a female living in such 'female-bonded'² systems should not do is transfer to another established group, in the manner of males, since she would then live her life amongst strangers, without the benefit of kin assistance.

Chacma baboon (*P. c. ursinus*) females, however, appear to provide an interesting exception to this general rule. In the Suikerbosrand Nature Reserve, south-southeast of Johannesburg, females have been seen to transfer between troops with a frequency⁶ that makes it difficult to argue that these are stochastic accidents. Anderson⁶ proposed that such transfers, in the absence of predation, represented attempts to increase reproductive success through the improvement in mate choice opportunities. However, female transfer has not been recorded from other chacma study populations and so may represent merely one, rare, consequence of the fact that female baboons, though philopatric, are not female-bonded. In the absence of within-group competition, it is argued that female baboons focus their social attention on males, leading to reduced

ties with female kin.⁷ While there is doubt about this,⁸ it is true that, unlike other subspecies, troop fission in chacmas is not characterized by the departure of matriline and appears linked to particular males.⁸⁻¹⁰

Is it the case that female transfer and male-focused fission are equivalent expressions of dissatisfaction with life in the natal group? The fact that our two study troops (ST, VT) at De Hoop Nature Reserve¹¹ now each contain an adult female born elsewhere confirms that female transfer is not restricted to Suikerbosrand, while observation of the process of transfer provides us with a unique opportunity to assess the nature of the decision-making underlying each event. As the circumstances were very different, we describe each event below, before considering the implications for baboon socioecology.

1. A group of three baboons — an adult male (Jo) together with an adult female (Fl) and her dependent offspring — were first seen moving as an independent unit on 8.12.1997. Between this date and 1.3.1998, the unit was occasionally seen in the vicinity of both study troops without any evidence of antagonism from either. On 2.3.1998, it was recorded as being within 30 m of ST. From this date until 3.4.1998, its presence in ST was intermittent and peripheral, although we observed resident females grooming both the new male and female. Between 6.4.1998 and 29.4.1998 the unit was mostly absent from ST, being seen on its own as well as with a third troop (LT), on which occasion we also observed an ST female (Be) in its company, she having gone directly from ST to LT in order to sexually solicit Jo. This female remained with the unit in LT for four days before returning to ST. When the unit itself returned to ST on 29.4.1998, Jo immediately consorted Be. From this date to 21.6.1998, the unit was recorded as present in ST, with the female generally being very peripheral. On this date, ST foraged near VT and when VT moved off, the small unit moved off with them. On 22.6.1998, ST and VT had an aggressive inter-troop

encounter, which ended with the two troops moving in opposite directions. The unit male, Jo, remained with VT while the female and her infant crossed back into ST. On the next day (23.6.1998), Jo was observed attempting to consort a VT female. Later that day ST approached to within 30 m and the unit female and her infant were observed. Jo made no effort to interact with her. From this point until the present (30.6.1999), Jo has remained with VT. Subsequent observations on ST have been more sporadic, owing to a shift in their home range, but Fl and the infant were still observed with them on 17.8.1998. She was the lowest ranking female in the troop.

2. In March and April 1998, an epidemic killed 44 animals in two baboon troops, one of which was VT, while the other was a neighbour, HT.¹¹ On 20.5.1998, the six remaining members of HT (not five as originally reported) — two subadult males (Ry, La), three adult females (Li, Ei, Fa) and a juvenile female (Xe) — were observed on the periphery of VT. Li was pregnant and Fa was sexually swollen. Although the HT unit was not seen on 25.5.1998, it was, otherwise, consistently with VT until the period beginning 29.6.1998, after which it occasionally moved on its own, either joining up at some point during the day or sleeping at a different site. Prior to 22.10.1998, the male La left the troop and by that date so had Ry and Li. On 18.11.1998, Ei was recorded as absent. La subsequently spent some days with the troop in mid-1999 while the others formed a small group that avoids VT when they are in the vicinity. The female Fa has, with the juvenile Xe, remained in VT, giving birth on 10.3.1999.

We collected data on the behaviour of the HT unit from the time of its arrival. La, due to the absence of other adult males in VT,¹¹ was immediately top-ranking, a status he held until, after a period of instability and aggression, he ceded it to Ry. Soon after this La left. Ry was thus the alpha male at the time of his own departure. In opposition to the two males, the three females were both spatially and socially very peripheral. They were lower-ranking than all VT females, a status indicated, despite the absence of directed aggression, by their avoidance of resident females. Activity data indicated that HT females were never seen to groom VT females, confining their few social interactions to males and juveniles. While HT females were as likely to have a VT female as their nearest neighbour as

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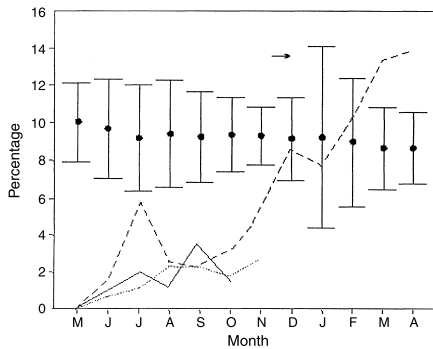


Fig. 1. The proportion (with 95% confidence limits) of all 30-min scan samples of activity in which data were collected on individual resident females in VT. We use this as a metric of 'centrality', since we attempted to place ourselves in such a position during scans in order to maximize the number of visible animals. The data indicate that the representation of individual females was constant. In contrast to this, we only infrequently collected data on the three HT females: Ei (dotted line), Li (continuous line), and Fa (broken line), which we take as a measure of their peripheralness.

they were to have another HT female, they kept a significantly greater distance from the former [10.8 ± 7.9 (s.d. m)] than they did from the latter (6.3 ± 5.2 m. $t = 3.64$, d.f. 200, $P < 0.001$). However, once the other two HT females departed, Fa showed a dramatic shift into the centre of the group (Fig. 1, arrow) that has been sustained after the birth of her infant.

These two events add to the sparse accounts of the fusion of wild primate groups.¹²⁻¹⁵ They also confirm, for baboons at least, that it can occur in the absence both of ecological competition^{13,14} or of predation risk setting a lower limit to independent group size.⁴ None of the groups competed for resources and, in the wake of the epidemic, the HT unit would, in any case, have experienced a short-term release from local competition. While leopards occur in the reserve, there have been no sightings in the home ranges of our troops; besides, both small units voluntarily spent time alone after joining the larger troop. At the same time, neither of these events represents a classic example of fusion. In both, the immigrating unit itself dissolved, with one or more members emigrating, resulting in the observed long-term outcome whereby each troop gained a single non-natal adult female.

This is interesting for two reasons. First, it is clear that these transfers were the unintended consequence of female association with males. In each case, fusion was driven by a male, or males, who gained a reproductive advantage by doing so. Whereas the adult sex ratio

in the unit of three was 1:1, joining ST increased this to 2.67 females per male (3 males: 8 females). The same is true for the HT unit, where the ratio increased from 1.5 females to 2.4 on joining VT (5 males: 12 females). It is known that male baboons can assess sex ratio¹⁶ so, from their point of view, fusion made excellent sense. Subsequent decisions to depart were equally likely to be based on an ability to gain access to females. Reproductive access in chacma baboons is determined by dominance rank¹⁷ and both La and Jo departed after the loss of, or failure to gain, alpha status. Unfortunately, we cannot explain the departure of Ry, who left VT while dominant. Nevertheless, the point remains that females who are associated with males, either by design or default, cannot deflect them from the pursuit of reproductive opportunities elsewhere and, in being reluctant to exist without a male presence, must therefore follow them into strange troops. The socioecological significance of this is that the populations of small, one-male units argued to be the constraint-free condition of savanna baboons⁷ are rarely likely to be achieved. Given stochastic variation in sex ratio, either additional males will join small units⁹ or the males in those units will merge them into others. Indeed, in the Drakensberg, the one population where such an outcome is most likely, and where females do follow males to form new units⁸, the occurrence of one-male units is no greater than chance.¹⁸

Second, while females may passively follow males into troops, our data indicate that the resultant female transfer is a consequence of the fact that they do not necessarily passively follow them out again. Despite being very low ranking, peripheral, and without adult kin, two females chose to remain in their new troops. Both could easily have followed the males, as Ei and Li did. Their failure to do so, given that our observations suggest that Jo and Ry were the probable fathers of Fl's and Fa's infants, has a significant bearing on our analysis of female relationships. We have argued elsewhere⁸ that fission in chacma baboons is linked to the departure of the fathers of offspring, something which the independent existence of the small unit of three suggests may be the case at De Hoop. Yet, here we have two females, opting to remain alone in non-natal troops, despite the known occurrence of infanticide in the population (unpublished data). Chacma females are unusual. Although they are female-bonded in at least three populations with

very different competitive regimes, these bonds do not underpin alliances as expected⁷ and do not deter them from leaving their natal troops in the company of males with whom they may or may not have close social ties other than shared parentage,⁸ and with females who also need not be friends.⁸⁻¹⁰ Our observation that they are capable of choosing to live among strangers after inadvertent translocation, and to adjust to their changed circumstances (see Fa's shift in Fig. 1) simply compounds our ignorance of the fundamental basis of their sociality, while suggesting that unraveling it will be of value to our understanding of primate socioecology.

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