Infants as a commodity in a baboon market

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We used data from adult female chacma baboons, *Papio cynocephalus ursinus*, to provide the first test of hypotheses on interchange trading and the structure of a biological market (Noë & Hammerstein 1994, *Behavioral Ecology and Sociobiology*, **35**, 1–11) within a primate group. The interchange commodities selected were grooming and handling of infants less than 3 months of age. Patterns of grooming in relation to infant handling showed strong evidence for interchange. Grooming for infant access was initiated by potential handlers and was significantly likely to be nonreciprocated. More critically, the data show that infant 'supply' created a market effect: grooming bout duration (the price 'paid' for handling) was inversely related to the number of infants present in the group. In addition, there was an inverse relationship between grooming bout duration and the rank distance between mothers and handlers, suggesting that higher-ranking mothers could demand a higher price for infant handling. Where rank distance was high, females were able to handle infants without grooming. Dominance could thus be used to disrupt the infant market effect. If biological markets models are to be fully applicable to primate groups (and those of other social mammals) then the potentially distorting effect of dominance needs to be incorporated into the framework.

The biological markets approach to the analysis of social dynamics represents, potentially, a valuable alternative to models based on reciprocal altruism. The problem of defection, which afflicts the latter (Roberts & Sherratt 1998; Barrett et al. 2000), is avoided by the central tenets of biological markets. These are (1) that different commodities can be traded for mutual benefit and (2) that partner choice is enabled by competition within trader classes (Noë & Hammerstein 1994). Where, therefore, animals can acquire something of benefit by offering a commodity of their own, and where there is a choice of trading partner, cheaters cannot prosper and cooperation emerges in the context of a particular market. Empirical exploration of these assumptions has recently begun (Noë et al. 1991; Stopka & MacDonald 1999; Bshary 2001), as has their extension to permanently social groups (Henzi & Barrett 1999; Barrett & Henzi 2001).

In a study of female chacma baboons, *Papio cynocephalus ursinus* (Barrett et al. 1999), we argued that allogrooming was such a commodity and suggested that differences in the patterning of grooming interactions between populations could be explained by the nature of the

'market forces' operating within them (Noë & Hammerstein 1994). Baboon females from the Drakensberg Mountains, South Africa where there was very little competition for resources and where, consequently, the 'dominance gradient' (Henzi & Barrett 1999) was shallow, could effectively only trade grooming for itself. Their grooming bouts, therefore, were characterized by closely time-matched reciprocal grooming bouts. In contrast, we found that time matching was much weaker among females living in a population with a harsher competitive regime.

Within the latter population, at De Hoop in the southern Cape, South Africa, it was suggested that a steep dominance gradient permitted the exchange of grooming for goods other than grooming itself ('interchange trading': Hemelrijk & Ek 1991), since dominant females would be able to control access to resources for which other females would then have to trade. We viewed the weaker time matching and dominance effects at De Hoop as reflecting this potential for interchange (Barrett et al. 1999). Our data therefore accord with the expectations of the biological markets approach without providing a direct test of its central assumptions. To do so requires the crucial demonstrations that different commodities are interchanged and that levels of supply and demand as well as competition within trader classes underpin fluctuations in commodity value (Barrett & Henzi 2001). In

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this paper we address these issues, providing confirmation of suppositions regarding the former (Barrett et al. 1999) and the first empirical evidence for the latter in a social mammal.

The Interchange Commodity

Interchange commodities can be of several types (see Barrett & Henzi 2001). Subordinate animals may trade grooming for tolerance by dominant animals around resources (e.g. drinking sites: Kapsalis & Berman 1996) or for support in aggressive interactions. Interchange can also be expected to occur between other trader classes; males, for example, may trade grooming for sexual access to females. In this paper, we consider the interchange of grooming for access to young infants. As with infants of other primate species, newborn baboons are a source of great attraction to other animals, and mothers receive high levels of social attention, usually in the form of grooming, in the first 3 months post partum as other animals attempt to 'handle' and 'inspect' these new arrivals (Altmann 1980; Nicolson 1987; Kenyatta 1995).

Infant handling therefore makes an ideal test case for investigating interchange grooming for the following reasons.

(1) It is easy to observe and score.

(2) Trader classes are easy to identify (mothers versus handlers).

(3) Levels of supply (number of young infants) fluctuate through time.

(4) Demand is consistently high, as all adult females are keen to interact with young infants.

(5) Handling is not 'free'. Baboon mothers are notably reluctant to allow their offspring to be handled, probably because of the potentially high costs to their reproductive success (Nicolson 1987). The increased social attention that mothers receive suggests that grooming is the price 'paid' for handling.

Predictions

If infant handling in return for grooming represents interchange trading between female baboons, two preliminary predictions must necessarily be satisfied before proceeding further.

Initiation and directionality of grooming bouts

(1) Grooming interactions that involve infant handling are more likely to be initiated by the handler rather than the mother.

(2) Grooming behaviour associated with infant handling is less likely to be reciprocated by the mother.

Interactions within trader classes

If these conditions are satisfied, it is then possible to test predictions concerning interactions within and between trader classes. Within the mother trader class, demand for access to other females' infants might be predicted to be lower since these females have infants of their own. Alternatively, interest in other females'

offspring as commodities may remain high regardless of motherhood, but mothers may be able to make a reciprocal exchange of access to infants, rather than interchanging grooming for access. Under both these hypotheses, we can predict that:

(3) grooming as a means of buying access to infants is less likely to occur between mother–mother dyads than between mother-nonmother dyads; while, if the second hypothesis is true, we can predict further that

(4) mothers trade infant handling reciprocally.

Interactions between trader classes: supply, demand and outbidding

Between trader classes, levels of supply and demand should influence the price that animals must pay and conflict should exist over the exchange rate, resulting in outbidding within the handler trader class. As the number of available infants varies, we predict that:

(5) the length of grooming bout associated with infant handling varies according to the supply of infants. Specifically, the 'price' is higher when few infants are available.

In addition, where populations are characterized by a strong dominance gradient and large power differentials, the difference in rank between a mother and a handler may also influence the exchange rate of the commodity: females within the mother trader class can exploit differences in rank to extract a higher price from low-ranking trader class females. That is, low-ranking females will have to provide proportionally longer grooming bouts in order to outbid the competition from potential handlers of higher rank. Given that the De Hoop population has a steep dominance gradient (Barrett et al. 1999), we predict:

(6) a negative relationship between grooming bout length and the rank distance between mother and handler.

METHODS

Study Site and Animals

We collected observational data between August 1997 and October 1998 from one main study troop of baboons (troop size varied between 38 and 50 during this period) in the De Hoop Nature Reserve. All females with an infant under the age of 12 months in August 1997 were selected as focal subjects for the larger project of which this study is a part. All females that gave birth during the study were subsequently included in the sample to give a total of 12 mothers and infants. For the purposes of the following analyses, we extracted data on infants from the ages of 0–3 months. Infants of this age possess a distinctive natal coat and are the most attractive to other animals. Limiting the data in this way ensures that all infants are equally attractive and avoids confounds brought about by age differences between infants. Consequently, only 10 subjects are included in the following analyses since two infants were 9 months old when the study began.

Data Collection

All individuals were recognizable from natural markings and were followed on foot at a distance of 5–10 m from dawn (0500–0730 hours, depending on the time of year) to dusk (1700–2000 hours) on each day of observation. Sampling consisted of a combination of scan samples taken at 30-min intervals during which we recorded the activity of all visible animals and 10-min focal animal samples during which we recorded all social interactions of mother and offspring on a continuous basis. We divided the day into four equal time zones during which each female was sampled at least once per time zone per month to give a minimum of 80 min of data (range 80–120 min) per mother–infant pair per monthly sample period. Data presented here come from 200 h of focal animal sampling.

In addition to grooming data collected during focal animal samples, we also collected female allogrooming sessions ad libitum throughout the day whenever we observed the initiation of a bout. We defined a grooming bout as a continuous period of allogrooming involving the same two animals. A change of identity of one of the animals or a shift in activity for more than 10 s signalled the end of a bout. Any one bout could contain one or more grooming episodes, which were defined by the identity of the groomer. A reciprocated bout comprised at least two episodes. For each bout, the identity of the participants and the time spent grooming by each partner (to the nearest second) were recorded. Grooming data collected in this manner were entered into a dedicated grooming database and analysed separately from the focal data (see Barrett et al. 1999, 2000).

Analyses

To test the above predictions, we extracted the following data from the grooming and mother–infant databases. From the grooming database, we partitioned data according to whether the bout was infant related (defined as a bout in which a female other than the mother handled or attempted to handle the infant). Noninfant-related bouts were those in which no infant was in contact with or within arm's reach of the participants. To prevent inflation of N, we again followed the method of Barrett et al. (1999, 2000). For each female, therefore, we extracted all grooming bouts in which she was designated as the initial groomer and from these selected at random a single grooming bout for each of the dyads of which she was a member. This gave a sample of 48 infant-related bouts and 89 noninfant-related bouts. While this approach prunes the data set severely, it is justified since, as in our previous analyses, our predictions apply to any single grooming bout. Analyses conducted on the full data set, while analytically invalid, provide the same results.

From the focal sample mother–infant database, we extracted all incidences of infant handling. This was defined as any physical interaction between an infant and an adult female other than its mother. Handling events were categorized as follows: (1) the handler removed the infant from contact with its mother to inspect and manipulate it; (2) the handler touched and manipulated the infant while it remained in contact with the mother; (3) the handler touched the infant and then tried to remove it from the mother who resisted strongly and kept the infant in contact; (4) the handler greeted the infant (grunts/lipsmacking) and nuzzled it while the infant remained in contact with the mother. No finer distinctions were made with regard to the following analyses since the intention was to test ideas regarding the trading of commodities and not the nature of handling per se. Handling bouts were categorized initially as (1) grooming followed by handling; (2) handling followed by grooming and (3) handling without grooming. Since there were only two instances of (2) and there was no other difference in the nature of these interactions compared with (1), these two categories were collapsed into a single category (1) handling with grooming.

To avoid over-representation of particular mother–handler dyads, we again took all the handling episodes for each mother and partitioned them according to infant age. Then, for each month of life, we extracted randomly one handling episode for each female with whom the mother interacted during that period. This gave us a sample of 107 handling bouts. Where infant handling was accompanied by grooming, the length of the grooming bout was recorded to the nearest second. However, of the 30 bouts in which handling was accompanied by grooming, only 19 of these had complete timed grooming records. This was due to the nature of the sampling schedule, which meant that animals were often already engaged in grooming at the start of the sample. Although these selection procedures are wasteful of data, they provide a rigorous test of our hypotheses and have been used effectively in other analyses (Barrett et al. 1999, 2000). Since our predictions are directional, we used one-tailed tests, unless otherwise stated, with P set at 0.05.

RESULTS

Initiation and Directionality of Grooming Bouts

Focal data on handling sessions revealed that all 19 infant-related grooming bouts were initiated by handlers rather than mothers. Data from the grooming data set showed the same pattern, with infant-related grooming bouts significantly more likely to be initiated by handlers than by mothers (handlers initiating: 41 dyads; mothers initiating: 7 dyads; $\chi^2_2 = 24.08$, $P = 0.0001$).

For handling bouts accompanied by grooming, 23 out of 30 (77%) involved nonreciprocal grooming of the mother by the handler. Mothers reciprocated grooming on only seven occasions (23%). This may represent an overestimate of nonreciprocal grooming since, as explained in the Methods, some grooming bouts were already underway when focal samples began. However, data from the 19 handling sessions with complete timed grooming show that 89.5% ($N = 17$) of these bouts were nonreciprocated. Data from the grooming database also revealed that infant-related (IR) bouts were significantly

Table 1. ANOVA on grooming bout duration of adult females

Ln time	Sum of squares	df	Mean square	F	P
Main effects					
(combined)	92.625	2	46.313	38.136	0.0001
Bout type	6.205	1	6.205	5.109	0.025
Bout direction	64.461	1	64.461	53.080	0.0001
Two-way interactions					
Bout type×Bout direction	0.168	1	0.169	0.139	0.710
Model	99.925	3	33.308	27.427	0.0001
Residual	162.731	134	1.214		
Total	263.656	137			

Bout type: infant related/noninfant related; bout direction: nonreciprocated/reciprocated.

more likely to be nonreciprocated than were noninfant-related (NIR) bouts (IR: nonreciprocated: 75%, $N=36$; reciprocated: 25%, $N=12$; NIR: nonreciprocated: 57.3%, $N=51$; reciprocated: 42.7%, $N=38$; $\chi^2_1=4.52$, $P=0.034$, two-tailed; analysis performed on raw frequencies).

Maternal response to handling depended on whether it was accompanied by grooming. Avoidance and threats towards handlers were extremely rare when grooming preceded handling (2/22, 9.1%), and mothers were more likely to sit passively and allow handling to take place (20/22, 90.9%). In cases where handling was not accompanied by grooming, mothers were more likely to threaten and/or avoid the handler (30/74, 40.5%), although the most common response was again to permit handling passively (44/74, 59.5%). These differences in maternal response depending on whether handling was accompanied by grooming were significant ($\chi^2_1=7.50$, $P=0.009$, two-tailed, $N=96$; in the remaining cases, mothers solicited grooming by the handler and were excluded from this analysis).

A two-way ANOVA revealed that both grooming bout type (IR versus NIR) and whether the bout was reciprocated significantly influenced total grooming bout length (Table 1). IR bouts tended to be shorter overall and were less likely to be reciprocated ($\bar{X} \pm$ SD; nonreciprocated bouts: IR: 127.1 ± 154.8 s, $N=36$; NIR: 187.5 ± 249.5 s, $N=51$; reciprocated bouts: IR: 369.5 ± 244.2 s, $N=12$; NIR: 692.4 ± 506.4 s, $N=38$). However, there was no interaction between these two effects, that is, IR bouts were not shorter merely because they were more likely to be nonreciprocated. With regard to variation in the types of handling performed, there was no relationship between the duration of grooming bout and handling category (category 1: median grooming bout duration 197 s; category 2: 80.5 s; category 3: 153 s; category 4: 73 s; Kruskal–Wallis ANOVA: $\chi^2_3=3.06$, $P=0.383$).

Interactions within Trader Classes

There was no overall difference in the level of handling shown by cycling, pregnant or lactating females (number of handling incidents: cycling: 41; pregnant: 35; lactating: 31; $\chi^2_2=1.42$, $P=0.492$, two-tailed). In line with our prediction, handlers in mother–mother dyads were
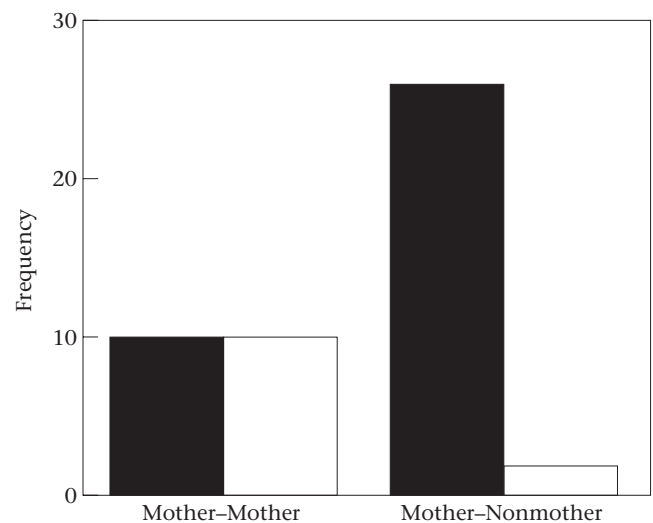

Figure 1. Frequency of nonreciprocated (■) and reciprocated (□) grooming bouts for mother–mother and mother–nonmother dyads.

significantly more likely to handle infants without grooming the mother than were handlers in mother–nonmother dyads (mother–mother: with grooming: 17%, $N=8$; without grooming: 83%, $N=39$; mother–nonmother: with grooming: 36.7%, $N=22$; without grooming: 63.3%, $N=38$; $\chi^2_1=5.04$, $N=107$, $P=0.025$). The grooming data set also revealed that, while mother–mother grooming occurred at a lower frequency than mother–nonmother grooming, reciprocated and nonreciprocated bouts were equally common whereas, in mother–nonmother dyads, nonreciprocated grooming bouts occurred significantly more frequently than reciprocated bouts ($\chi^2_1=13.54$, $P=0.0001$, two-tailed; Fig. 1). Contrary to prediction, however, only four of all mother–mother handling sessions involved reciprocal handling of infants.
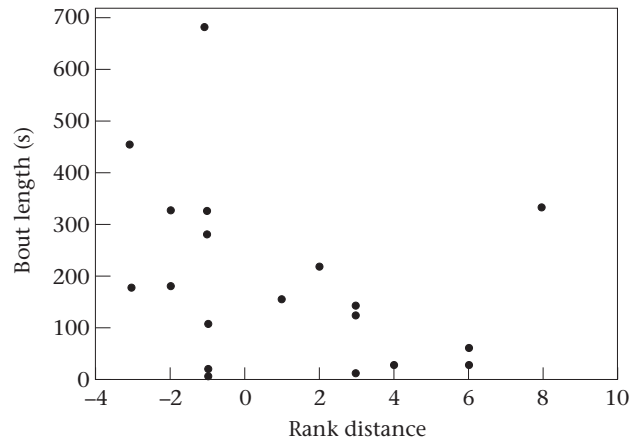
Supply, Demand and Outbidding

We analysed data only from handling incidents accompanied by grooming. Since biological markets theory considers commodities to be inalienable and
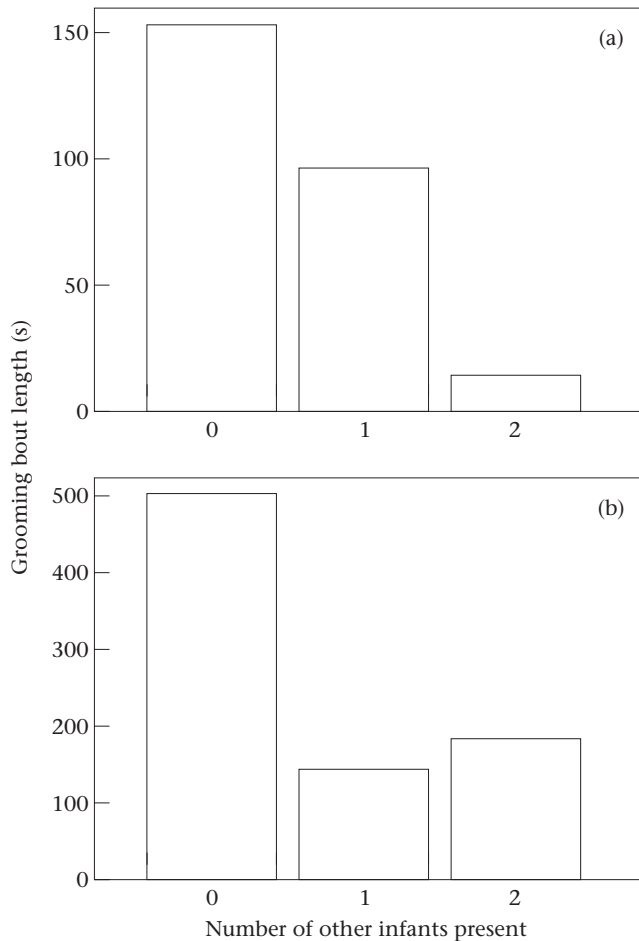
Figure 2. Variation in median grooming bout duration (s) with availability of infants present in the troop where (a) handlers outranked mothers and (b) mothers outranked handlers. Note that the Y axis scales and the number of other infants present differ.

Figure 3. Relationship between handlers' grooming bout duration and rank distance.

unable to be obtained by force (Noë & Hammerstein 1994), handling incidents where the infant was taken by force from the mother could not be included, since by definition, they do not form part of the grooming market. We partitioned the data set into cases where the mother was lower ranking than the handler and cases where the mother was higher ranking. This was to control for any effect of dominance on interchange, which might lead to differences in exchange rate between females. There was a significant effect of infant availability on grooming bout length for cases where the mother ranked below the handler (Kruskal–Wallis: $\chi^2_2=4.57$, $P=0.05$; Fig. 2a), and a strong, but nonsignificant, trend in cases where the mother ranked above the handler ($\chi^2_2=3.60$, $P=0.083$; Fig. 2b). In both cases, an increase in the number of infants led to a reduction in grooming bout length.

As predicted, there was a significant negative correlation between rank distance and the amount of time that handlers groomed mothers ($r_S=0.406$, $N=19$, $P=0.042$; Fig. 3). The higher ranking the handler compared to the mother, the less time was invested in grooming. There are two extreme points in Fig. 3. The grooming bouts represented by these points involve the same high-ranking

female (SA, rank 2), an individual who showed a general tendency to spend more time grooming than other females (mean time spent grooming by females ± SD=2273 ± 4769 s. SA at 18 376 s therefore lies 3.85 SDs above the mean. No other female exceeded 1 SD above the mean value; unpublished data). Although these data points follow the general pattern of a reduction in grooming time with increasing rank distance, exclusion of these points improves the strength of the correlation substantially ($r_S=0.566$, $N=17$, $P=0.009$).

In addition, we found that rank had a strong influence on whether interchange took place. Rank distance was significantly higher when handling took place without grooming (median rank distance: handle with grooming: 2.00, handle without grooming: 4.00; Mann–Whitney U test: $Z=-2.252$, $N_1=30$, $N_2=77$, $P=0.012$). Similarly, for handling with grooming, mothers were just as likely to rank above as below the handlers (mother's rank>handler's rank: 13 cases; mother's rank<handler's rank: 17 cases; Wilcoxon signed-ranks test: $Z=-1.45$, $N=30$, $P=0.147$, two-tailed). However, for handling without grooming, mothers were significantly more likely to rank below the handlers (mother's rank>handler's rank: 21; mother's rank<handler's rank: 56: $Z=-3.70$, $N=77$, $P=0.0001$, two-tailed).

DISCUSSION

Our findings confirm that female baboon grooming has value in relation to at least one other commodity. Data on initiation, reciprocation and maternity indicate that females without young infants were prepared to groom to gain access to others' infants. In the case of mother–mother dyads, the lower frequency of handling in return for grooming did not occur as a consequence of interchange trading being replaced by reciprocal trading in infants.

More importantly, the finding that the availability of infants affected the duration of infant-related grooming bouts provides the first empirical indication of market effects in a primate group. The fewer infants present,

the longer handlers groomed. It is conceivable that the proximate explanation for this centres on the fact that mothers received more attention, leading to increased tension, when there were fewer infants present. Increased grooming would then be required to reduce maternal stress sufficiently (Boccia 1987; Boccia et al. 1989) for a mother to release the infant. However, this argument cannot apply to dominant mothers and subordinate handlers, as the balance of power here lies with the mother. In this case, it appears that dominant females used their higher market value to extract more grooming. If this is so, then it is also possible that other mothers exploited the rarity of infants within the group to extract more grooming from potential handlers. This would mean that mothers played a more active role in setting the 'price' for handling than would occur if tension reduction alone set the market value of infants.

At the same time, infant-related grooming bouts were shorter than noninfant-related grooming bouts, whether reciprocated or nonreciprocated. Females appear, therefore, to groom only as long as is necessary to obtain maternal tolerance. This may be because the returns on grooming diminish faster in the context of trading infant access than when trading grooming for itself. Although we did not time handling incidents accurately, there was no indication that females who groomed for longer were permitted to handle an infant for longer. Focal data show that all handling incidents were short (less than 1 min; unpublished data) and that mothers were at best tolerant, rather than willing, participants. In addition, increased grooming duration had no effect on the 'intensity' of handling. Together with the fact that infant-related grooming was generally shorter than grooming in other contexts, this fluctuation in the value of the commodity (i.e. the amount and quality of handling obtained did not change with the effort expended to obtain it) is a clear indication that a market is operating.

On the strength of these results, it seems appropriate now to extend work on simian biological markets to those arenas where interchange is most commonly expected, such as access to resources, but where determining temporal parameters and units of analysis is intrinsically more difficult (Barrett & Henzi 2001). In doing so, attention will need to be paid to the finding that dominance effects could, in some instances, completely override market effects. When rank distance was high, handlers were able to gain access to infants without grooming. Put simply, dominance relationships allowed females to obtain infant access by force.

In its original formulation (Noë et al. 1991), commodities within a biological market were assumed to be inalienable, so that animals had no choice but to trade. However, empirical work suggests that it is, in fact, possible for dominance, coercion and punishment (sensu Clutton-Brock & Parker 1995) to act as market forces and to play a significant role in the generation of market effects (see Barrett & Henzi 2001; Bshary 2001). In this particular case, however, the threat of punishment or coercion by high-ranking animals does not constitute a market force, but is a means by which market forces are disrupted.

This does not negate the applicability of biological market models to primate groups, since it is apparent that, despite these effects, animals do trade grooming to their mutual benefit, are able to choose their partners and do attempt to get good value for their efforts (Barrett et al. 1999, 2000). However, the fact that dominance effects allow some animals to circumvent the market needs to be accommodated within this framework. Indeed, this may be essential since dominance hierarchies are very common in primate groups, and those of other social animals, and these group-living situations are the ones in which a market approach is likely to be most productive (see Barrett et al. 2000).

The results of the present study and our previous work (Barrett et al. 1999, 2000; see also Henzi & Barrett 1999; Barrett & Henzi 2001) also suggest that female chacma baboons may deal with social events over a very short timescale, optimizing access to commodities on a daily (or even shorter-term) basis. The impact of the almost constant availability of baboon infants on female social dynamics is therefore likely to be strong. This is so, not because their presence influences patterns of alliance formation in the future as has been suggested (e.g. Maestripieri 1994a, b), but because it means that access to infants must always feature as a component of females' decisions regarding partner choice within the market place.

Acknowledgments

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