

Monkeys, markets and minds: biological markets and primate sociality

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12.1 Introduction

The sight of a monkey group, huddled together in pairs, each individual taking turns to comb diligently through the other's fur inevitably brings to mind the old cliché, "you scratch my back and I'll scratch yours" and makes it obvious why primate grooming behavior is often seen as the quintessential act of cooperation and reciprocity. Among the monkeys and apes, grooming is also seen as the defining act of sociality; the fact that individuals put considerable effort into their grooming relationships, groom some group members more than others, and work to sustain time for grooming in the face of opposing pressures (Sade 1972, Dunbar & Sharman 1984), suggests that grooming helps to serve an individual's social goals, as well as enabling animals to stay clean and healthy. Understanding how primates cooperate and perform successfully in the social world means, to a great extent, understanding the dynamics of grooming.

Traditionally, it has been assumed that dominance and competition are the factors that explain the intensity with which female primates, in particular, engage in grooming (e.g. Seyfarth 1977, Harcourt 1988). Competition among female primates arises as a consequence of group living. Living together in a cohesive social group can itself be seen as a cooperative act; joining together with others enables animals to receive benefits, like reduced predation risk or decreased vulnerability to infanticidal males (van Schaik & Kappeler 1997, Henzi & Barrett 2003), that are unavailable to solitary animals. However, living in a group is not cost-free; the unavoidable corollary of living in close proximity to others is conflict over access to scarce local resources, such as food or predator-risk reducing spatial positions (van Schaik 1989, van Schaik & Kappeler 1997). Although these effects may be ameliorated by the fact that females often reside in kin-based groups, they nonetheless remain trapped by the need to remain safe, on the one hand, and the need to secure sufficient resources for themselves and their offspring, on the other. This dilemma, seen in both proximate and ultimate perspective, generates the subtle and complex patterns of cooperative interaction that are associated with female-bonded primate social systems.

Among the most important of these cooperative interactions, and the ones most frequently linked to grooming in a causal manner, are the coalitions that females form during aggressive encounters, whereby one individual comes to the aid of another to help fight off an attacking individual (Silk 1987). The consensus view is that, among the primates, females form long-term mutually-ben-

official alliances with specific individuals in order to buffer themselves against the negative effects of competition within their groups. This buffering is thought to take the form of coalitionary support during agonistic interactions combined with the use of grooming to build trust and alleviate stress. Grooming, thus, has two (non-exclusive) functions within this scenario; it builds bond strength and thereby establishes the trust on which coalitionary relationships may be built (Dunbar 1984) and/or it acts as a currency that can be exchanged in anticipation of future coalitionary support (Seyfarth & Cheney 1984).

12.2

The problem with chacma baboons

This idea that grooming is a means of servicing coalitionary relationships is neat, coherent and fits well with notions that monkeys and apes are highly 'political' animals (see e.g. Byrne & Whiten 1988). However, there is a problem with the above scenario: chacma baboons, (*Papio hamadryas ursinus*), our chosen study animal, very rarely form coalitions, despite the fact that females sustain grooming relationships and compete over access to resources (Ron et al. 1994, 1996, Silk et al. 1999, Barrett & Henzi 2002). At De Hoop, our current study site, for example, we have seen only two female-female coalitions in approximately 30000 observer-hours. Moreover, recent work on yellow baboons in Amboseli, Kenya, reveals that females form coalitions against other adult females at extremely low rates in this population as well (1-4 interventions per 100 disputes) (Silk et al. 2004). Low rates of coalition formation may therefore be characteristic of all baboons, and not just the southern African sub-species. Silk et al. (2004) suggest that coalitions confer significant individual benefits on the females that participate in their formation but, as suggested by Henzi & Barrett (1999), their overall rarity makes it unlikely that they are the organizing principle of female social strategies.

Another pertinent fact is the finding that chacma females from the Drakensberg Mountains continue to form grooming relationships and adjust their time budgets to conserve grooming time despite the fact that the distribution of resources in their environment means that they experience almost no competition for food and consequently show little aggression (Henzi et al. 1997). Specifically, once the size of the female cohort of a group exceeds a critical number, Drakensberg females cut back the number of different individuals with whom they engage in grooming. This allows them to increase the length of individual grooming bouts with their chosen partners and, more importantly it seems, keeps levels of grooming reciprocation high (Henzi et al. 1997); female clique size is reduced at precisely the point at which reciprocal grooming with all other female group members can no longer be sustained.

The significance of these findings is further highlighted by other data from Amboseli revealing that grooming has significant fitness benefits for baboons, even though grooming is not causally related to coalition formation in this population. Females that are highly social and who groom frequently have sig-

nificantly higher offspring survival rates than less sociable females (Silk et al. 2003).

Among baboon females, then, grooming remains significant and has positive fitness effects even in the virtual absence of coalition formation. Consequently, the notion that the function of grooming is to cement coalitionary alliances cannot be taken as a general explanation for the prevalence of grooming across the primates as a whole. On a more personal and immediate level, the rarity of coalition formation among chacma females meant that, in our own studies, we had to start thinking about grooming and its dynamics differently, resulting in a simple and very obvious insight into the problem; namely, that a comprehensive explanation of the role of grooming in primate societies should encompass its utilitarian benefits, as well as its social ones (Barrett et al. 1999, Henzi & Barrett 1999, Barrett & Henzi 2001).

It is clear that grooming retains its original hygienic value, despite its social importance, since animals spend time grooming themselves as well as directing it to others, and because the grooming they receive from others is generally directed at areas they cannot easily reach (Barton 1985). The targets of this grooming are ectoparasites such as fleas and lice (Tanaka & Takafushi 1993). A greater parasite load means a greater loss of blood, greater irritation, and increases the probability of infection (Johnson et al. 2004), so keeping levels low is of clear benefit to animals. In addition, it is possible that grooming has thermoregulatory benefits by maintaining the loft of the fur, thus aiding heat retention and dissipation. It is also clear that the physical contact that grooming involves is highly pleasurable for the recipient and is, in fact, associated with the production of β -endorphins (Keverne et al. 1989). This latter feature cannot be viewed in the same utilitarian light as the removal of parasites, as it is presumably a derived feature that proximately reinforces grooming behavior. Nevertheless, it can result in grooming being exchanged for its own hedonic benefits, rather than for 'political' reasons.

Grooming is also costly for its participants. Not only are there opportunity costs associated with grooming another animal (an individual could be engaged in other activities like foraging, or indeed being groomed themselves) but there is also a risk of acquiring parasites from grooming partners if the parasites are able to move from one animal to another during the course of a grooming bout (see Johnson et al. 2004 for a theoretical approach based on the ideal free distribution). Removing another animal's parasites therefore comes with the simultaneous cost of acquiring a few of them oneself; a problem that will be exacerbated in larger groups because these tend to have higher average parasite loads than small groups (Johnson et al. 2004). Grooming is therefore a cooperative act since animals cannot obtain all the grooming they require to be parasite-free by their own actions, and the benefits of grooming another must be traded off against the costs of doing so.

12.3 The social market place

While this idea is obviously not new, the focus on the social function of grooming has pushed aside the rather more mundane role that grooming serves. By highlighting the broader utility of grooming, it becomes easier to appreciate that grooming is a valuable commodity in itself. The fact that an animal must trade with other individuals in order to reduce its parasite load means that, regardless of its ability to facilitate other social interactions, grooming is a valuable service that one animal can supply for another. Johnson et al. (2004) go further than this, however, by emphasizing that levels of parasite infestation can produce patterns of behavior (e.g. group fission) that have traditionally been attributed solely to complex social processes. Social dynamics may actually be linked to parasite loads in a fundamental way, making it impossible to divorce the hygienic from the social function of grooming in the way that some authors have suggested (e.g. Dunbar 1988).

A more utilitarian perspective on grooming also frees us from the assumption that coalition formation is inevitably tied to grooming; although females potentially are able to trade grooming for this service, there is no necessary link between these two behaviors from our perspective. Other conceptual approaches to the issue require that they are connected (e.g. Dunbar 1988, van Schaik 1989), even though the evidence to support such a mandatory link is equivocal at best (Henzi & Barrett 1999).

This notion of grooming as a tradable commodity thus leads neatly to the adoption of biological market (BM) theory as an explanatory framework. BM theory, as put forward by Ronald Noë and Peter Hammerstein (Noë et al. 1991, Noë & Hammerstein 1994, 1995), holds that (i) where individuals control resources or can provide a service to others, these constitute commodities that can be exchanged but not taken by force (they are 'inalienable'); (ii) trading partners are chosen from a range of alternatives, via a mechanism of outbidding competition, in such a way that profit is maximized. This, in turn, means that the prevention of defection is not a driving force in a BM framework, in contrast to models based on the iterated Prisoner's Dilemma (Axelrod 1986). (iii) Supply and demand determine the bartering value of commodities exchanged; thus, within primate groups, animals may trade grooming with each other on a mutualistic basis in order to reap the benefits that grooming itself offers (reciprocal traders), or they can exchange grooming for other commodities that are, in some sense, value equivalent (interchange traders) (Hemelrijk & Ek 1991). It should therefore be possible to distinguish 'trader classes' of females that exchange grooming in different ways. Possible sources of interchange commodities are tolerance around feeding or drinking sites, mating opportunities, tolerance and access to infants (for further details see Barrett & Henzi 2001). Coalitionary support is also a potential interchange commodity for species other than baboons, although there are reasons to suspect that this is less likely to occur than other exchanges (see below).

In the absence of coalitions and alliances, adult female baboons generally gain access to resources on the strength of their own power (females can gener-

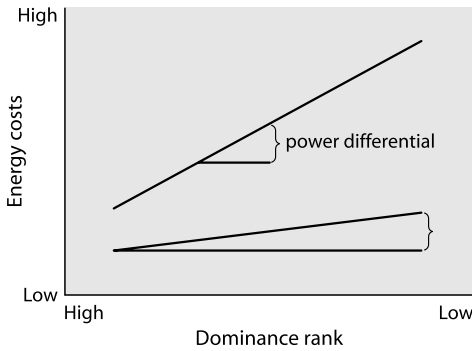


Fig. 12.1. A notional graph to illustrate the concept of a power differential. As dominance rank gets lower, the energy costs associated with receiving aggression from others increase. High-ranking females can therefore exert a much greater effect on another female's fitness than low-ranking females. The two slopes represent groups with different dominance gradients. When gradients are steep (upper line), the negative effect exerted by one female on another can be achieved at lower rank distances than in a group where the gradient is shallower. Adapted from Barrett & Henzi (2001) with permission.

ally be placed in a linear, transitive dominance hierarchy, which describes priority of access to resources). Consequently, we predict that interchange trading should occur only when the 'power differential' between two participants is great enough that access to the commodity cannot be achieved by the less powerful individual alone. Power differentials among adult females can be expressed in terms of the distance between the animals' respective dominance ranks, and the gradient (or 'steepness') of the hierarchy (Barrett & Henzi 2001). As Fig. 12.1 shows, the same power differential may represent a difference of only one rank position in troops where the dominance gradient is steep (upper line) but can encompass the whole dominance hierarchy in troops where the gradient is shallow. Thus, the power differential between the highest- and lowest-ranked females in the latter group is equivalent to the differential between two adjacently-ranked females in the former.

Gradients are expected to be shallow when competition is low and resources are non-monopolizable. In such cases, reciprocal traders should dominate the market place since females cannot exert sufficient power over others to induce interchange trading. As competition increases and resources become monopolizable, gradients are expected to become steeper. Rank distance will therefore exert a stronger influence over females' ability to obtain access to resources, and they will be in a position to trade grooming for access to commodities; interchange traders should therefore come to make up a significant proportion of the market. Importantly, this implies that reciprocal grooming should make up a significant proportion of grooming under all circumstances in all groups, regardless of dominance gradients. This is because all females will always have the ability to exchange this commodity with each other; a notion similar to Chapais's notion of low-competence cooperation (Chapais, this volume). Interchange

traders, on the other hand, should only be seen under competitive circumstances (cf. Chapais's competence-dependent cooperation).

12.4

Why markets?

So far, so good. But does the notion of a market place really add value over a standard optimality analysis of behavior? Does a view of grooming as valuable in its own right necessarily require buying into a whole new theoretical framework? Are terms like 'commodities' or 'trader classes' really essential to understanding how females use grooming for their own particular ends? Not surprisingly, perhaps, we would argue that the answer to these questions is 'yes' and that a BM framework is more than just a new bottle for some rather old wine. The value of BM from our perspective is three-fold. First, unlike other models of cooperation, BM explicitly focuses on partner choice as a factor influencing the kinds and levels of cooperation that one sees; it thus recognizes the inherent dynamism represented by primate social groups. This means that, as well as giving some insight into the ultimate function of cooperative behavior, a BM framework also places great emphasis on the proximate mechanisms by which these cooperative outcomes are negotiated.

This focus on the process by which individuals choose partners in relation to the state of the market means that 'noisy' relationships can be transformed into highly informative ones: the variance around a mean level of interaction between two individuals does not have to be viewed as potential error, but can be investigated as a contingent response to fluctuations in the supply and demand of the commodities on offer. In addition to the relative balance between reciprocal and interchange traders in the market place, potential partners can also vary in value depending on their health, reproductive state, seasonal changes in the competitive regime, and on the presence or absence (through migration or death) of other individuals. A BM approach can deal with this kind of dynamic change within groups in a way that simply cannot be matched by analyses based on a static assessment of the costs and benefits of interacting with others.

Second, a market-based analysis does not treat primate groups as monoliths in which all females are assumed to show the same response to a given competitive regime (Barton et al 1996); rather, it takes a more individual-based approach in which traders are predicted to behave differently depending on what they are trading and with whom (see also Silk et al. 2004, who make a similar argument for individual benefits in the context of coalition formation). This is in contrast to more standard socioecological models that characterize groups as 'despotic' or 'egalitarian' and implicitly assume that all females will follow the same set of behavioral 'rules' (see e.g. Sterck et al. 1997). In a BM formulation, a female can be both egalitarian and despotic in her interactions at the same time; she may trade in a reciprocal (egalitarian) manner with one female, but interchange (despotically) with another. Again, this emphasis on individual dynamics over time is a more realistic approach to understanding primate social interactions. It exploits potentially informative variability within and between females, rather

than attempting to smooth out all the bumps and wrinkles in order to force them into a specific category of social interaction.

Third, and on a more practical level, perhaps, BM offers a way out of the kin selection-reciprocal altruism impasse. While BM was originally envisaged as a way of explaining how unrelated individuals (even those of different species) could achieve cooperation, there is actually no reason why kin should not trade commodities with each other if trade is necessary for each of them to achieve their goal. As Silk (this volume) and Chapais (this volume) both point out, one should not mistake kin-biased behavior for kin selection, nor should we expect individuals to always favor kin for cooperative tasks. A BM approach does not force an immediate distinction between kin selection and reciprocal altruism as explanations for cooperation, but allows one to remain agnostic on this thorny issue, while including factors like relatedness as variables likely to influence partner choice and commodity exchange rates.

In addition to these benefits concerning the analysis of cooperation within groups, we also feel that the BM approach has the potential to add to other areas of research beyond understanding cooperation. As detailed below, we believe that a view of primate groups as market places, with trade as central to group social dynamics, can help to shed light on other areas of evolutionary significance, such as the cognitive differences that have evolved within the primate order.

12.5

When is a primate group also a market?

There is one more point about a BM framework that needs emphasizing before we go on; any attempt to investigate whether market forces structure the grooming dynamics of primate groups requires a focus on the dynamic part of the equation, and not just the grooming. The BM approach is concerned with the manner in which individual behavior reflects changes in the market place and the supply and demand of valuable commodities. In other words, it is concerned with responses to variation in local circumstance. If circumstances do not vary, then it becomes impossible to test whether supply and demand for commodities structure the market, since by definition both of these variables will remain constant. Valid tests of a BM framework therefore require fluctuation in the market; if this is not the case, then one may rightly conclude that market forces do not explain behavior, but for the wrong reason; if markets do not vary, then market forces will not be apparent, but this does not mean that they do not exist at all. As is recommended in all cases where a particular theoretical framework is applied, *a priori* reasons for why dynamic market effects are expected should be generated, rather than merely assuming that they are present.

The other reason for emphasizing this dynamic element is that BM has been seen by some as an alternative to Seyfarth's (1977) model of primate grooming when, as Noë & Hammerstein (1995) originally pointed out, the latter is actually a form of market model. As in a standard BM formulation, the key components of Seyfarth's model are partner choice and competition for partners that differ in value. However, the crucial difference between the BM approach and Seyfarth's

(1977) model is that the latter is entirely static; it assumes that the value of high-ranking females remains constant over time. Seyfarth's model also deviates more significantly from a BM approach in that the competition between females does not take the form of 'outbidding' competition, whereby females who supply a better quality product (or ask a lower price) do better within the market. Instead, competition applies on a 'first come, first served' basis where females are able to prevent others from grooming merely by virtue of their rank; high-ranking females get to choose first and they remove females from the 'grooming pool'. In doing so, they prevent other females from entering into a 'bidding war' because the excluded females never get an opportunity to engage with such partners and make them a better offer. This again results in a static, as opposed to a dynamic, market place, where partner choice precludes outbidding rather than promoting it. In this sense then, Seyfarth (1977) does not present us with a true market-based model.

Finally, not all instances of grooming need represent 'market trading': in some instances, individuals will groom for purposes related to tension-reduction, bonding with offspring and the like, in a manner that is not dictated by market forces. Again, this means that it is important to give *a priori* reasons as to why market effects should be in operation, and to test this assumption, rather than merely proceed under it.

12.6

Testing the framework: market forces and grooming reciprocity

So, how well does market theory do when put to the test? As a first step in exploring the applicability of a market-based approach, we tested whether grooming reciprocity between females was influenced by dominance gradients and power differentials, using data from two contrasting populations of South African chacma baboons. Data from two troops living in the Drakensberg Mountains of Kwa-Zulu Natal were compared with two troops at De Hoop, an area of coastal fynbos (Mediterranean scrub vegetation) in the Western Cape (see Barrett & Henzi 2002 for an overview of this site), matched for female cohort size.

Differences in the level of food competition experienced by females in the two populations were substantial. In the Drakensberg Mountains, the sparse and relatively even distribution of food (Henzi et al. 1992) meant that agonistic events between females occurred at a rate of only one in every 500 hours of observation, whereas at De Hoop, individual females were engaged in aggression at least once per hour on average (Barrett et al. 1999, Barrett et al. 2002). Consequently, females at De Hoop could be ranked in a strong linear dominance hierarchy, whereas this was not possible for the two mountain troops. We inferred from this that interchange trading would be possible at De Hoop since power differentials were likely to be high, whereas this was unlikely to be the case in the Drakensberg. In the latter population, we predicted that females would be limited to reciprocal exchange, able only to trade grooming for its own intrinsic value.

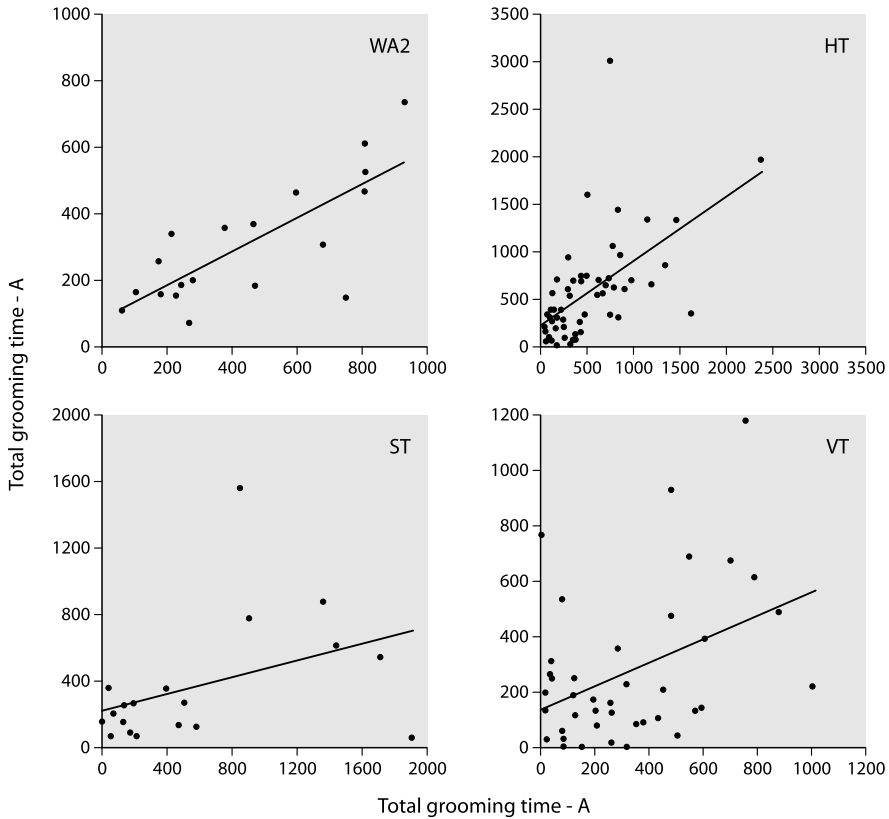


Fig. 12.2. Time-matching across four chacma baboon troops from two different South African populations. WA2 and HT are from the Drakensberg Mountains, Kwa-Zulu Natal, and ST and VT are from De Hoop, Western Cape. Troops were matched for female cohort size (WA2 and ST: $n = 7$; HT and VT: $n = 12$). In each case, there is a significant relationship between the amount of time spent grooming by the initiator of bout (groomer 1) and its reciprocating partner (groomer 2). However, time-matching is more precise for the Drakensberg populations in terms of both explained variance and a slope that more closely approximates a 1:1 fit (WA2: $r^2 = 0.588$, $b = 0.50$; HT: $r^2 = 0.588$, $b = 0.67$; ST: $r^2 = 0.163$, $b = 0.25$; VT: $r^2 = 0.168$, $b = 0.42$). See Barrett et al. (1999). Reprinted from Proceedings of the Royal Society, Series B, London.

In line with our prediction that reciprocal traders should make up a significant share of the market, regardless of the potential for interchange trading, we found that females in both populations showed significant levels of ‘time-matching’; that is, there was a significant positive correlation between the grooming contributions of individuals to a grooming bout (Barrett et al. 1999) (Fig. 12.2). The fact that females showed a significant tendency to match their partners’ grooming contribution (they ‘give as good as they get’; Barrett et al. 2000) suggested that being a good value partner required ‘fair trade’. Experimental studies of capuchin monkeys support this notion that individuals are capable of gen-

erating expectancies about what they can expect to receive based on what their partner gets (Brosnan & de Waal 2003).

It is also interesting to note that individuals did not supply their grooming partners with a single lengthy bout of grooming, which was then reciprocated in kind. Rather, individuals divided their grooming into a number of short bursts that were traded back and forth over the course of the bout (see Barrett et al. 2000). This ‘parceling’ of grooming fits with Connor’s (1995) theoretical demonstration that such behavior increases the costs of finding an alternative partner by ensuring that one always remains a valuable partner, thus removing any temptation to defect. The need to be a good value partner in a market place where many other individuals can supply the commodity in question, plus the parceling of bouts into short grooming bursts, appears to keep females honest and well out of the clutches of the Prisoner’s Dilemma.

12.7

Partner control as well as partner choice?

In the Drakensberg, females time-matched more precisely than those at De Hoop; the relationship between individual partners’ contributions was much stronger for the Drakensberg troops in terms of both the amount of explained variance and a slope coefficient that was closer to a one-to-one fit (see Fig. 12.2). Originally, we suggested that this reflected the limited potential for interchange trading in the Drakensberg (Barrett et al. 1999), with the result that the market place contained only reciprocal traders. The poorer fit at De Hoop was attributed to the fact that dominance effects, and hence the potential for interchange, introduced more noise into the relationship found, thus resulting in poorer time-matching.

However, it is also possible that high power differentials at De Hoop provide dominant animals with more ‘leverage’ (*sensu* Lewis 2002) to extract a higher amount of grooming from subordinates during reciprocal bouts (so that, for example, one unit of grooming from a dominant requires two in return from a subordinate). This in turn could be due to a market effect created by coercion, punishment or other forms of partner control (Barrett & Henzi 2001, Bshary & Nöe 2003). Support for this interpretation is provided by a significant relationship between rank distance and time-matching of bouts in the De Hoop population; subordinate individuals tended to groom for much longer than dominant individuals within bouts. Overall, for each unit increase in rank, there was a 28 second discrepancy in the amount of grooming provided by the subordinate animals compared to the dominant. This suggests that dominant individuals were indeed able to use their increased power to extract a higher price in grooming from their subordinate counterparts.

The introduction of partner control into the mix represents a departure from the original BM formulation, which dealt only with trade and outbidding in the absence of physical force or coercion. However, as Noë (2001) points out, multiple sources of power are needed to understand cooperative interactions completely. Thus, while it is true that the original BM formulation dealt only with

inalienable resources, this does not imply that market forces cannot coexist with the use of coercion or other forms of leverage (Ronald Noë, pers. com.). In line with Bshary & Nöe's (2003) views on cleaner fish, partner control seems to be crucial to an understanding of the baboon market.

Moreover, Bowles & Hammerstein (2003) note that human economic models which take account of power have long existed, and that market theory in economics now "takes as its foundational assumptions the incomplete nature of contracts (biologically speaking, the possibility of cheating, exploitation etc.)" (p. 157). Another factor that may also be relevant is that of asymmetric price transmission, whereby variation in supply and demand is not passed on to consumers and producers equally. This can cause prices to 'stick' at artificially high or low levels depending on whether transmission fails to consumers or producers, respectively (e.g. Azzam 1999, Goodwin & Holt 1999, Bunte & Peerlings 2003). Thus, we should view partner control as itself determined by a market situation in which partner choice options are exercised.

Overall then, these initial results showed how differences in ecology, and hence competitive regime, have the effect of setting up differential market forces that influence the strength of grooming reciprocity seen between partners. This, in turn, leads to an asymmetry in the payoff for grooming bouts between distantly-ranked animals compared to closely-ranked animals (see Barrett et al. 1999 and Barrett & Henzi 2001 for a more detailed discussion).

12.8

Time-matching in other primate species

Time-matching and rank effects have also been investigated in samango monkeys (Payne et al. 2003), capuchins and captive bonnet macaques (Manson et al. 2004). Among samango monkeys, time-matching occurred at approximately the same level as the Drakensberg baboons and overall levels of reciprocated grooming were similar (50% and 40%, respectively). This is a point worth noting because samango monkeys have been characterized as an archetypal 'egalitarian' species (Rowell et al. 1991), with the reciprocal nature of female grooming held up as a key characteristic of egalitarian societies in general. The fact that 'despotic' baboons show a pattern of grooming similar to that of the 'egalitarian' samango illustrates our point that a BM approach cuts across static categorical designations, and emphasizes that individual females and populations will show patterns that reflect their individual circumstances.

Similarly, capuchins and bonnet macaques also time-matched significantly (Manson et al. 2004). This study demonstrated, too, that the length of time that an individual spent grooming was a significant predictor of whether its partner would reciprocate at all. However, when the two species were analyzed separately, time-matching remained significant only for the capuchins and the relationship was much weaker than in either the baboons or samangos. Interestingly, immediately-reciprocated bouts accounted for only 5–7% of the total grooming observed among the two bonnet macaque groups and only 12–27% among the capuchin monkeys. Moreover, among the macaques, grooming was signifi-

cantly unbalanced over longer time spans (although this needs to be interpreted cautiously since it is difficult *a priori* to determine the timeframe over which data should be analyzed; Barrett et al. 1999). This figure is much lower than for baboons and samangos suggesting that reciprocation is of less importance to capuchins and macaques and that the nature of the market place thus differs. One major source of difference is likely to be the fact that, unlike baboons and samangos, female capuchins (O'Brien 1993, Di Bitteti 1997, Parr et al. 1997) and bonnet macaques (Sinha 1997) are known to direct grooming down the dominance hierarchy from high-ranking to low-ranking animals. It is therefore possible that a higher proportion of capuchin and bonnet macaque grooming represents appeasement of subordinates by more dominant animals; it is a signal of 'benign intent' towards subordinates (Silk 1996), rather than an example of market-based trade for hygienic/hedonic benefits.

Despite these differences in reciprocity, rank effects were nevertheless apparent in both bonnet macaques and capuchins, with distantly-ranked dyads showing greater grooming discrepancy than closely-ranked dyads. However, for each unit difference in rank distance, a 5.8 second discrepancy in grooming was predicted for the capuchins and a 2.25 second discrepancy was predicted for the bonnet macaques; values far lower than the 28 second discrepancy predicted for the baboons. As Manson et al. (2004) suggest, rank may therefore provide a relatively poor measure of a partner's market value in these species. Alternatively, grooming simply may be a more valuable commodity for baboons compared to capuchins and bonnet macaques. As wild terrestrial animals, baboons are more likely to have higher ectoparasite loads than arboreal animals, like capuchins, or captive animals, like the bonnet macaques in Manson et al.'s (2004) study. The value of grooming is likely to be greater among baboons in much the same way that a glass of water is worth more if one is dying of thirst in the Sahara desert than if one is sitting in the middle of a lake.

12.9

Shifting power relations and the balance of trade

In addition to these cross-population and cross-species effects, a market-based approach can also help explain behavioral differences within populations of the same species over time. By monitoring temporal ecological variability, it is possible to test whether females are able to track the value of commodities and adjust their behavior accordingly. As such, it entails a more dynamic and individual-based approach to issues of power and dominance among females. Therefore, the ability to test for such effects requires that ecological conditions vary sufficiently to have an impact on the competitive regime. Fortunately, this was possible at one of our study sites, De Hoop, where the ecological regime of one of our study troops, VT, changed markedly over a short period of time (see Barrett et al. 2003 for details). This involved the loss of an entire habitat type, a dry lake bed, through natural flooding. The net result of this was a significant reduction in food competition as the troop was forced to range and feed in areas where resources were more uniformly distributed and less monopolizable.

As a consequence of this change in habitat availability, aggressive interactions dropped from over two agonistic interactions per female per hour to less than one interaction per female per hour (Barrett et al. 2003). This was because, during the low competition post-flood period, there was little benefit to be gained from using dominance to exclude females from food resources. As a result, the dominance gradient became shallower and power differentials were significantly reduced (Fig. 12.3a). Conditions at De Hoop therefore became much more like those in the Drakensberg. Related to this, we also found that aggression was targeted much more towards females of adjacent rank during the low competition period, so that there was a negative relationship between aggression rates and rank distance (Fig. 12.3b). No such significant relationship had existed during the period of high competition, indicating that females were equally likely to direct aggression to distantly-ranked, as well as closely-ranked, opponents (Fig. 12.3b). Thus, the changes in the competitive regime produced by the flood resulted in dominant females losing some of their leverage over low-ranking females; acting aggressively no longer imposed such severe costs on subordinate females or achieved high benefits for dominant females.

Given this loss of leverage by high-ranking females, and the more relaxed competitive regime reminiscent of the Drakensberg, patterns of grooming were predicted to show increased levels of time-matching, reflecting both the loss of opportunity for interchange trading for feeding tolerance and the reduced leverage of dominant females to secure themselves a better rate of exchange through the threat of potential force. In line with this prediction, time matching was more precise during the period of low competition than during the period of high competition and much more like that of HT, the Drakensberg group of equivalent size (De Hoop VT: $r^2 = 0.298$, $b = 0.558$; Drakensberg HT: $r^2 = 0.331$; $b = 0.67$) (Fig. 12.4; Barrett et al. 2003). In addition, the relationship between rank distance and grooming time discrepancy found prior to the flood was no longer present during the subsequent period when competition was low (Barrett et al. 2003). Thus, our notion that, during the high competition period, the exchange rate for reciprocal bouts was determined by the capacity for interchange plus the increased leverage of dominant females was supported by these data.

Our most recent analyses (Henzi et al. 2003) have tackled long-term patterns of grooming in relation to ecological variability and show the same patterns as these within-bout analyses. During the period of high resource competition, we found that female grooming clique size (the number of other individuals that a given female grooms) and partner diversity were higher than during the post-flood period of low competition. This is because the steeper power gradient meant that more females were in a position to exchange tolerance for grooming when competition was high. In the absence of strong competition during the post-flood period, females needed to exchange grooming only for itself, which they were able to do with a smaller set of closely-ranked partners (Henzi et al. 2003).

These results are particularly interesting because, when making our predictions regarding changes in social dynamics, we also took Seyfarth's model and determined the predictions this would make if it contained a dynamic element. According to this model, when resource competition is high, competition among

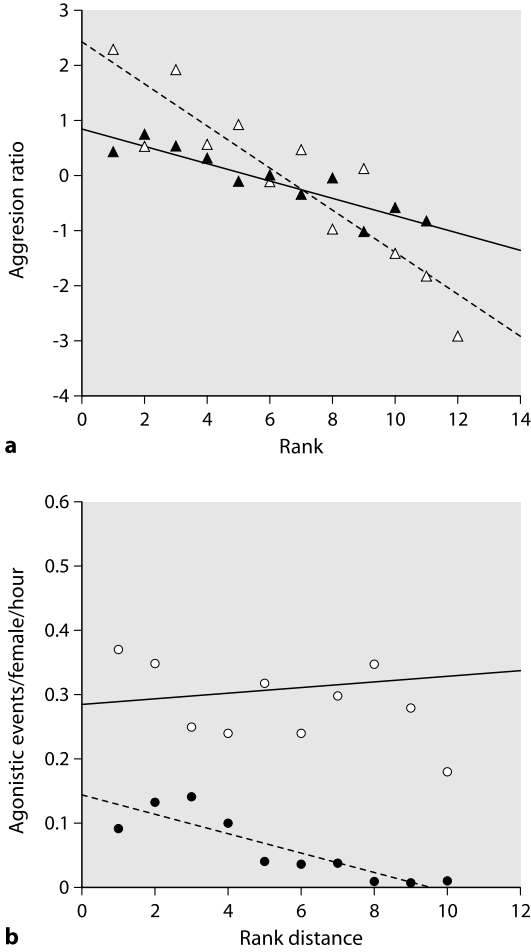


Fig. 12.3. (a) Relationship between aggression ratio (aggression given by a female – aggression received by a female) and rank for De Hoop females. The aggression ratio represents the dominance gradient of the group (Barrett et al. 2003). During the post-flood low competition period (closed triangles, solid line), the relationship between aggression ratio and rank has a significantly shallower slope than during the pre-flood, high competition period (open triangles, dotted line), indicating that the dominance gradient was reduced during the post-flood period (low-competition period: $b = 0.16$; high competition period: $b = 0.39$; $t_{19} = 3.5$, $p < 0.005$). **(b)** Relationship between overall rates of aggression and rank distance between females at De Hoop. During the low competition period (closed triangles, solid line), aggression rates decline significantly as rank distance increases ($r^2 = 0.77$, $p = 0.001$), indicating that aggression is mainly directed at females of adjacent rank. During the high competition period (open triangles, dotted line), there is no significant relationship between the two ($r^2 = 0.025$, $p = 0.645$), indicating that aggression is directed to females of all ranks (see Barrett et al. 2003). Reprinted with permission from Elsevier.

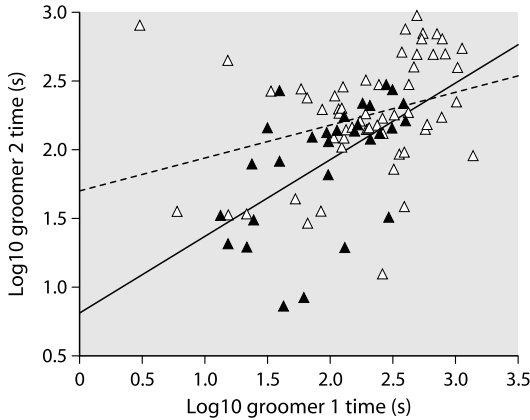


Fig. 12.4. Time-matching between De Hoop females during the periods of high competition and low competition. Time-matching is more precise during the low competition period (closed triangles, solid line), when dominant females' leverage is reduced, than during the high competition period (open triangles, dotted line) as indicated by greater explained variance and a slope that more closely approximates a 1:1 fit (low competition period: $r^2 = 0.298$, $b = 0.558$; high competition period: $r^2 = 0.099$, $b = 0.237$) (see Barrett et al. 2003). Reprinted with permission from Elsevier.

low-ranking females to gain access to high-ranking females should result in a grooming distribution where females spend most of their time grooming those of adjacent rank. Consequently, under conditions when competition is reduced and the pressure to seek out high-ranking females is relaxed, a wider grooming distribution is predicted. As should be apparent, our results are directly opposed to this prediction, demonstrating that even when a dynamic element is brought into Seyfarth's (1977) model, it still does not function as a true market-based model. This probably stems from the model's assumptions about why females seek particular partners. The fact that baboon females increase the rank diversity of their partners at times of high competition suggests that, as mentioned above, partner choice and dynamic outbidding competition structure the market, and not exclusion by dominants; when there is a greater need to interchange grooming for tolerance, high-ranking females are more often sought out as partners by all females and they are able to gain sufficient access to achieve these goals. Alternatively, Payne (in prep.) suggests that high-ranking females may use their increased leverage during high competition periods to 'extort' grooming from a wider variety of females, forcing lower-ranked females to give them more grooming. According to this argument, females do not groom to gain tolerance, but to avoid increased intolerance from dominant females. Either way, these findings support Chapais's (this volume) ideas regarding partner choice in relation to kinship. Baboon females apparently choose their partners in relation to their competence at providing a particular service, rather than directing all behavior preferentially to kin because of presumed inclusive fitness benefits.

Lazaro-Perea et al. (2004), in a study of wild marmosets, also found evidence for competence-dependent trade. In this study, the breeding female in a marmo-

set group tended to groom non-breeding females in an asymmetrical manner, giving much more than she received. This was interpreted as ‘payment’ for the services that non-breeding subordinate females had to offer; subordinate females are known to carry and share food with infants, are more active in territorial defense, and participate in alarm calling and mobbing behavior (Lazaro-Perea et al. 2004). These findings are particularly gratifying because they come from a species of non-female bonded New World monkey, showing that a market-based approach applies more broadly than just female-bonded societies in general, and Old World monkeys in particular.

12.10

The baby market: supply, demand and leverage

Although the above findings are consistent with a BM interpretation, and imply that interchange trading occurs, they do not actually show that this is the case. In order to provide full support for the BM framework, we need to show that the behavioral interaction of two trader classes is determined by fluctuations in the supply and demand of a commodity that can be exchanged for grooming.

To demonstrate interchange grooming in the De Hoop population, we exploited the fact that new-born infants are a source of great attraction for female baboons. Adult females frequently attempt to interact with both infants and their mothers in the first few months *post partum*, despite the fact that mothers are very reluctant to expose their young infants to the attentions of other group members. This set-up allowed us to measure the impact of grooming on an individual’s ability to interact with new infants. If grooming increased tolerance around infants, then females could potentially ‘buy’ access to these commodities by grooming the mother (Henzi & Barrett 2002; see also Muroyama 1994 who initially made this suggestion with reference to allomothering in patas monkeys). More specifically, the length of the grooming bout associated with infant handling should vary according to the supply of infants so that the ‘price’ (in terms of grooming bout length) should be higher when fewer infants were available. In order to test for this, we partitioned our data set into cases where the mother was lower ranking than the female handling the infant (‘handlers’ hereafter) and cases where the mother was higher ranking. This was both to control for the effects of dominance on interchange indicated in our previous work and to test whether dominance-related differences in leverage influenced exchange rates between mothers and handlers.

As predicted, grooming bout lengths were significantly influenced by the number of infants present in the group for cases where the handler outranked the mother and there was a strong trend in cases where the mother ranked above the handler (Henzi & Barrett 2002). Specifically, an increase in the supply of infants led to a reduction in the grooming bout length needed to gain tolerance, representing a classic market effect within the group. The influence of partner control within the market place was also apparent in these analyses, with higher-ranking mothers apparently able to gain more grooming than lower-ranking mothers for a given supply of infants. Plotting the relationship between the

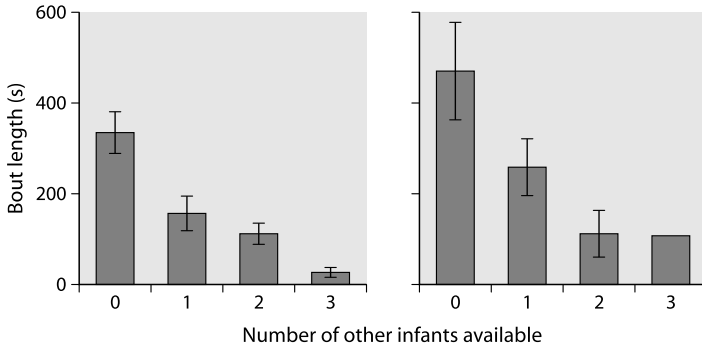


Fig. 12.5. The baby market. As the number of other infants present, in addition to the focal infant in the group, increases, so the amount of grooming given to its mother to obtain tolerance decreases. The value of the commodity (infants) is thus dictated by the supply of infants relative to the demand for handling.

rank distance of handlers and mothers against grooming time revealed a significant negative correlation; higher-ranking mothers could demand a higher price for access to their infants (Henzi & Barrett 2002). This was interpreted as a form of asymmetric price transmission; for dominant mothers, an increase in the supply of infants was not transmitted to handlers in form of reduced price. Instead, their price seemed able to stick at a higher level compared to the situation when handlers outranked mothers. However, re-analysis of these data with an enlarged data set reveals that, while a much stronger market effect is present across all females (Fig. 12.5a,b: two-way ANOVA, number of other infants available: $F_{3,32} = 3.276$, $p = 0.034$), there is no significant main effect of maternal rank ($F_{1,32} = 0.929$, $p = 0.342$) nor any interaction between maternal rank and infant number ($F_{3,32} = 0.881$, $p = 0.461$), and the correlation between rank distance and grooming bout length is no longer significant ($r_s = -0.279$, $n = 40$, $p = 0.08$, two-tailed; Fig. 12.6). However, a trend is still apparent in the data, at least for instances where there are one or fewer other infants available (Fig. 12.5a,b), and it is possible that partner control and asymmetric price transmission can only be exercised by the very highest-ranking females. The inclusion of more middle-ranking females into the dataset suggests that, overall, market forces prevail; the supply of infants is the main factor that determines the exchange value of grooming in the baby market.

Lazaro-Perera et al. (2004) also looked for interchange trading in their study of marmosets. Contrary to their predictions, breeding females did not groom other females more in times of greater need; for example, when there were more dependent infants in the group or following inter-group encounters. Payne et al. (2003) obtained similar results from samango monkeys, suggesting either that services are not, in fact, interchanged or that the exchange of services is not immediate, a point we return to below.

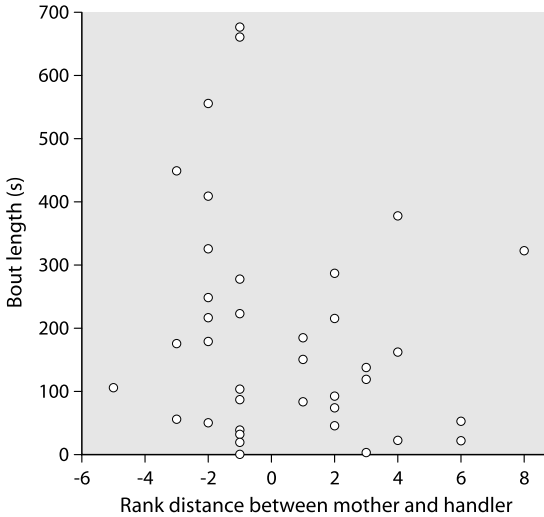


Fig. 12.6. Relationship between the rank distance of mothers relative to handlers and the grooming bout length given to mothers. There is a non-significant trend for higher-ranking mothers to receive relatively more grooming than lower-ranking mothers in exchange for infant-handling.

12.11 A market for brain power

The value of a market-based approach to understanding patterns of primate sociality seems clear and, on the strength of these results, it seems appropriate to extend work on primate markets to other species and to other arenas where commodity exchange is to be expected, such as access to resources, mating opportunities and coalitional support. The manner in which market-based trading influences other aspects of primate social behavior, such as reconciliation and other forms of conflict-management, is also worth considering (see Aureli & Schaffner, this volume). In addition, we feel that a BM approach may also pay great dividends in studies of primate cognition and tests of the ‘Machiavellian intelligence’ (Byrne & Whiten 1988) or ‘social brain’ hypotheses (Dunbar 1998). In particular, we suggest that differences in market structure may help explain differences in monkey and ape cognitive capacities, which seem to exist, yet remain poorly characterized (Barrett et al. 2003).

In primate market places, individuals track the price of commodities and respond flexibly to changes in supply and demand as we have shown. This requires cognitive and behavioral flexibility; an ability to learn rapidly and to update one’s view of the world swiftly in the light of new information. A market-based approach to primate cognition therefore agrees with the ‘Machiavellian intelligence’ hypothesis (Byrne & Whiten 1988) that sociality has driven brain evolution. It differs, however, by discarding the assumption that animals have been selected to cope with increasingly elaborate strategies and counter-strategies,

the goals of which are to 'outwit' the competition. We argue that brain size and structure have, instead, been driven by a need to track short-term fluctuations in commodity value.

Monitoring the market place is intrinsically complex; the value of a particular partner is contingent on the value of others. Each of these values may shift with changes in reproductive state, health, dominance and ongoing social behavior. Those who are good value today may not be so tomorrow. This constant state of flux means that keeping tabs on the social market is very different from the other kinds of contingent monitoring that primates must do, such as tracking fluctuations in fruit availability (Milton 1988). Fruits, unlike conspecifics, do not make decisions in response to primate behavior (except in an evolutionary sense). This inherent contingency in primate market places thus requires the ability to track the contingencies between one's own behavior in relation to others. More importantly perhaps, it also requires the ability to track the behavior of third parties in relation to each other and the behavioral consequences that this may have for one's own behavior. This has clearly selected for what Call (2001) refers to as a 'knowledge-based' understanding of others, as evidence from monkeys and, to an even greater degree, apes has shown. Nevertheless, there remains a cognitive difference between monkeys and apes that, although not precisely identified, is apparent when comparing their performance on psychological tests (Tomasello & Call 1997, Hare et al. 2001, 2003).

Our suggestion is that these differences arise as a consequence of both increased spatial and temporal dispersion in ape market places compared to those of monkeys. While monkeys are all highly gregarious and live in cohesive groups in which individuals encounter every member of their group every day, the apes (in particular, the chimpanzee and orangutan) live in more fragmented societies due to the impact of food competition, which forces females to forage in small parties or on their own. The apparent exceptions to this distinction, group-living gorillas and fission-fusion spider monkeys, are less problematic than they appear. Among gorillas, group living may be a relatively recent adaptation in response to infanticide by adult males (Harcourt & Greenberg 2001), and fission-fusion is likely to have been the ancestral ape state. The nature of spider monkey fission-fusion is not well studied and may differ from apes in important ways. If, however, their behavior is truly ape-like, then we have an ideal test case; we would predict that they manifest ape-like cognitive abilities.

In fission-fusion societies, individuals see each other only at infrequent intervals, often weeks apart, yet each recognizes and remembers the members of its community and is capable of maintaining long-standing relationships. In such systems, there will be greater pressures on individuals to mentally represent those animals that are not currently present and to retain and manipulate information about them for substantially longer periods of time than is common in spatially- and temporally-stable monkey groups, where animals are only out of view for hours at the most. This is not to say that monkeys are incapable of representation; their high performance on delayed response tasks shows that they are able to represent objects in their absence (see Tomasello & Call 1997 for a review). Rather, the issue at hand is the length of time over which this information must be retained and manipulated. Thus, while the studies we have

reviewed here reveal that baboons are highly competent market-traders, they also highlight the fact that most of the social decisions made by these animals occur over a very short timeframe; females respond to current need (access to an infant, high resource competition) when making their grooming decisions, with little indication that they plan strategically for the future by grooming in anticipation of future need (see also Barrett & Henzi 2002).

In a fission-fusion society, however, monitoring the state of the social market place requires the ability to track and update any changes observed in the interactions of others after coming into contact after a period of absence, and animals must use individuals' absence, as well as presence, to predict reliably the occurrence of certain behaviors in others. Thus, while all anthropoid primates are capable of tracking 'third-party relations' (relationships between two other animals without reference to self) (Tomasello & Call 1997), the ability to generate a causal understanding of such behavioral interactions in the absence of certain individuals would seem to be much more demanding cognitively. Thus, the key to social survival in dispersed systems is the ability to work with a social world that is partially virtual, rather than purely physically instantiated. The fact that chimpanzees are apparently able to represent the relative spatial locations of crude stone tools (hammer stones and anvils) and to use this information in a flexible manner (Boesch & Boesch 1984) supports the notion for a similar capacity in the social domain.

Recent work by Boroditsky (2000) arguing that, in humans, the sense of time emerges via a metaphorical analogy from a sense of space provides us with a means of extending our argument beyond the spatial domain. A sense of space could, with sufficient additional cognitive control, be used to develop an extended sense of time. This would then enable animals to predict future states of the market place, as well as track current changes, in a very effective way and to be able to project key aspects of social interaction and relationships onto an uncertain future. An animal with this predictive capacity would have a clear advantage over one that could only track current states and respond after the fact. Evolutionarily, once animals had a well-developed ability to understand a virtual spatial world of trading partners, this could have scaffolded the development of an understanding of temporally-dispersed trading partners as well, enabling animals to sequence social events into causal chains. This ability would enable animals to start predicting the likely consequences of behavior beyond the immediate present, enabling them to plan ahead effectively and to inhibit responses that could have negative repercussions (Barrett et al. 2003; see also Tulving 1983, Suddendorf & Corballis 1997).

One important point to note here is that we are not arguing that a dispersed social system *per se* selected for these higher cognitive abilities. After all, there are many species of lemurs and other prosimians that have dispersed social systems (see e.g. Eberle & Kappeler 2002), but that apparently have brains somewhat smaller than their testes (Peter Kappeler, pers. com.). Rather, it is the specific historical contingency of evolutionary events in the anthropoid line that produced this state of affairs. The shift to a diurnal lifestyle and group living that arose with the evolution of the anthropoids created the selection pressures for social market places like those described above. The skills needed to trade

grooming for other goods, to respond to fluctuations in the value of goods, and to play individuals off against each other were honed in the context of these stable diurnal social groups, which is why both monkeys and apes have relatively large brains, relative to prosimians and other mammals.

The evolution of the great apes as ripe fruit specialists then gave rise to dispersed social systems in which the group-based social skills of these animals were placed under the new selection pressures we outline above. A further point to emphasize is that only the social changes within the market place created the pressure to expand brain size; the ephemeral and dispersed nature of fruit supplies served to create a more fluid social system, but did not have any impact on brain size *per se* according to our hypothesis (cf. Potts 2004). Thus, ours is not a general explanation of the consequences of dispersion on brain size and intelligence, since we assume that most of the skills needed for dealing with a market-based system were already in place by the time such systems arose. Instead, it is a historically-based hypothesis dealing with the particular evolutionary pathway taken by the anthropoid apes (see also Potts 2004).

12.12 (Neuro)biological markets

In humans, the ability to plan ahead, to contemplate the future and reflect on the past, are all faculties associated with the pre-frontal cortex (PFC) (see Fuster 1989). Miller & Cohen (2001) have suggested that the actions of the PFC enable a high level of 'cognitive control' of exactly the kind that we suggest is required in a dispersed market place; namely, the ability to take charge of one's actions and direct them towards future, unseen goals. Put simply, they suggest that the role of the PFC is to guide activity flow along the neural pathways needed to solve the task, ensuring that these pathways are activated even when there is strong competition from more frequently used, but inappropriate, pathways (Miller & Cohen 2001). The impressive expansion of the PFC across the primate order suggests that monkeys, apes and humans will differ in their ability to achieve cognitive control. Both the frontal lobes (Semendeferi et al. 1997) and the PFC (Fuster 1989, Passingham 1993) of monkeys are significantly smaller than those of humans and apes (in the latter case, 11% of total cortical volume, compared to 17% and 36% for chimpanzees and humans, respectively; Fuster 1989). Neurobiological evidence thus backs up our argument that monkeys should be more limited than apes and that, by the same token, apes should be more limited than humans in their ability to plan ahead effectively over more than a few hours, or to inhibit behavior in order to achieve long-term goals.

The PFC is not the only element crucial for producing cognitive control, however. The allocation of such control is thought to be dependent on the anterior cingulate cortex (ACC), an area variously associated with error detection, response selection and, most relevant here, conflict monitoring (Carter et al. 1998, Botvinick et al. 1999, Bush et al. 2000). By detecting conflict, the ACC is able to signal to the PFC that additional control needs to be allocated to a task. It has also been suggested that the upgrading of the ACC would have been critical for

enabling animals to generate a ‘virtual group’ of spatially-dispersed individuals since it is linked to generating a sense of self in relation to others (“the troop in the head”: Skoyles & Sagan 2002). In this respect, it is intriguing that spindle cells, a class of large projection neurons found principally in the ACC region, are found only in apes and humans and not in monkeys (Nimchinsky et al. 1999). Allman et al. (2001) have speculated that these cells are involved in coordinating widely distributed neural activity involving emotion and cognition, fitting well with our speculations on the need for greater cognitive control within a dispersed hominoid market place.

12.13

Implications for primate cognition and cooperation

Having introduced the notion of improved cognitive control as the key to coping with a dispersed market place, we can predict how cognitive abilities should differ between monkeys and apes. In essence, apes should possess an analogical reasoning ability that monkeys lack, show greater abilities to solve problems that require the completion of sub-tasks while keeping an overall goal in mind, better inhibition of pre-potent responses, increased planning abilities and finally, an ability to construct and sequence longer causal chains of events. Apes are known to show higher performance than monkeys in both causal (Limongelli et al. 1994, Visalberghi & Limongelli 1995) and analogical reasoning tasks (Thompson & Oden 2001), but there have been, as yet, few attempts to test for differences in the latter two abilities. Anecdotal evidence suggests that monkeys show extreme ‘myopia for the future’ (Roberts 2002), while recent work reveals that apes show extended memory for accumulated quantity (Beran & Beran 2004). Most importantly, we can also predict that, compared to apes, monkeys will show no evidence of generating ‘contingency plans’ for future events.

This has implications for the nature of monkey trading within a market, bringing us back to our initial arguments concerning the value of grooming to female primates. If our hypothesis is correct, and monkeys are unable to plan for the future, then grooming should only be exchanged for something immediately obtainable (like access to infants) or something that does not require any monitoring of checks and balances over time. This cognitive perspective therefore provides a further reason why coalitionary support is unlikely to be traded for grooming, at least among monkeys, because the need for support is unpredictable and highly variable across time. Coalitionary support may thus be needed immediately leaving no time for support to be ‘bought’ from others. However, the ‘myopia’ of monkeys means that they will be unable to plan ahead and groom potential partners before they are needed. In any case, this would be a wasted effort due to the myopia of the partners themselves who may fail to retain the relevant information regarding the price paid. Coalitions are thus most likely to occur when there are immediate and direct benefits for the females taking part, as seems to be the case at Amboseli (Silk et al. 2004a), rather than as a result of trading favors over time in a reciprocal manner (see also Stevens & Hauser 2004 who argue for similar cognitive limitations on reciprocal altruism).

Trading for something like feeding tolerance is different, both because it may be immediately obtainable and because some form of 'attitudinal reciprocity' can work as a mechanism (De Waal 2000c); regular grooming may change the general attitude of the groomee towards the groomer, putting them in a more relaxed state about the groomee, so that grooming could have a long-term effect with little loss of value over time and without requiring extensive 'book-keeping'. The same may be true for helping behavior (Lazaro-Perea et al. 2004). However, it seems unlikely that reducing tension in a partner would have the effect of increasing the willingness of such a partner to take aggressive risks on another's behalf and engage in coalitionary support (we thank Ronald Noë for pointing this out).

A focus on tolerance, how it is traded and the timeframe over which it operates, is the logical next step in our analyses, since it has important implications for our assumptions about what can and cannot be traded. If the cognitive timeframe over which baboons operate is fairly short, animals will be unable to groom too far in advance to achieve their goals. If so, then grooming "is not a hard currency but chocolate money that melts away" (R. Noë, pers. com.). Determining whether baboons are dealing in hard cash or perishable goods, and how this affects exchange rates over time, is an important goal for the future.

12.14

Summary and conclusions

Data from baboons, and an increasing number of other primate species, support the notion that primate groups represent 'biological markets', within which individuals 'trade commodities' with each other (e.g. grooming, tolerance, helping behavior) according to the laws of supply and demand. Grooming reciprocity among female chacma baboons is driven by market forces generated by the ecological and competitive circumstances under which they live, so that levels of cooperation vary across both space and time. Females also interchange grooming for tolerance around infants, with the 'price' of grooming set by the local supply of infants as economic theory predicts. Thus, the dynamic, individual-based approach of BM theory, with its emphasis on partner choice, is a much more appropriate framework within which to analyze primate cooperation than alternative models, like those based on the iterated Prisoner's Dilemma (Axelrod 1986).

Market-based theories can also shed light on other aspects of primate sociality, including the evolution of primate cognition. Monitoring a social market place that is in a constant state of flux requires high levels of cognitive and behavioral flexibility, but does not require that primates have to be especially 'Machiavellian' in their attitude to others. Differences between ape and monkey market places in terms of the spatial and temporal dispersion of individuals, and the timeframe of social decision-making provide us with a plausible and testable hypothesis concerning the evolution of primate social intelligence.

This, in turn, has implications for human evolutionary psychology and, specifically, the notion of 'massive modularity', the idea that selection has produced a mind comprised of computational algorithms designed to solve specific re-

curing problems. If, as we suggest, primate groups, including those of humans (La Cerra & Bingham 1998), constitute market places, then a massively modular psychology seems unlikely; the contingency inherent in a market means that what constitutes a fair trade today may actually be a dodgy deal tomorrow. A computational cheat-detection module, for example, triggered by certain conditions such as ‘taking the benefit without paying the cost’ (Cosmides & Tooby 1992) will be doomed to giving the wrong answer most of the time, because the truth of such a statement is entirely contingent on the state of the market. As La Cerra & Bingham (1998) point out, a more flexible form of decision-making is needed under such circumstances; one that can cope with these ever-changing contingencies and one for which the human PFC is well designed.

In line with this, it is clear from the work of Gächter & Herrmann (this volume) and Millinski (this volume) that human decisions regarding cooperation and cheating are contingent on the context in which individuals find themselves. While these may be emotionally-mediated actions, as opposed to perfectly rational ones, they are not automatic, involuntary or mandatory as a modular response would require. Nor do these decision ‘mistakes’ reflect the operation of ancient decision-making mechanisms selected for in small kin-based groups; if female baboons, who live in small kin-based groups, can differentiate among their kin according to the services they have to offer, as our work demonstrates, then it seems unreasonable to expect human decisions to be based on a much more crude rule of thumb. Rather, our decisions are the creative, flexible and contingent responses of a primate well versed in the workings of a biological market, with a flexible mind and brain to match.

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