Supply and demand determine the market value of food providers in wild vervet monkeys

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Animals neither negotiate verbally nor conclude binding contracts, but nevertheless regularly exchange goods and services without overt coercion and manage to arrive at agreements over exchange rates. Biological market theory predicts that such exchange rates fluctuate according to the law of supply and demand. Previous studies showed that primates pay more when commodities become scarcer: subordinates groomed dominants longer before being tolerated at food sites in periods of shortage; females groomed mothers longer before obtaining permission to handle their infants when there were fewer newborns and males groomed fertile females longer before obtaining their compliance when fewer such females were present. We further substantiated these results by conducting a 2-step experiment in 2 groups of free-ranging vervet monkeys in the Loskop Dam Nature Reserve, South Africa. We first allowed a single low-ranking female to repeatedly provide food to her entire group by triggering the opening of a container and measured grooming bouts involving this female in the hour after she made the reward available. We then measured the shifts in grooming patterns after we added a second food container that could be opened by another low-ranking female, the second provider. All 4 providers received more grooming, relative to the amount of grooming they provided themselves. As biological market theory predicts, the initial gain of first providers was partially lost again after the introduction of a second provider in both groups. We conclude that grooming was fine-tuned to changes in the value of these females as social partners.

biological markets | cooperation | economic behavior | primates | reciprocity

Trading in humans and cooperation in animals are part of a continuum in which both human and nonhuman agents usually have to take 3 crucial steps: (*i*) choose a partner, (*ii*) determine how much to invest to obtain the desired commodities, and (*iii*) prevent being short-changed by the chosen partner. While research in economics traditionally concentrates on factors that determine the price of commodities, quantitative aspects have gained much less attention in studies of nonhuman cooperation (1). Over the past decades, cooperation research has focused mainly on the question of partner control rather than on the relative values of goods and services exchanged. By contrast, the biological market paradigm (2, 3) focuses on the link between steps *i* and *ii* and predicts that the law of supply and demand affects the exchange rates in nonhuman "trading" in a similar fashion as in human economic exchanges. Here we test this prediction in 2 wild vervet monkey groups by measuring changes in grooming patterns after experimentally changing the number of individuals that could provide food to their group.

We envisage the exchange of commodities in primate groups as trading on a market with exchange rates fluctuating from day to day depending on supply and demand. Monkeys trading goods and services have to agree on exchange rates to avoid overt conflicts, but lack the option of negotiating verbally and concluding binding contracts. Not all commodities exchanged among nonhuman primates can be adapted in quantity or quality during each interaction, but 1 service, grooming, can be adjusted easily. Grooming can be exchanged against grooming itself, but also against other goods or services, lending it currency-like characteristics. Commodities bought with grooming include tolerance at food sites (4–9), access to newborns (10, 11), compliance of females (12), and support in conflicts (13–15), although results on grooming–support exchanges have been mixed (16–18). Monkeys do not necessarily track value fluctuations for each commodity on the market separately, however, but they may change their general attitude toward group members (19) in accordance with the accumulated value of the different commodities each one of them has on offer. Mechanistically the value attributed to a partner is likely to be expressed in physiological parameters such as titers of neurohormones and neurotransmitters implicated in trust and pair bonding (20–25).

We created an artificial market in 2 groups of wild vervet monkeys in the Loskop Dam Nature Reserve (South Africa) and caused sudden changes in the market value of a few animals in such a way that these affected all other group members and could easily be perceived by them. After an initial phase in which we gathered baseline data on grooming (phase 0), we allowed a single low-ranking female in each study group to produce a bonanza of food for herself and her group members by triggering the opening of a container (Movie S1) in 16 trials spread over a period of 9 weeks (phase 1). These first 2 stages resemble a study previously done in captivity with long-tailed macaques (26). In that experiment, a single individual that could produce a small food reward and share it with up to 2 other animals experienced an increase in social status. We developed this paradigm further to show the quantitative effects of a shift in supply on grooming patterns. This requires a manipulation either of the amount of reward per provider or of the number of providers. We opted for the latter approach because it is very hard to control the amount of food each individual will obtain once the provider made it available. In phase 2 of the experiment we therefore introduced a second provider in each group, another low-ranking female with a second food container (Movie S2) that only she could open. The same amount of food (5 apples per trial sliced in small pieces) was now divided over the 2 containers that were made available simultaneously, but that were not necessarily opened simultaneously. In economic terms we thus replaced a monopoly by a duopoly. Agents enjoying a monopoly should obtain stronger leverage over their
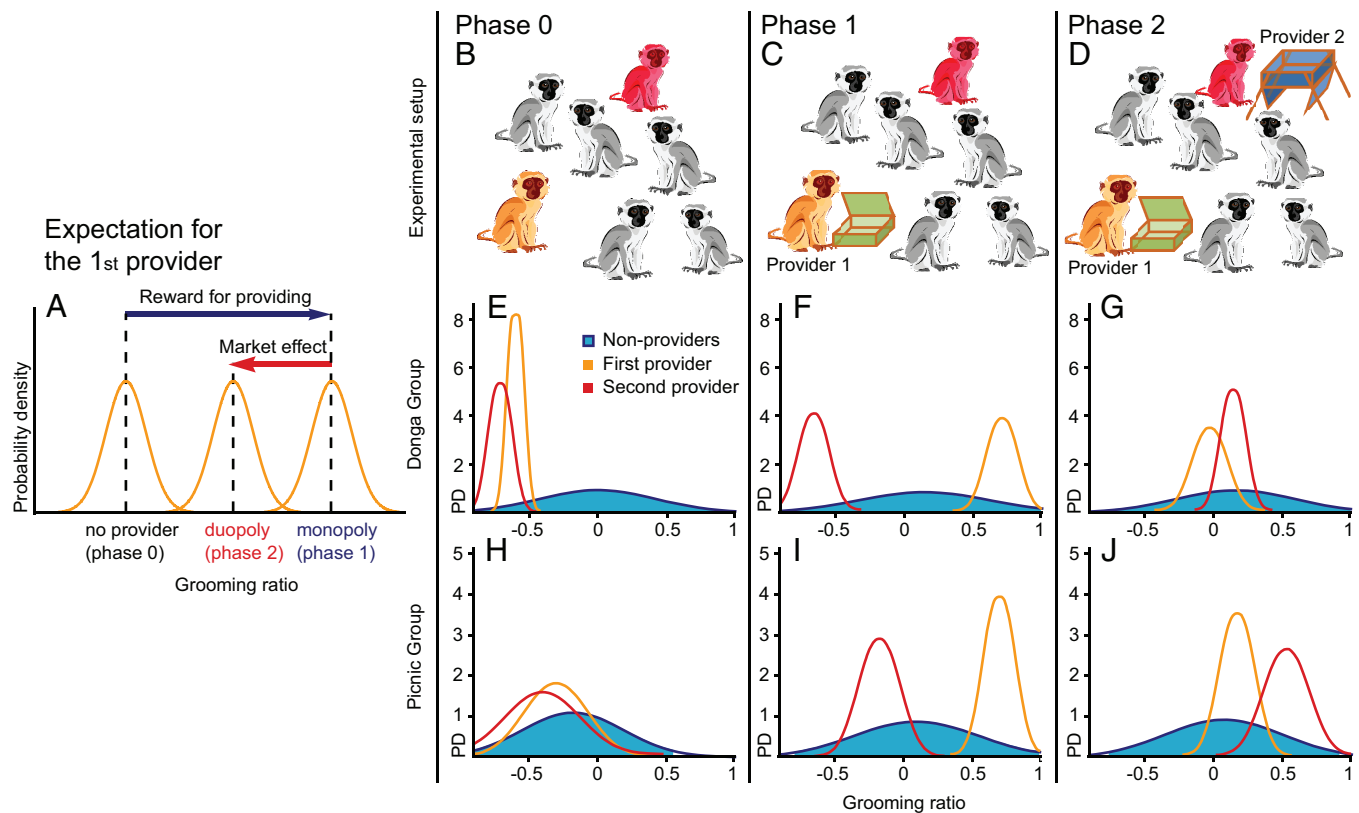
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Fig. 1. Mean estimates of the grooming ratios for the food provider. (*A*) Expected effects. In phase 0 of the experiment each individual has a specific ratio of grooming received versus grooming given. In phase 1 (monopoly) the grooming ratio of the single food provider should increase (reward for providing). But, as soon as an additional provider is introduced in phase 2 (duopoly), the grooming ratio of the first provider should decrease again as a consequence of the increased supply of food providers (market effect). (*B–D*) Schematic representation of the 3 experimental phases. Probability density (PD) functions are shown of mean estimates for grooming ratios of nonproviders (blue), first provider (orange), and second provider (red) in phase 0 with no provider (*E* and *H*), phase 1 with one provider (*F* and *I*), and phase 2 with 2 providers (*G* and *J*) for the Donga group (*E–G*) and the Picnic group (*H–J*).

exchange partners than members of a competitive duopoly. This leads to our main prediction: grooming ratios should increase in favor of the provider in phase 1 and decrease again with the introduction of a competitor in phase 2, as depicted in Fig. 1*A*. We used the ratio of grooming given relative to grooming received as our main parameter, because we expected that group members could pay the providers both by grooming them more and by demanding less grooming from them.

There is considerable discussion about the function of grooming in primates. A first basic assumption is that grooming entails a net cost to the groomer and provides a net benefit to the groomee. In free-ranging groups, grooming is very likely to have an opportunity cost in the form of lost foraging time and lowered vigilance (27). Captive animals, in contrast, sometimes groom excessively, out of boredom, or in the form of a pathological stereotypy, thus removing the incentives to reduce grooming payments to a minimum. However, even in the wild primates groom each other much more than can be explained by its hygienic function, the most likely ultimate function of allo-grooming (22). The proximate mechanisms that make monkeys enjoy being groomed include the release of several neurotransmitters and neurohormones implicated in the brain's reward circuit, analogous to the reaction of human subjects to touch (22, 23). Enjoying being groomed is a bit like enjoying eating: the proximate mechanisms are such that the system easily overshoots the original ultimate goals. Additional functions may be served, such as building up fat reserves when eating or strengthening the bonds between individuals when grooming. In primates the latter is now probably more important than the hygiene of the fur (22).

The crucial question here is not, however, what the exact function of grooming is, but whether grooming is sufficiently costly to underlie market forces, in the sense that animals prefer grooming another animal shorter rather than longer if the effect remains the same. We follow the tradition of estimating the amount of grooming by the length of time a grooming bout lasts. Although the value of a unit of grooming time may drop as the grooming bout progresses, it seems safe to assume that longer bouts have higher value than shorter ones within the same dyad. Expressing the value of grooming in time units also makes our results more easily comparable with a recently published formal market model that used time units to express the value of services (28). We felt confident that grooming patterns underlie market forces, because market effects had already been shown in several studies apart from our own (7–12).

We chose low-ranking females as providers, because lower-ranking individuals in primate species with clear dominance hierarchies tend to groom higher-ranking members of their group more than vice versa (among others, refs. 4, 5, 8, 9, 29, and 30). The reason behind this is that a dominant individual can offer several resources, apart from grooming, that the subordinate cannot match in value: support in agonistic conflicts, tolerance at resources, or even simply restraint in aggression. We therefore expected to see much stronger effects in low-ranking providers than in high-ranking ones.

What exactly are our providers offering their group members? Each provider opened a container with enough pieces of apple to give every group member a good chance of getting hold of some food in a free-for-all determined mainly by dominance. At

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first sight, providers would not seem able to give food to some members more than to others, which implies that partner control strategies, such as reciprocal altruism (30) or tit-for-tat (31), cannot play much of a role. Reciprocal altruism has been construed in a narrow and in a broad fashion. Models using the narrow interpretation, which are usually based on variations of the 2-player iterated prisoner's dilemma, allow precise predictions about the behavioral contingencies of 2 partners in repeated interactions. The few studies in which these predictions have been tested in primates yielded negative results (32, 33). This narrow interpretation does not apply to our experiment, because a priori our providers cannot make a strategic choice that is simultaneously contingent on behavior of group members that treated them differently in the previous "round."

In a much broader interpretation, reciprocal altruism encompasses all forms of partner control mechanisms in which individuals reward or punish their partners on the basis of past behavior. One way in which our providers could give some group members an advantage over others is by making the timing of opening contingent on the past behavior of the group members near the container, assuming that being near gives a competitive advantage. This way the provider could, to a limited extent, individualize the commodity offered. This still does not mean that providers can play dyadic games with all their group members simultaneously, but they could exert some partner choice this way. Partner choice is the core mechanism driving biological markets, but is not taken into account in reciprocal altruism and other partner control models.

In summary, these considerations lead us to expect (*i*) baseline grooming ratios to be skewed in favor of more dominant individuals, (*ii*) grooming patterns to change strongly in favor of the first providers, but to become less favorable again when the second providers are introduced, and (*iii*) providers to open the containers preferably in the presence of those grooming them most.

Results

The grooming ratio can shift in favor of a provider in several ways: either the provider can groom less or her group members can groom her more, or both. It is perhaps easier to adjust a grooming ratio to one's own advantage by grooming less than by persuading the other to groom longer, but this does not warrant strong predictions about shifts in absolute grooming bout lengths. We therefore used grooming ratios per dyad, calculated as time being groomed minus time spent grooming divided by total grooming time, which yields values between −1and 1. In the experimental phases, grooming data were recorded during 1 h after the containers were opened. We had expected to see changes in grooming patterns before the containers were opened too, but in practice we could not measure this. Early in the series of trials the animals were too excited to sit down for a grooming session with food visible in the closed container and at a later stage the providers often opened the containers almost immediately, leaving no time for grooming sessions [see supporting information (SI) Table S1 and *SI Text*].

In the preexperimental phase 0 we measured baseline grooming ratios, which were highly correlated with the relative rank difference of the corresponding dyads [Mantel test (ref. 34), combined probabilities (ref. 35): $\chi^2 = 25.69$, $P < 0.001$; see Fig. S1]; i.e., the larger the rank difference was, the more lopsided the grooming effort was in favor of the dominant.

The grooming ratios of the providers differed significantly among the 3 phases (Friedman test, combined probabilities: first provider, $\chi^2 = 26.25$, $P < 0.001$; second provider, $\chi^2 = 18.59$, $P < 0.001$). After showing that the overall experiment yielded a highly significant result, we proceeded with a number of post hoc sign tests. The grooming ratios for the first providers in each group changed according to expectation (Fig. 1*A*): the ratio

increased significantly in favor of the provider from the nontest phase 0 to test phase 1 (single provider: $\chi^2 = 15.25$, $P < 0.01$). Grooming ratios for the first provider dropped significantly again when the second provider was added in phase 2 ($\chi^2 = 15.25$, $P < 0.01$), but remained significantly above the control values of phase 0 ($\chi^2 = 15.25$, $P < 0.01$). As expected, the grooming ratios for the second providers did not change significantly between phases 0 and 1 [$\chi^2 = 3.54$, not significant (NS)], but their ratios shot up when they became providers themselves in phase 2 ($\chi^2 = 15.25$, $P < 0.01$). The provider effect was so strong that it more than counterbalanced the dominance effect. The strongly negative grooming ratios of the low-ranking females we measured in phase 0 turned into positive values once they became providers. To evaluate whether these changes for providers were indeed outside the range of fluctuations found in the nonproviders (e.g., because of seasonal changes), we estimated mean changes in grooming ratios for both providers and nonproviders, using a hierarchical bootstrap resampling procedure to deal with dependencies among dyads (36) (Fig. 1 *I* and *J*). The differences in grooming ratios between the nontest phase 0 and phase 1 were significantly greater for the first providers than for the group of nonproviders (Donga group, $P < 0.0001$; Picnic group, $P = 0.0005$; combined probabilities, $\chi^2 = 54.65$, $P < 0.001$). Grooming ratios increased significantly for both second providers compared to the nonproviders in phase 2 (Donga, $P < 0.001$; Picnic, $P = 0.040$; combined probabilities, $\chi^2 = 102.72$, $P < 0.001$). Comparing grooming differences between the nontest phase and phase 2, we found a significant difference between the first provider and the group of nonproviders in the Donga group, but not in the Picnic group (Donga, $P = 0.0029$; Picnic, $P = 0.91$; combined probabilities, $\chi^2 = 11.90$, $P < 0.025$).

These changes in grooming ratios were not because of a change in behavior of a few individuals, but were visible in a broad range of dyadic relationships (Fig. 2). In 13 of 15 dyads the providers groomed less in an absolute sense, compared to the preexperimental phase. In 4 dyads, 2 in each group, the nonproviders groomed the providers more. Three of these 4 were among the 13 in which the nonproviders were groomed less.

We also verified whether providers attempted to give specific individuals a head start by opening the container preferentially in their presence. They could be expected to do so for 2 classes of individuals: (*i*) long-term friends or kin with whom they had a positive relationship and (*ii*) animals that groomed them specifically in the context of the trials. Providers did not open the containers preferentially when their preferred grooming partners from phase 0 were nearby (Donga group, Spearman rank correlation, first provider, $r_s = 0.31$, $n = 9$, NS, and second provider, $r_s = 0.52$, $n = 9$, NS; Picnic group, Spearman rank correlation, first provider, $r_s = 0.13$, $n = 6$, NS, and second provider, $r_s = -0.25$, $n = 6$, NS), but in both groups we found, in phase 1, that an individual that happened to be the nearest neighbor at the moment of opening was significantly more likely to groom the provider (single provider: Donga group, $\chi^2 = 33.69$, df $= 9$, $P < 0.001$; Picnic group, $\chi^2 = 13.5$, df $= 6$, $P = 0.036$; combined probabilities, $\chi^2 = 25.06$, df $= 4$, $P < 0.001$). During test phase 2, this effect was also found for the first providers (combined probabilities for the first providers of both groups: $\chi^2 = 10.33$, df $= 4$, NS), but not for the second providers (combined probabilities for the second providers: $\chi^2 = 6.38$, df $= 4$, NS). Thus, the first providers were likely to be engaged in grooming sessions with individuals that were near the container when it opened and thus probably got more food than latecomers (see SI for details of statistical tests).

Discussion

In agreement with an earlier study (26), we found that grooming ratios shifted to the advantage of female vervets that produced food bonanzas. Our crucial result, however, lies in the quanti-
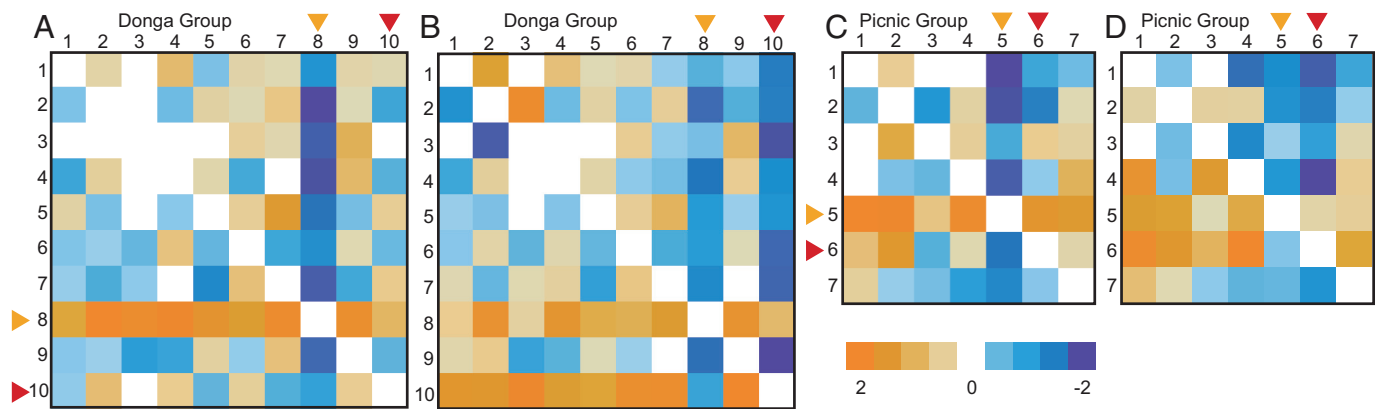
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Fig. 2. Changes in dyadic grooming ratios. Differences are shown between phase 1 and phase 0 for the Donga group (*A*) and the Picnic group (*C*) and between phase 2 and phase 0 for the Donga group (*B*) and the Picnic group (*D*). Individuals are ordered by rank, and 1 equals the highest ranking animal. Rows, groomers; columns, groomees. Values were calculated by subtracting grooming ratios of phase 0 from those of phase 1 or 2, respectively. As original ratios ranged between −1 and 1, differences could range between −2 (blue, maximum shift in favor of groomer) and 2 (orange, maximum shift in favor of groomee). First providers are indicated by orange arrowheads and the second producers by red arrowheads.

tative shifts of the exchange rate between grooming and providing food: the positive effect on the grooming ratios of the first providers was roughly half as strong after we added a second provider in each study group, confirming a central tenet of biological market theory (2, 3, 28). Similar market effects have hitherto been reported only for primates exchanging grooming for access to naturally occurring commodities (4, 5, 8–12).

Grooming ratios were adapted rather quickly to changing circumstances and we therefore assume that this reflects strategic behavior that forms part of the natural repertoire of vervets. Allowing some animals to produce food sources for themselves and their group members by opening a container is obviously rather artificial. However, it is not necessarily uncommon or unnatural for a primate group to gain access to a large food source because of a single group member. Two phenomena come to mind: animals giving a food call after finding a large resource (37–40) and experienced "leaders" (41) guiding their group to crucial resources (42–44). Neither phenomenon is found in all primates, or unique to primates, but both are sufficiently common to make the existence of mechanisms encouraging food providers likely. Our providers might be comparable to leaders, which in primates can be high- as well as low-ranking females (43, 44), because in both cases the same individual produces a communal resource repeatedly, thus giving their group members time to recognize their special skills. In all 3 cases, food calls, leading, and our experiment, the animal producing the resource may act on purely selfish motives. Leaders and providers may forage for themselves and produce food for others as a by-product and food calls might be given only upon finding large and shareable resources to protect the caller against predators by improving the "safety-in-numbers" (37, 41, 45).

A provider can be expected to open the food container sooner or later out of pure self-interest, as long as she gets some food herself without experiencing unusual harassment. Why would group members pay for something they would obtain by simply waiting long enough? We assume that vervets, like many other animals, discount future benefits and value a reward more the sooner it becomes available (46). In addition there was a clear opportunity cost of waiting near the closed food container, because the group could not continue its normal foraging routine.

It seems reasonable to assume that only a limited amount of grooming—irrespective of who provides it—is needed to induce the providers to open their containers. In that case, each of the nonproviders would have been better off if others provided all

of the grooming needed. The nonproviders would thus be caught in a collective action dilemma, a situation that resembles the notoriously unstable *n*-players prisoner's dilemma (47). So why did the whole group change its grooming behavior to the advantage of the providers or, in other words, how could an individual willing to groom the provider do better than an animal that did not groom her?

The provider could make the timing of opening dependent on the presence or the absence of specific group members. The providers were indeed reluctant to open their containers in the presence of high-ranking animals. Providers were also more likely to be groomed by nonproviders that were near the containers at the moment they were opened than by nonproviders that were farther away. We see 4, not necessarily mutually exclusive, interpretations of this phenomenon: (*i*) those that ate more during a trial were more inclined to groom, (*ii*) grooming improved long-term bonds and the providers preferably opened the containers in the presence of group members they trusted, (*iii*) grooming and opening the container were exchanged in a reciprocal altruism-like fashion, and (*iv*) grooming ratios reflected the stress level of the providers rather than their market value.

(*i*) Grooming sessions often follow longer periods of foraging. A simple explanation would therefore be that those with fuller bellies were inclined to groom more. This can explain more grooming by those that obtained most of the resource, such as the provider and others near the container at the moment of opening, but this cannot explain the shifts in grooming ratios we observed.

(*ii*) Nonproviders could have groomed the provider to improve their affiliative bond with her. Candidate neurobiological mechanisms are those usually connected to trust, pair bonding, and friendship, such as increased titers of oxytocin, vasopressin, and endorphins, which notably follow friendly forms of touching (reviewed in refs. 24 and 25). The attitude toward a group member can be improved by any good or service received from that individual, but grooming is the standard service every vervet has handy.

Grooming to gain trust is reminiscent of a mechanism De Waal (19) labeled "attitudinal reciprocity," which is a generalized bookkeeping mechanism based on multiple interactions in which the more recent interactions tend to weigh more than those from a more distant past. "Attitudinal partner choice" would be a more accurate term in the present case, but the idea

remains the same: the animals are assumed to be driven by emotions reminiscent of those felt by humans toward friends.

(*iii*) Grooming the provider can also be interpreted as contingent on the provider's behavior; in other words, the provider is prepaid in the expectation of returns during the next trial. This would imply a more accurate form of bookkeeping in the sense of De Waal's "calculated reciprocity" (19) and would suggest cognition to be in the driver's seat. For this reciprocal altruism-like mechanism to work the groomers must have been willing to invest in a future reward that could be reaped 1 or more days later. Investments in uncertain returns over such long periods could be beyond the cognitive capacities of monkeys, however (48). Calculating providers should have been ready to make spiteful decisions costly to themselves, and also to those who groomed them, by not opening the container to punish those not willing to shift the grooming ratio in their favor. The provider could eventually have punished specific individuals by waiting till they were at some distance from the container. It is highly unlikely that our providers used this rather complicated tactic, however, because they opened the container almost immediately in the later trials (Table S1).

(*iv*) An explanation for dynamic changes of primate grooming patterns that does not invoke the law of supply and demand (10, 49) is based on the idea that the proximity of group members causes stress to those controlling interesting commodities. More attention would cause more stress, which in turn would require more grooming to calm the provider. This stress hypothesis has notably been suggested for "baby markets": the level of anxiety of mothers would increase with the number of females vying for their infants simultaneously and the amount of grooming needed to calm the mothers would increase accordingly (10, 49). However, the stress hypothesis also predicts that high-ranking handlers, who cause more stress (50), would have to groom longer than low-ranking ones. The opposite was found, however (9–11, 29), which makes sense from a market perspective: high-ranking individuals can compensate low amounts of grooming by offering tolerance, restraint, and/or support, which all have higher value the higher ranking the donor is. In our study higher-ranking individuals also groomed the commodity providers less than lower-ranking ones. Moreover, in the relaxed period after the consumption of the reward during which we measured grooming times, the providers were no longer under extraordinary attention.

The question remains whether the grooming patterns observed after the containers were opened could indeed be interpreted as rewarding and/or prepaying the providers. Not all group members groomed providers more; some also accepted shorter grooming bouts from the providers compared to the preexperimental phase. Again this makes sense if one thinks in terms of mechanisms of price setting in a market: during a grooming session both partners can test their momentary market value by ending a grooming bout and monitoring their partner's reaction. Providers were probably confronted with less dissatisfaction if they groomed others only briefly, while at the same time their own signs of dissatisfaction carried more weight. A price-setting process is dynamic and grooming ratios can thus be adjusted in several ways: one party grooms less, or the other grooms more, or both.

In conclusion, the adjustment of grooming ratios can be understood as a continuous bargaining process in which bargaining positions depend on the perception of the other's value as a partner in a long-term perspective. Grooming plays a dual role in this process: it functions both as a currency, because of its direct influence on the reward system of the groomee, and as a commodity, because it can be traded directly for access to infants, for tolerance, and so forth. Grooming can thus be used to balance asymmetries in trades of other commodities. In our experiment this balance shifted suddenly, and grooming patterns were quickly adjusted, when we experimentally created a monopoly, and shifted again when we turned the monopoly into a duopoly. Thus, free-ranging monkeys can accurately adjust to shifting markets, although they cannot rely on language for bargaining and have no obvious way of concluding binding contracts.

Methods

Observer Team. The observer team consisted of the first author and 7 different assistants: E. van de Waal (September 2005 to January 2006), S. Lemoine (February to May 2006), V. Dufour and S. Aubel (May and June 2006), E. Hellard and A. Brotz (June to August 2006), and E. Hellard and D. Carter (September 2006).

Research Area and Subjects. We used 2 free-ranging vervet monkey groups, *Chlorocebus aethiops*, in the Loskop Dam Nature Reserve, Mpumalanga Province, South Africa. Loskop is located at 180 km northeast of Pretoria, covers ≈25,000 ha, is on average 1,000 m above sea level, and consists mainly of "bushveld" (tall grasses and thick acacia bushes). Winters (May to October) are dry and cold and summers (November to April) are hot and humid.

Both study groups were habituated to human observers before the start of the experiments. Their home ranges of ≈3 km² each were ≈3 km apart. The Donga group had a period of fast turnover of adult males before the study period but the total group size never exceeded 15. We observed 3–5 adult males, 7 adult females, 1–2 subadult individuals, and 1–2 infants at a time. The Picnic group had 2–3 adult males, 4 adult females, 1 juvenile, and 2–6 infants at a time. The dominance hierarchies remained stable throughout the study period. For the experiment, we selected the 2 lowest-ranking females that would accept manipulating the containers as food providers.

Experiment Protocol. The experiment had 3 phases: a period without a provider (phase 0, September 2005 to April 2006, 221 observational sessions for the Donga group and 191 for the Picnic group, of which we randomly chose 55 sessions per group for analysis), a period with 1 provider per group (phase 1, May to June 2006, 16 trials per group, always the same female as a provider), and a period with 2 providers per group (phase 2, August to September 2006, 22 tests per group, the same first provider plus a second one). Both experimental phases were preceded by a period of training in which the providers learned to touch the lid of their specific food container.

The groups were followed every second day during phase 0 and 2 days in a row every 4 days during the 2 testing phases 1 and 2. In phases 1 and 2 we waited until the animals reached a suitable area (open with big trees nearby for the vervet monkeys to rest safely) before positioning the food container. After a provider opened the container, we recorded all grooming interactions within the following 60 min. Each approach to and opening of the containers by the providers was recorded with digital video cameras (Samsung VP-D361i and Panasonic NV-GS11). One observer (C. Fruteau) continuously followed the provider while 2 assistants recorded the interactions of the rest of the group. All agonistic and affiliative interactions were recorded continuously (51) and the distance between every visible vervet and the experimental containers was recorded in 30-s intervals. Grooming bouts were timed to the nearest second. A bout was considered to have ended when either the direction of grooming changed or there was a break of 20 s. A trial was aborted if 1 or both of the providers did not open their container during 1 h, which happened 5 times in phase 2 for the Donga group and once in phase 2 for the Picnic group. The procedure for phase 2 was identical to the trials in phase 1, except that 2 containers were placed simultaneously at ≈2 m distance from each other (Movie S2). The reward was the same as in phase 1 and evenly distributed over the 2 containers. Both providers were followed by 1 observer, each, while a third observer recorded the interactions between the remaining members of the group.

Observations were distributed throughout the day but the majority of the data were taken from 6 a.m. to 1 p.m. and from 4 p.m. to 6 p.m. We used Pendragon Forms (professional edition 4.0.00) on Palm Zire 31 handheld computers for all behavioral data. Births, immigrations, disappearances, and intergroup encounters were recorded on a daily basis.

Food Containers. We worked with 2 containers (50 × 55 × 15 cm) with wooden frames that were both covered with a plastic mesh on all sides and reinforced with a metallic grid on top, allowing the vervets to see and smell the food (Fig. S2*A* and Movie S1). The second container stood on 50-cm legs and had a split bottom, causing the food to drop to the ground (Fig. S2*B* and Movie S3). The containers were filled with a total of 5 chopped apples per test. This was sufficient to ensure that most adults got a share. The obvious differences in

form and color made it easy for both providers and nonproviders to attribute a specific device to a specific provider. The containers were unlocked by remote control (a car door locking device) as soon as the provider touched the lid.

Training of Providers. To habituate all animals to the food containers and to train the providers to operate them, we conducted a training phase with 24 trials per group from October 2005 to mid-January 2006 for the first providers and a training phase with 12 trials per group for the second providers in July 2006. We provided 5 chopped apples per trial and we opened the container by remote control as soon as the selected provider touched it. The trials were not time restricted; i.e., we waited until the providers dared to come and open their container. During the first training phase, dominant individuals tried to monopolize the food as soon as the container was opened, which led to serious harassment of the low-ranking providers. We placed 2 extra apples (also cut into pieces) outside the container as soon as the provider had opened the container to reduce this harassment. This additional food supply was not necessary for the second training phase, where harassment of the providers was much lower. It took only 1 trial for 3 of the providers to come to touch the container by chance. The second provider of the Donga group touched the container for the first time in the fifth trial. Throughout the training phases, the time required by the providers to open their container dropped quickly:

first providers, Donga group, from 35 min to <1 min, and Picnic group, from 120 min to <10 min; second providers, Donga group, from 55 min to <2 min, and Picnic group, from 75 min to <10 min. None of the providers attempted to open the container attributed to the other provider after the training phase.

Statistical Tests. We give only combined probabilities for both groups whenever the same effects were found in both. Raw data and separate probability estimates are given in Tables S1–S5. Rank order and linearity indexes were determined with the MATMAN software (34), and all other computations were made with MATHEMATICA 6.0 (52).

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