



Is grooming used as a commodity in wild white-handed gibbons, *Hylobates lar*?

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Biological market theory is an extension of the idea of reciprocal altruism, as a mechanism to explain altruistic acts between unrelated individuals in a more flexible system of exchanging commodities. In nonhuman primates, social grooming has been used to test predictions in both contexts: reciprocal altruism or biological markets. Specifically, in species in which males cannot coerce females to mate, males may attempt to interchange grooming for mating, particularly when females are fertile and mating opportunities are more likely to arise. We tested whether wild white-handed gibbon males from Khao Yai National Park, Thailand, increased their grooming activity when the female partner was fertile. Adult females and males of our study population are codominant (in terms of aggression), they live in pairs or small multimale groups and mate promiscuously. We analysed grooming episodes during 2760 observation-hours in 12 groups separately for females' reproductive condition (cycling/pregnant/lactating) based on noninvasive measures of ovarian hormone activity. We found that males groomed females more than vice versa and more grooming was exchanged when females were cycling than during pregnancy or lactation. The number of copulations/day was elevated when females were cycling, and females copulated more frequently with males on days when they received more grooming. When males increased their grooming efforts, females also increased their grooming of males, perhaps to equalize give and take. Although grooming might be reciprocated because of intrinsic benefits of receiving grooming, we conclude that males also interchange grooming as a commodity for sexual opportunities during a female's fertile period.

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Trading commodities and services in identical or different currencies has been suggested as a mechanism adopted in animals to solve conflicts of interest and resulting in successful reproductive strategies (Noë 2006a). In nonhuman primates, for example, social grooming is an affiliative behaviour commonly offered and exchanged for itself in reciprocal fashion (Gomes et al. 2009; Schino et al. 2009) or interchanged, for example, for tolerance (Ventura et al. 2006; Port et al. 2009), coalitional support (Seyfarth & Cheney 1984; Hemelrijk 1994;), food (de Waal 1997) and mating opportunities (Gumert 2007; Norscia et al. 2009). Proposed benefits of receiving grooming are broad and range from ectoparasite and debris removal (Reichard & Sommer 1994; Mooring et al. 1996;

Hawlena et al. 2007) to tension reduction through the release of β -endorphins (Schino et al. 1988; Keverne et al. 1989). Taking into account associated costs of social grooming such as decreased vigilance and time lost for other activities (Maestripieri 1993; Cords 1995), its evolution and maintenance has traditionally been explained by kin selection and reciprocal altruism (Kapsalis & Berman 1996; Brosnan & de Waal 2002). More recently, the idea of biological markets has been offered as an extension to 'classical' reciprocal altruism theory, in which social behaviours such as acts of grooming are valuable commodities that can be exchanged to form and/or maintain partnerships (Noë et al. 1991; Noë & Hammerstein 1994, 1995; Noë 2001, 2006a; Barrett & Henzi 2001). The smallest biological market may include only two players (Hammerstein 2001), although most biological markets usually have more than two traders, which can exchange commodities to their mutual benefit. Competition may occur between members of the same trader class, while cooperation may occur between members of different trader classes. Empirical studies assessing whether biological markets can explain the dynamics of primate male–female interactions are still limited, but

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the economic paradigm has been successful in demonstrating, for example, interchanges of social acts for mating opportunities in some species (Barrett & Henzi 2001, 2006; Noë 2001, 2006a). None the less, debate and disagreements about the circumstances in which the two approaches, biological market theory and reciprocal altruism, can be applied to biological systems still persist (e.g. Noë 2006b; Schino & Aureli 2010). We chose to apply biological market theory to our data set with the intention of adding empirical data to the discussion and to promote further clarification of each approach. In short, the key difference between the two theories is encapsulated in the opportunity, in biological market theory, to provide service to others in the absence of force and to be able to choose among partners, at least theoretically, through a mechanism of outbidding each other in the value of the same or an equivalent commodity offered and received. Lastly, in biological market theory, the exchange of commodities between members of different trader classes should be influenced by supply and demand, such that individuals offering a rare commodity are expected to be able to increase their demands for resources or services received from trading partners.

Owing to a slower reproductive rate and greater overall parental effort (through pregnancy and lactation), receptive mammalian females are generally considered a limiting resource for male reproductive success (Trivers 1972), which may allow females to influence male behaviour by exercising mate choice. The potential of mate choice as a selective force has been recognized since Darwin (1871), and market effects have been accredited throughout the literature to sexual selection, which may have led to males that have evolved traits and skills that increase their ability to attract and obtain females as sociosexual partners (Setchell 2005). This suggests that under conditions in which males cannot force females to copulate, sexual selection promotes males who invest in efforts to gain mating opportunities.

Grooming can be a commodity interchanged for mating opportunities (e.g. longtailed macaques, *Macaca fascicularis*: Gumert 2007; Verreaux's sifaka, *Propithecus verreauxi*: Norscia et al. 2009). Broad support comes from observations of primate species in which males groom females more frequently when females are swollen or receptive to mate (i.e. chimpanzees, *Pan troglodytes*: Hemelrijk et al. 1992; hamadryas baboons, *Papio hamadryas*: Colmenares et al. 2002). These observations are in line with predictions of biological market theory asserting that if an exchange of grooming and mating occurs, partner value would influence grooming payments if multiple exchange partners are available. An important variable in partner value is the precise female reproductive state, which has not been addressed adequately in previous grooming–mating interchange studies, and assessing variation in the price of a social commodity based on the influence of partner supply is a central point of the theory of biological markets.

The aim of this study was to test whether grooming functions as a commodity in wild white-handed gibbons at Khao Yai National Park, Thailand, and how results may be interpreted more appropriately under biological market or classical reciprocal altruism theory. More specifically, we were interested in assessing how male-to-female grooming activity would vary across females' reproductive states (i.e. cycling, pregnancy and lactation) and whether grooming was interchanged for mating opportunities. Gibbons of this population provide an interesting opportunity to study grooming in relation to mating opportunities for several reasons. First, pressure for males to invest in grooming as a commodity varies across groups owing to variation in the number of males. White-handed gibbons at Khao Yai National Park live in single- and multimale groups of usually two or three adult males (Reichard 2009). Males in single-male groups face less competition

for mating opportunities than males in multimale groups. Consequently, one would expect, at least theoretically, more competition between members of this trader class (i.e. males) and that all males in multimale groups would invest more in social grooming with the female. Males in multimale groups can be categorized as primary or secondary male partners based on interaction patterns with the female (Barelli et al. 2008a). Primary males regularly duet and engage in a larger share of grooming and copulations with a female whereas secondary males duet with the female only under rare circumstances and copulate less frequently with her (Barelli et al. 2008a; Reichard 2009). Because of the predictable involvement of primary males in grooming and copulations versus a low involvement of secondary males, we focused primarily on potential female–primary-male exchanges/interchanges. Second, gibbon groups are organized as single-female breeding units, which reduce males' opportunities to find additional mates or trading partners within a social unit. Although extrapair copulations have been observed in this and other gibbon species (Palombit 1994; Reichard 1995; Lappan 2007), mating opportunities occurring with neighbouring females do not contribute to a potential interchange system of grooming and mating opportunities, because grooming has so far never been observed between neighbouring males and females, suggesting that female extrapair copulations (EPCs) are unrelated to grooming. Thus, if a biological market for trading sexual opportunities across groups exists, a different currency than social grooming must be used. Third, white-handed gibbons have a very slow, ape-typical life history with long gestation and particularly long lactation periods (Reichard & Barelli 2008). Because gibbon females have long interbirth intervals it is more likely that adjustments in grooming intensity will occur according to female reproductive stage and that these will be more easily detected than in primate species with more temporally compressed reproductive events such as annual breeders. Fourth, sexual activity in white-handed gibbons is not confined to specific months or seasons and extends beyond the fertile phase. Copulations occur at similar frequencies during cycling and pregnant stages, and in both reproductive conditions females mate multiple times (Barelli et al. 2008a). Moreover, they display moderate sexual swellings, which males use to allocate their mating activities (Barelli et al. 2008a). Thus, gibbon males detect changes in female reproductive status and adjust their mating behaviour accordingly. What is not clear, however, is whether social grooming follows a similar trend and contributes to males' mating opportunities. Finally, gibbons are considered a codominant species (Carpenter 1940), because sexual dimorphism in body and canine size is minimal, which prevents males from forcing females to copulate and thereby fulfils a precondition of biological market theory.

To test whether grooming is a commodity in this species, we made the following predictions. (1) If grooming is exchanged/interchanged following biological market rules in dyadic male–female interactions, grooming should be adjusted according to changes in the value of exchanged/interchanged good(s). Since female white-handed gibbons may copulate during all reproductive conditions, but only fertile periods are critical for males to accomplish fertilization, males will increase grooming efforts during periods of increased female fertility, that is, increased male-to-female grooming will be observed when females are cycling compared to other reproductive states. (2) Because primary males in multimale groups experience more direct male–male competition over access to mating opportunities than males in single-male groups, we predicted that primary males' grooming investment will be on average higher than that of males in single-male groups or secondary males in multimale groups. Thus, if grooming functions as a commodity that enhances a male's chances of mating, testing the different types of group composition will clarify whether biological market effects do exist. However, considering the

definition of reciprocal altruism as follows 'when an actor incurs immediate costs (while the recipient gains immediate benefits) and receives delayed benefits that depend on the future behavior of the recipient' (Schino & Aureli 2009, page 46), we should not exclude the possibility that this somewhat simpler approach may sufficiently explain gibbons' exchange of commodities, in which case we would predict that grooming should be exchanged either for itself or for other services regardless of a female's reproductive state. We thus predicted that females would match males' grooming during periods of high fertility as well as during periods of nonfertility, and they would also interchange grooming for copulation regardless of the female's reproductive state.

METHODS

Study Site and Animals

We studied a population of white-handed gibbons residing in the Mo Singto–Klong E-Tau study area of Khao Yai National Park, Thailand (2168 km²; 101°22'E, 14°26'N; ca. 130 km northeast of Bangkok). The Park is part of the large Dong Phrayayen–Khao Yai Forest Complex (DPKY) World Heritage site (UNESCO World Heritage Centre 2005) which covers an area of 6199 km² (Lynam et al. 2006). The Mo Singto–Klong E-Tau study area spans approximately 8.5 km² of continuous seasonally wet evergreen forest in slightly hilly terrain (730–890 m above sea level) located in the central portion of the Khao Yai Mountains. Precipitation varies from 2000 to 4900 mm annually (Kitamura et al. 2004), and mostly occurs during the wet season (May–October).

Approximately 2800 h of direct observations of 12 habituated white-handed gibbon groups were made from July 2003 to April 2005. Seven groups were pair living while five comprised two adult males unrelated to the respective group's female and were considered multimale (Barelli et al. 2007, 2008a; Table 1). In multimale groups, we distinguished between primary and secondary males based on singing and mating patterns, that is, primary males engaged in duet singing and performed the majority of copulations with the group female (Barelli et al. 2008a).

Behavioural observations were carried out by C.B. and three experienced Thai field assistants. Each observer followed one of the 12 study females from dawn to dusk (average observation time: 8.24 h/day) while collecting faecal samples for assessing female reproductive condition and concurrently recording sexual swelling scores. All mating activity involving the focal animal was recorded as well as all grooming acts (bout frequency and duration) that involved the focal female or the adult male(s) present in the group.

Table 1

Group composition and female reproductive status of wild white-handed gibbons at Khao Yai National Park, Thailand

	Group	Group composition	Reproductive stage
1	A	2AM, 1AF	C
2	B	1AM, 1AF	X
3	C	1AM, 1AF	C, L
4	D	2AM, 1AF	P, L
5	H	1AM, 1AF	C, P, L
6	J	2AM, 1AF	P, L
7	N	1AM, 1AF	C
8	NOS	2AM, 1AF	C, P
9	R	1AM, 1AF	C, L
10	S	1AM, 1AF	C
11	T	2AM, 1AF	C, L
12	W	1AM, 1AF	P, L

AM: adult male; AF: adult female; C: cycling; P: pregnant; L: lactating; X: postreproductive.

A grooming act was considered to have ended if there was no grooming activity for more than 1 min. To determine whether male-to-female grooming events occurred when females were more sexually receptive than in periods in which they were not, female reproductive status was assessed using previously validated measures of faecal progesterone metabolites. This enabled us to determine reliably whether a female was cycling, including the day of ovulation, pregnant or in a state of lactational amenorrhoea (Barelli et al. 2007; Barelli & Heistermann 2009). The fertile phase of an ovarian cycle was defined as a period of 5 days, comprising the presumed day of ovulation plus the following day and the 3 days preceding ovulation (Barelli et al. 2007). Days outside the 5-day fertile period were considered the nonfertile phase of the female menstrual cycle. Sexual swellings were scored daily after visual inspection of anogenital tumescence, and swelling size was assessed intraindividually in comparison to the size of a female's ischial callosities following a previously established procedure (Barelli et al. 2007). Three swelling stages were distinguished: 'no swelling', 'partial swelling' and 'maximum swelling' (for details see Barelli et al. 2007, 2008a).

Twelve focal females were followed systematically during one or more reproductive conditions for approximately 3 months each. Data on reproductive status were available for eight cycling stages, seven lactating stages and five pregnancies, plus one potentially postreproductive status (Table 1). Although hormonal concentrations of two females (Brenda (group T) and Sofi (group S)) were within the ranges of those shown by cycling females, their profiles were not regular. However, because they did not carry a nursing infant and precise back counting from well-known subsequent births indicated that they could not have been pregnant during data collection, we considered them cycling and therefore included their data.

After controlling for factors such as reproductive status, reproductive phase, and sexual swelling, we found that grooming interactions between females and secondary males were too rare and variable to be reliably modelled. Thus, we excluded secondary males from our quantitative analyses, but consistently maintained social organization (pair-living versus multimale groups) as a variable in statistical analyses. Contributions and participation of secondary males in exchange/interchange of grooming with females was evaluated qualitatively in the discussion of results.

Statistical and Data Analyses

Grooming rates and female reproductive status

To test whether grooming rates (min/h observed, calculated per day) differed across females' reproductive states we used a generalized linear mixed model (GLMM, Baayen 2008a) with a Gaussian error structure, identity link function and female identity included as a random effect. We restricted our analyses to groups in which females were observed in at least two reproductive states and for at least 4 days each, which left us with data for eight groups and a total of 227 observation-days. We ran three models of grooming rate as the response variable: (1) one that included all grooming in which females were involved; (2) one with only the grooming that females gave to primary males; and (3) one with only the grooming that females received from primary males (square-root transformed). We tested the significance of reproductive status on grooming interactions using likelihood ratio tests comparing the fit of the full model to the corresponding reduced model excluding reproductive status. Since likelihood ratio tests for fixed effects in a mixed model are potentially unreliable, particularly if the number of cases per level of the random effect is relatively small (Bolker et al. 2008), we also used Markov chain Monte Carlo (MCMC) sampling to test statistical significance. This method allows reliable

estimation of confidence intervals and *P* values for fixed effects in mixed models (Baayen 2008a). In these models we generally considered autocorrelation (see below).

Mating activity and female reproductive status

To test whether number of copulations per day differed between reproductive states we used a GLMM with Poisson error structure, log-link function and social group included as a random effect. However, since the data were overdispersed, we used a permutation test to establish statistical significance (Adams & Anthony 1996; Manly 1997). We permuted the number of copulations per day across reproductive status but only within social groups, using 1000 permutations and including the original data as one permutation. As a test statistic we used the difference in AIC (Akaike's information criterion) between the two models without and with reproductive status included (further on termed DAIC). Again, we restricted the analysis to groups in which females were observed in at least two reproductive states and in each of them for at least 4 days (leaving a total of eight groups and 227 observation-days).

Grooming rates and mating activity

To test whether grooming received by females from primary males (min/h observed, calculated per day) correlated with the number of copulations, we first correlated the two variables (using the Spearman correlation coefficient) separately for each combination of group and reproductive status. We restricted the analysis to dyads in which (1) at least one copulation occurred, (2) at least one grooming event was performed, and for which (3) we had at least 3 observation-days. To account for multiple testing, we combined results by first comparing numbers of positive and negative correlations, using binomial tests, and second by combining *P* values using Fisher's omnibus test. This method combines a number of independent *P* values into a single chi-square-distributed variable with degrees of freedom equalling twice the number of *P* values (Haccou & Meelis 1994). To rule out confounding effects of sexual swelling and reproductive phase (fertile or nonfertile), we also ran correlations separately for each combination of group, reproductive status (cycling, pregnant and lactating), sexual swelling and reproductive phase, including only combinations fulfilling the aforementioned criteria. Since sample sizes per correlation were partly rather small we used a binomial test comparing the proportions of positive and negative correlation coefficients.

Grooming exchange between sexes

To test whether grooming that females received from primary males correlated with grooming that females gave to primary males, we used essentially the same analysis as for the correlation between grooming and number of copulations. Here, we considered only data sets with at least 3 days per dyad and in which both female and male groomed at least once. To test grooming exchange asymmetries between females and primary males we used a Wilcoxon signed-ranks test applied for the same set of data with the exception that here we considered only samples with at least 6 days per dyad (the smallest sample size potentially revealing significance). In these analyses we could not account for temporal autocorrelation (see below).

Grooming rate and female swelling stage

We tested for a relation between female swelling status and the rate of grooming (min/h observed) using a GLMM with Gaussian error function and identity link. In this we included female swelling stage (as a covariate, i.e. continuous predictor), female reproductive status and an autocorrelation term (see below) as fixed effects and female identity as a random effect. For the analysis we square-root transformed grooming rate.

Further considerations

The behaviours we analysed (i. e. grooming and copulations) were likely to show some temporal autocorrelation (i. e. residuals for data points observed close to one another in time being more similar than residuals from more distant data points). To protect our analyses against a lack of independence, we introduced an autocorrelation term into the GLMMs, which we derived as follows. First, we ran the full model and derived the residuals from it. We then calculated, for each data point separately, the weighted average of the residuals of all other data points, with the weight being equal to 1/time lag to the other data points, whereby only residuals for data points from the same social group were considered. The resulting variable was then included as an additional fixed effect in the full model. Time lag was measured in days.

We calculated GLMMs using the function 'lmer' provided by the package 'lme4' (Bates et al. 2008) for R version 2.8.1 (R Development Core Team 2008). We derived MCMC *P* values using functions 'pvals.fnc' and 'aovlmer.fnc' from the R package 'languageR' (Baayen 2008b). The 'autocorrelation term' and permutation test were calculated using an R function and an R script written by R.M. For GLMMs with Gaussian error structure we checked for the assumptions of normally distributed and homogeneous residuals being fulfilled by visual inspection of plots of residuals against fitted values. Also, after transformations the latter assumption was occasionally not fully fulfilled, but deviations were generally moderate and hence we are confident that the results can be trusted. Wilcoxon tests were generally exact (Mundry & Fischer 1998) and calculated using SPSS 15.0 for Windows (SPSS Inc., Chicago, IL, U.S.A.). Spearman correlations were exact for sample sizes up to eight, based on 10 000 permutations for larger samples, and were calculated using a program written by R.M. We present two-tailed *P* values throughout.

RESULTS

On average, Khao Yai white-handed gibbons groomed for 4.1 min/h ($N = 12$ groups, $N = 2760$ observation-hours), which was about 7% of the average daily activity period of about 8.24 h. With regard to grooming given and received by females to and from primary and secondary males, no obvious pattern emerged (Table 2). Qualitative inspection of grooming activities confirmed an earlier observation (Reichard 2009) that some secondary males would not groom a female (see group NOS) and that primary males usually gave more grooming to females than secondary males (but see group J). Also, females' allocation of grooming to secondary and

Table 2

Grooming exchanged between female and male gibbons at Khao Yai National Park, Thailand

Group	Social organization	Grooming given to		Grooming received from	
		Primary males (min/h)	Secondary males (min/h)	Primary males (min/h)	Secondary males (min/h)
A	Mm	0.36	0.89	1.25	1.17
D	Mm	2.65	1.04	1.67	0.32
J	Mm	0.73	0.97	0.14	0.88
T	Mm	1.64	1.25	1.19	1.07
NOS	Mm	5.04	0.88	3.02	0.00
B	P-I	3.16		2.44	
C	P-I	2.84		1.19	
H	P-I	2.14		2.95	
N	P-I	0.49		0.71	
R	P-I	2.38		2.27	
S	P-I	3.34		1.70	
W	P-I	1.01		0.92	

Mm: multimale group; P-I: pair-living group. Amount of grooming between females and primary males and between females and secondary males is combined for all reproductive stages, phases and sexual swelling conditions.

primary males was very flexible: two females groomed a secondary male more and, in one case, the amount of grooming given to primary and secondary males was almost equal. In the group in which the female (group A) groomed the secondary male more than the primary male, the secondary and primary males groomed the female equally. Finally, in the group in which the female groomed both males about equally (group J), she received more grooming from the secondary male (Table 2).

Effects of Sex and Female Reproductive State

Overall, primary males groomed females significantly more than females groomed primary males (16 Wilcoxon tests, conducted separately for each combination of group ($N = 12$) and reproductive status, combined using Fisher's omnibus test: $\chi^2_{32} = 233$, $P < 0.001$). In fact, of 16 combinations of group and reproductive status, females groomed primary males more often in only one case. To rule out confounding effects of sexual swelling and reproductive phase, we also compared grooming rates after splitting the data by sexual swelling and reproductive phase (fertile or nonfertile), in addition to group and reproductive status. Still, in 17 of 20 data sets the primary male groomed the female more than vice versa ($N = 10$ groups, Fisher's omnibus test: $\chi^2_{40} = 146.8$, $P < 0.001$), which indicates that our observation of primary males generally grooming females more than females grooming them is a robust finding for this population.

Grooming was clearly elevated when females were cycling compared to when females were lactating or pregnant (GLMM: $P_{\text{MCMC}} < 0.001$; Fig. 1). This was also the case when considering only the rate at which females groomed primary males or only the rate at which primary males groomed females (both P_{MCMC} and $P_{\text{likelihood ratio test}} < 0.001$). Similarly, the number of copulations per day between females and primary males was larger when females were cycling than when they were pregnant or lactating (permutation test: $\text{DAIC} = 70.2$, $P = 0.001$; Fig. 2).

Exchanging Grooming for itself

On days on which females received more grooming from primary males they also gave more grooming in return (Spearman

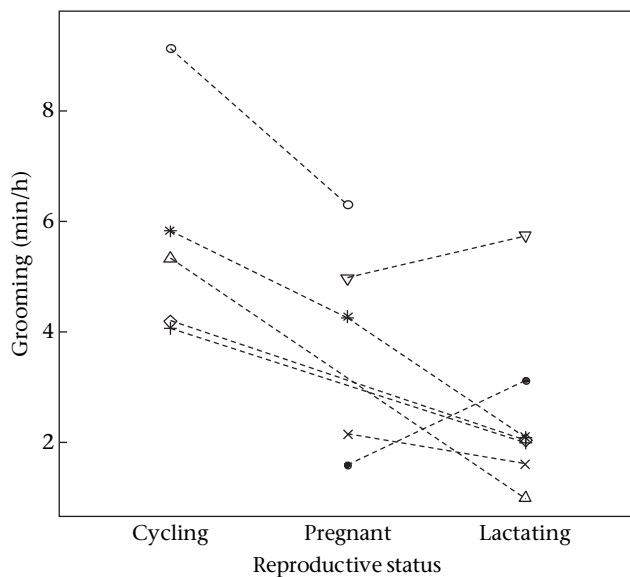


Figure 1. Rate of grooming between females and primary males in relation to female reproductive status. Each group is represented by two or three symbols, connected by a dashed line. $N = 8$ groups (groups in which females were observed in only one reproductive status were not included) and 2–7 observation-days.

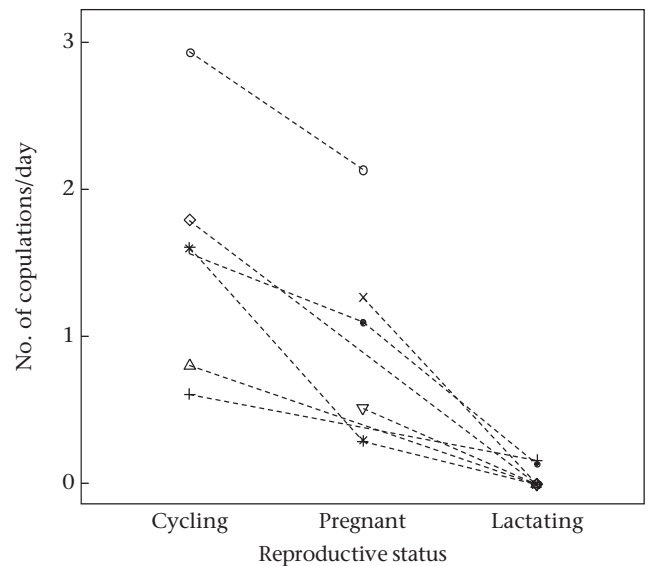


Figure 2. Number of copulations per day between females and primary males in relation to female reproductive status. Each group is represented by two or three symbols, connected by a dashed line. $N = 8$ groups (groups in which females were observed in only one reproductive status were not included) and 2–7 observation-days.

correlations, conducted separately for each combination of group ($N = 12$) and reproductive status: all 20 correlations > 0 ; average $r_s = 0.66$; Fisher's omnibus test: $\chi^2_{40} = 193$, $P = 0.001$). Repeating this analysis separately for each combination of group, reproductive status, sexual swelling and reproductive phase, we found 33 positive, one correlation equal to zero, and only three negative correlations (binomial test: $P < 0.001$, average $r_s = 0.60$; Fig. 3).

Exchanging Grooming for Mating Opportunities

Females copulated more with primary males on days when they received more grooming from those males. When correlating the number of copulations with the rate of primary male-to-female grooming, we found a positive correlation in 14 of 15 combinations of group ($N = 12$) and reproductive status (binomial test: $P < 0.001$; average $r_s = 0.29$), and overall the correlations were highly significant (Fisher's omnibus test: $\chi^2_{30} = 52.1$, $P = 0.007$). Repeating this analysis separately for each combination of group, reproductive status, sexual swellings and reproductive phase (fertile, nonfertile), we found 17 positive and only seven negative correlations (binomial test: $P = 0.064$, average $r_s = 0.20$).

Grooming, Sexual Swellings and Mating

Primary males did not groom females more when females were maximally swollen than when they were not swollen ($P_{\text{MCMC}} = 0.63$, $N = 8$ groups, 215 observation-days), despite the fact that male grooming generally increased during the fertile period of females compared to nonfertile reproductive stages.

DISCUSSION

Our first question was does grooming in wild white-handed gibbons qualify as a commodity? The results of this study support this idea; in fact, grooming was interchanged for other goods and for itself. Unfortunately, whether biological market theory exclusively explains gibbons' trading of services remained somewhat unclear. We detected a strong link between the intensity of primary

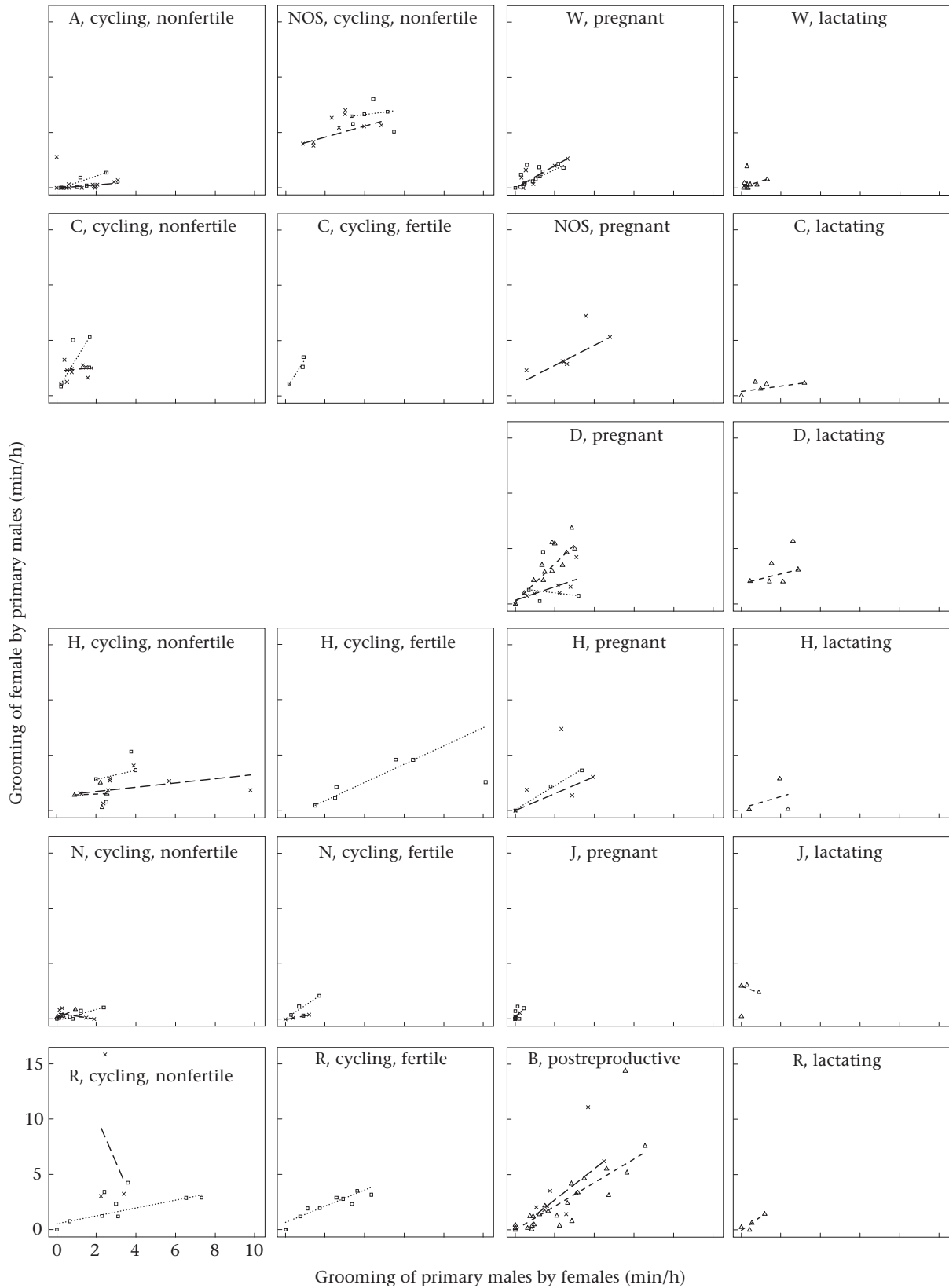


Figure 3. Relation between grooming of females by primary males and grooming of primary males by females. Each graph shows the relation for one combination of group (usually rows; see Table 1 for group letters), reproductive status (cycling, pregnant, lactating) and phase (fertile and nonfertile phases, columns). Within graphs, sexual swelling sizes are depicted separately (1: Δ , dashed line; 2: x, long-dashed line; 3: \square , dotted line). Lines represent robust regression lines based on minimizing the sum of the absolute deviations. Note that groups N and J are shown in the same row and that group NOS is depicted in the first two rows.

male-to-female grooming and female reproductive status, with males adjusting their grooming activity to the changing reproductive value of females. When females were cycling and their reproductive value was high, males increased their grooming effort, which supports predictions of biological market theory. However, females also responded to increased male grooming with an increase in their own grooming of males, which is more difficult to reconcile with a biological market framework. Although females' tendency to match their partners' grooming contribution has been suggested (under biological market theory) to be a requirement for being considered a fair/good trading partner (Barrett et al. 1999; Barrett & Henzi 2001, 2006), further investigation is needed to clarify this pattern. In a follow-up step it would be important to investigate which direct or indirect benefits females may receive from males in exchange for grooming and whether, for example, males may interchange female grooming for priority of access to food or protection of resources and/or infants. In a previous study we showed that gibbon females of this population have priority of access to food (Barelli et al. 2008b); at present, however, it is unclear whether males trade access to food sources for grooming or whether, because of codominance of the sexes, females can simply demand priority of access to preferred food sources. Based on our current results, we predict that females' priority of access to food is also part of a complex interchange system in gibbon pairs.

Another question we asked was do primary males groom females to exchange grooming for itself or for other goods, in particular mating opportunities? Our results seem to support both predictions. Primary males groomed females more than vice versa, and females likewise increased grooming, perhaps in an effort to match males' increased grooming during periods when they were cycling. Concurrently, we found strong support for an interchange of grooming for mating opportunities from the observation that mating frequencies increased on days when higher levels of male-to-female grooming occurred. Perhaps not all instances of grooming correspond to trading, but represent events related to other purposes such as social bonding, health or tension reduction. In fact, although a biological market framework may predict grooming–mating interchanges, it does not account for the mechanisms driving such an exchange. The proximate mechanism that enables individuals to engage in grooming–mating interchanges could be attitudinal reciprocity (de Waal 2000; Schino et al. 2007), rather than a calculated system of exchange. Since grooming is known to reduce tension (Schino et al. 1988), lower heart rate (Aureli et al. 1999) and decrease stress levels (Shutt et al. 2007), it could also promote a cooperative attitude between partners. This may explain our result that females groomed more on days when they were groomed more themselves. In fact, grooming seems to be associated with secretion of β -endorphins, which leads to a stronger positive emotional feeling towards the groomer (Keverne et al. 1989). Physiological mechanisms such as these may have evolved to motivate individuals to cooperate through reward and stress reduction, facilitating male sexual advances and consequently social interchange.

Another aspect we investigated was the relationship between female sexual swellings and male grooming effort because a previous study had suggested that males use sexual swellings as a cue to allocate mating activities (Barelli et al. 2008a). Based on these observations we expected that males would groom maximally swollen females more than nonswollen females. To our surprise, however, no relationship between sexual swelling size and primary male-to-female grooming was found. Grooming and variations in female genital swellings may indeed be independent of each other and males may use rather broad categories of cycling versus noncycling stages to gauge their grooming efforts. Perhaps a fine-tuned grooming adjustment in relation to female swelling

size is uneconomical if males use a rule of thumb to allocate grooming. It may also be hypothesized that primary males must sustain elevated grooming levels throughout a female's cycling period to ensure continuous spatial proximity and thereby maintain copulation opportunities. It is difficult to reconcile, however, the finding of a link between maximum sexual swellings and copulation frequencies in a previous study (Barelli et al. 2008a) and our current finding of a link between copulation frequency and male grooming effort, but no corresponding link between grooming and sexual swellings. A similar result was also found in long-tailed macaques (Gumert 2007), in which female swellings did not influence a market of grooming and males did not groom swollen females more than nonswollen females despite a grooming–mating interchange. Clearly, more data are needed to understand better the potential links between female sexual swellings and grooming–mating interchange markets in primates.

Limitations of the Study and Further Analyses

One limitation of our study is that it was not possible to integrate secondary males' grooming activity into the detailed grooming–market analyses because of their marginal involvement with females. Consequently, we could only provide preliminary, descriptive information on secondary males' grooming and were unable to test how secondary males fit into the biological market idea. This is unsatisfying because previous research has shown that secondary males are not excluded from mating with females (Barelli et al. 2008a). Thus, if a grooming–mating interchange market exists in gibbons secondary males should be active participants in it. Several lines of reasoning may explain the broad lack of or low participation of secondary males in grooming females. Perhaps our conclusion of a grooming–mating interchange system in gibbons is false and we overlooked a third variable that drives both primary males' grooming and mating patterns, although we believe this is unlikely. If such a third variable exists, we are not aware of it. An alternative, simple explanation would be that secondary males wanted to participate in grooming–mating interchanges but were prevented from doing so by primary males. Although plausible, we currently have no indication that primary males are able or willing to suppress grooming activities between females and secondary males. Overt aggression between primary and secondary males has so far only been observed during initial stages of multimale group formation (Reichard 2009), which was not the case during this data collection period. However, we cannot exclude the possibility that subtle dominance cues are given by primary males causing secondary males to engage less in grooming with females. It is also possible that secondary males trade commodities other than grooming for mating opportunities. Perhaps participation in territorial/resource defence for females, which has been hypothesized to be a driving force for the formation and maintenance of multimale gibbon groups (Savini et al. 2009), is sufficient for secondary males in interchange for mating opportunities. Finally, limitations of our data set may have caused an incomplete picture of secondary males' involvement in grooming and mating with females, which a longer study could address. In summary, it is currently unclear why secondary males are not involved more in the grooming–mating market that we have hypothesized operates for primary males and females, and further elucidation must await the collection of more data.

A second limitation might be related to variation in social organization. Because of a small sample size we combined primary males from single-male groups and multimale groups into a single category. However, with an expanded sample size it should be possible to differentiate the effects of multimale and single-male organization. In single-male groups the male has more leverage,

as the female's options to avoid grooming with the male are limited owing to a lack of alternative partners. In multimale groups, however, females have greater leverage, as primary and secondary males theoretically compete for mating opportunities, which is predicted to raise the grooming effort of males. A general prediction that needs testing with an extended data set is therefore that, overall, males in multimale groups would invest more in grooming than the single male of a pair-living group. Since biological markets are sensitive to 'demand' and 'supply', a fine gradient between male grooming effort and mating opportunities is expected to exist for each class of male, that is, sole male in a single-male group, primary male in a multimale group and secondary male in a multimale group. We were not able to address the outcome of market forces precisely with regard to the three classes of males.

Finally, we have presented a primarily male-centred analysis based on the notion that males have a strong incentive to trade commodities for mating opportunities. However, females are equal partners in biological markets between the sexes and their interests must also be investigated. If we consider that perhaps a majority of gibbon species are pair bonded and female choice might be more limited to a small number of sexual partners compared to larger multimale/multifemale societies, copulations are as valuable to females as they are to males, and females must ensure they achieve fertilization during a relatively short ovulation window. Moreover, in species in which females benefit directly from male services, for example the carrying or feeding of infants (e.g. [Ginther & Snowdon 2009](#)), it is easier to hypothesize interchange systems from the female's perspective. However, in white-handed gibbons, males do not participate directly in the rearing of young. Thus, direct benefits for females from grooming exchanges or interchanges with males are not obvious. Future studies must therefore address whether female gibbons engage in exchange of grooming or rather interchange for other commodities. We suggest that priority of access to food resources but also protection from resource exploitation by neighbouring females/groups or protection against male infanticide may be potential areas to explore.

Conclusions

Our study shows that biological market theory, which commonly focuses on large multimale/multifemale primates ([Gumert 2007](#)), may also be applied to a socially monogamous, but reproductively promiscuous primate. Gibbons are a sexually monomorphic species ([Plavcan & van Schaik 1997](#)) and intersexual dominance is absent. This gives males little direct control over females and sets the stage for a cooperative relationship between males and females that needs to be negotiated repeatedly and consistently between equal participants. In such a social environment the powers of demand and supply of goods and services are expected to become visible, and, as predicted by biological market theory, market forces exert more influence in situations in which social commodities can be obtained through cooperative trading of acts, rather than being acquired by force. Thus, biological market theory may be an appropriate model to investigate cooperation-based exchange systems in primates such as gibbons.

In accord with biological market theory, we observed that gibbon males increased their grooming effort as females became a more valuable resource to them. Why females responded to this with an increase in grooming and copulation frequency needs further investigation. At present, we conclude that males benefit from a grooming–mating interchange. Taken together, a variety of forces may influence the dynamics of grooming interactions in nonhuman primate species, which may respond flexibly to the changing relative value of social resources. In some dyads and some contexts, partners may reciprocate grooming, while in others

interchanges may occur for other benefits, including mating opportunities.

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References

- Adams, D. C. & Anthony, C. D. 1996. Using randomization techniques to analyse behavioural data. *Animal Behaviour*, **51**, 733–738.
- Aureli, F., Preston, S. D. & de Waal, F. B. M. 1999. Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. *Journal of Comparative Psychology*, **113**, 59–65.
- Baayen, R. H. 2008a. *Analyzing Linguistic Data*. Cambridge: Cambridge University Press.
- Baayen, R. H. 2008b. *languageR: Data Sets and Functions with 'Analyzing Linguistic Data: A Practical Introduction to Statistics'*. R Package Version 0.953. Vienna: R Foundation for Statistical Computing. <http://www.r-project.org>.
- Barelli, C. & Heistermann, M. 2009. Monitoring female reproductive status using fecal hormone analysis and preliminary data on patterns of genital swellings in relation to female cycle stage in captive and wild white-handed gibbons (*Hylobates lar*). In: *The Gibbons: New Perspectives on Small Ape Socioecology and Population Biology* (Ed. by S. M. Lappan, D. Whittaker & T. Geissmann), pp. 313–325. New York: Springer.
- Barelli, C., Heistermann, M., Boesch, C. & Reichard, U. H. 2007. Sexual swellings in wild white-handed gibbon females (*Hylobates lar*) indicate the probability of ovulation. *Hormones and Behavior*, **51**, 221–230.
- Barelli, C., Heistermann, M., Boesch, C. & Reichard, U. H. 2008a. Mating patterns and sexual swellings in pair-living and multimale groups of wild white-handed gibbons (*Hylobates lar*). *Animal Behaviour*, **75**, 991–1001.
- Barelli, C., Boesch, C., Heistermann, M. & Reichard, U. H. 2008b. Female white-handed gibbons (*Hylobates lar*) lead group movements and have priority of access to food resources. *Behaviour*, **145**, 965–981.
- Barrett, L. & Henzi, S. P. 2001. The utility of grooming in baboon troops. In: *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets* (Ed. by R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein), pp. 119–145. Cambridge: Cambridge University Press.
- Barrett, L. & Henzi, S. P. 2006. Monkeys, markets and minds: biological markets and primate sociality. In: *Cooperation in Primates and Humans: Mechanisms and Evolution* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 209–232. Berlin: Springer.
- Barrett, L., Henzi, S. P., Weigrill, T., Lycett, J. E. & Hill, R. A. 1999. Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society B*, **266**, 665–670.
- Bates, D., Maechler, M. & Dai, B. 2008. *lme4: Linear Mixed-effects Models Using Eigen and SVD*. R Package Version 0.999375-28. Vienna: R Foundation for Statistical Computing. <http://www.r-project.org>.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J.-S. 2008. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.
- Brosnan, S. F. & de Waal, F. B. M. 2002. A proximate perspective on reciprocal altruism. *Human Nature*, **13**, 129–152.
- Carpenter, C. R. 1940. A field study in Siam of the behavior and the social relations of the gibbon (*Hylobates lar*). *Comparative Psychology Monographs*, **16**, 1–212.
- Colmenares, F., Zaragoza, F. & Hernández-Lloreda, M. V. 2002. Grooming and coercion in one-male units of hamadryas baboons: market forces or relationship constraints? *Behaviour*, **139**, 1525–1553.
- Cords, M. 1995. Predator vigilance costs of allogrooming in wild blue monkeys. *Behaviour*, **132**, 559–569.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. New York: Modern Library.
- Ginther, A. J. & Snowdon, C. T. 2009. Expectant parents groom adult sons according to previous alloparenting in a biparental cooperatively breeding primate. *Animal Behaviour*, **78**, 287–297.
- Gomes, C. M., Mundry, R. & Boesch, C. 2009. Long-term reciprocation of grooming in wild west African chimpanzees. *Proceedings of the Royal Society B*, **276**, 699–706.

- Gumert, M. D. 2007. Payment for sex in a macaque mating market. *Animal Behaviour*, **74**, 1655–1667.
- Haccou, P. & Meelis, E. 1994. *Statistical Analyses of Behavioural Data*. Oxford: Oxford University Press.
- Hammerstein, P. 2001. Games and markets: economic behaviour in humans and other animals. In: *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets* (Ed. by R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein), pp. 1–19. Cambridge: Cambridge University Press.
- Hawlana, H., Bashary, D., Abramsky, Z. & Krasnov, B. R. 2007. Benefits, costs and constraints of anti-parasitic grooming in adult and juvenile rodents. *Ethology*, **113**, 394–402.
- Hemelrijk, C. K. 1994. Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Animal Behaviour*, **48**, 479–481.
- Hemelrijk, C. K., van Laere, G. J. & van Hooff, J. A. R. A. M. 1992. Sexual exchange relationships in captive chimpanzees? *Behavioral Ecology and Sociobiology*, **30**, 269–275.
- Kapsalis, E. & Berman, C. M. 1996. Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*) I. Criteria for kinship. *Behaviour*, **133**, 1209–1234.
- Keverne, E. B., Martensz, N. & Tuite, B. 1989. Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, **14**, 155–161.
- Kitamura, S., Suzuki, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Noma, N., Maruhashi, T. & Suckasam, C. 2004. Dispersal of *Aglaia spectabilis*, a large-seeded tree species in a moist evergreen forest in Thailand. *Journal of Tropical Ecology*, **20**, 421–427.
- Lappan, S. 2007. Social relationships among males in multimale siamang groups. *International Journal of Primatology*, **28**, 369–387.
- Lynam, A. J., Round, P. D. & Brockelman, W. Y. 2006. *Status of Birds and Large Mammals in Thailand's Dong Phrayayen-Khao Yai Forest Complex*. Bangkok: Wildlife Conservation Society and Biodiversity Research and Training Programme.
- Maestriperi, D. 1993. Vigilance costs of allogrooming in macaque mothers. *American Naturalist*, **141**, 744–753.
- Manly, B. F. J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. New York: Chapman & Hall.
- Mooring, M. S., McKenzie, A. A. & Hart, B. L. 1996. Grooming in impala: role of oral grooming in removal of ticks and effects of ticks in increasing grooming rate. *Physiology and Behavior*, **59**, 965–971.
- Mundry, R. & Fischer, J. 1998. Use of statistical programs for nonparametric tests of small samples often leads to incorrect *P* values: examples from *Animal Behaviour*. *Animal Behaviour*, **56**, 256–259.
- Noë, R. 2001. Biological markets: partner choice as the driving force behind the evolution of mutualisms. In: *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets* (Ed. by R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein), pp. 93–118. Cambridge: Cambridge University Press.
- Noë, R. 2006a. Digging for the roots of trading. In: *Cooperation in Primates and Humans: Mechanisms and Evolution* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 233–261. Berlin: Springer.
- Noë, R. 2006b. Cooperation experiments: coordination through communication versus acting apart together. *Animal Behaviour*, **71**, 1–18.
- Noë, R. & Hammerstein, P. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology*, **35**, 1–11.
- Noë, R. & Hammerstein, P. 1995. Biological markets. *Trends in Ecology & Evolution*, **10**, 336–339.
- Noë, R., van Schaik, C. P. & van Hooff, J. A. R. A. M. 1991. The market effect: an explanation for pay-off asymmetries among collaborating animals. *Ethology*, **87**, 97–118.
- Norscia, I., Antonacci, D. & Palagi, E. 2009. Mating first, mating more: biological market fluctuation in a prosimian. *PLoS One*, **4**, e4679.
- Palombit, R. A. 1994. Extrapair copulations in a monogamous ape. *Animal Behaviour*, **47**, 721–723.
- Plavcan, J. M. & van Schaik, C. P. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology*, **103**, 37–68.
- Port, M., Clough, D. & Kappeler, P. M. 2009. Market effects offset the reciprocation of grooming in free-ranging redfronted lemurs, *Eulemur fulvus rufus*. *Animal Behaviour*, **77**, 29–36.
- R Development Core Team 2008. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Reichard, U. H. 1995. Extra-pair copulation in a monogamous gibbons (*Hylobates lar*). *Ethology*, **100**, 99–112.
- Reichard, U. H. 2009. Social organization and mating system of Khao Yai white handed gibbons, 1992–2006. In: *Wild Gibbon Populations: New Understandings of Small Ape Socioecology, Population Biology and Conservation* (Ed. by S. M. Lappan & D. Whittaker), pp. 347–384. Berlin: Springer.
- Reichard, U. H. & Barelli, C. 2008. Life history and reproductive strategies of Khao Yai *Hylobates lar*: implications for social evolution in apes. *International Journal of Primatology*, **29**, 823–844.
- Reichard, U. H. & Sommer, V. 1994. Grooming site preferences in wild white-handed gibbons (*Hylobates lar*). *Primates*, **35**, 369–374.
- Savini, T., Boesch, C. & Reichard, U. H. 2009. Varying ecological quality influences the probability of polyandry in white-handed gibbons (*Hylobates lar*) in Thailand. *Biotropica*, **41**, 503–513.
- Schino, G. & Aureli, F. 2009. Reciprocal altruism in primates: partner choice, cognition, and emotions. *Advances in the Study of Behavior*, **39**, 45–69.
- Schino, G. & Aureli, F. 2010. A few misunderstandings about reciprocal altruism. *Communicative and Integrative Biology*, **3**, 561–563.
- Schino, G., Scucchi, S., Maestriperi, D. & Turillazzi, P. G. 1988. Allogrooming as a tension-reduction mechanism: a behavioral approach. *American Journal of Primatology*, **16**, 43–50.
- Schino, G., Polizzi di Sorrentino, E. & Tiddi, B. 2007. Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame of reciprocation. *Journal of Comparative Psychology*, **121**, 181–188.
- Schino, G., Di Giuseppe, F. & Visalberghi, E. 2009. The time frame of partner choice in the grooming reciprocation of *Cebus apella*. *Ethology*, **115**, 70–76.
- Setchell, J. M. 2005. Do female mandrills prefer brightly colored males? *International Journal of Primatology*, **26**, 715–735.
- Seyfarth, R. M. & Cheney, D. L. 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature*, **308**, 541–543.
- Shutt, K., MacLarnon, A., Heistermann, M. & Semple, S. 2007. Grooming in Barbary macaques: better to give than to receive? *Biology Letters*, **3**, 231–233.
- Trivers, R. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man, 1871–1971* (Ed. by B. Campbell), pp. 136–179. London: Heinemann.
- UNESCO World Heritage Centre 2005. Twenty-four new sites added to World Heritage List. *The World Heritage Newsletter*, **50**, http://whc.unesco.org/documents/publi_news_50_en.pdf.
- Ventura, R., Majolo, B., Koyama, N. F., Hardie, S. & Schino, G. 2006. Reciprocation and interchange in wild Japanese macaques: grooming, covefeeding, and agonistic support. *American Journal of Primatology*, **68**, 1138–1149.
- de Waal, F. B. M. 1997. The chimpanzee's service economy: food for grooming. *Evolution and Human Behaviour*, **18**, 375–386.
- de Waal, F. B. M. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behaviour*, **60**, 253–261.