

How do you measure pleasure?

A discussion about intrinsic costs and benefits in primate allogrooming.

Yvan I. Russell^{1-4,*}

Steve Phelps⁵

- 1. Junior Research Group “Evolution of Cooperation and Prosocial Behavior”, CRC Evolution of Social Behaviour, University of Göttingen, Germany.**
- 2. Institute of Cognitive and Evolutionary Anthropology, University of Oxford, UK.**
- 3. Department of Psychology, Middlesex University, UK.**
- 4. Department of Psychology, Brunel University, UK.**
- 5. Centre for Computational Finance & Economic Agents, University of Essex, UK.**

- Yvan Russell was partly funded by the German Initiative of Excellence of the German Science Foundation (DFG)**

Send correspondence to: yvanrussell@gmail.com

Keywords: grooming; value; sociality; primates; cost; benefit; game theory

Word count: 8,376 including references and figure captions

6,357 excluding references and figure captions

Abstract

Social grooming is an important element of social life in terrestrial primates, inducing the putative benefits of β -endorphin stimulation and group harmony and cohesion. Implicit in many analyses of grooming (e.g. biological markets) are the assumptions of costs and benefits to grooming behaviour. Here, in a review of literature, we investigate the proximate costs and benefits of grooming, as a potentially useful explanatory substrate to the well-documented ultimate (functional) explanations. We find that the hedonic benefits of grooming are well documented. However, we did not find convincing evidence for costs. If proximate costs do exist, they might consist of energetic, cognitive, opportunity costs, or some combination of all of these. Nonetheless, there remains the possibility that grooming costs are negligible, or even that the provision of allogrooming is rewarding in itself. We suggest empirical research to resolve this issue.

Introduction

In primate societies, allogrooming ('social grooming') is an integral part of life (Dunbar, 1988, 1991, 2010; Russell, 2007; Grueter et al., 2013). This refers to the act of one primate cleaning the other, by removing dead skin, dirt, and ectoparasites from the skin and fur (Hutchins & Barash, 1976; Nishida et al., 1999; Pérez & Veà, 2000; Tanaka & Takefushi, 1993; Tanaka, 1998). Allogrooming evolved in terrestrial species whose proximity to the ground made them vulnerable to becoming dirty and infested – hence, they needed to have their fur cleaned in hard to reach places (Grueter et al., 2013). However, grooming is more than merely hygienic (Dunbar, 1991): allogrooming apparently plays a role in maintaining social bonds between individuals within a group (Dunbar, 1988, 2010; Dunbar & Shultz, 2010; Silk et al., 2003) and promotes cooperation in primate societies (e.g., Dugatkin, 1997; Ventura et al., 2006). In the 'biological markets' approach (Noë et al., 1991; Noë & Hammerstein, 1995), animal sociality is construed as existing within a marketplace of individuals who vary in their desirability as trading partners. The goal of such studies (see Barrett & Henzi, 2001) is to define what is being traded and how. In this context, grooming is only one of many currencies that individuals can use in order to receive something in return. Grooming effort within a dyad is often asymmetric (not traded in equal amounts) due to an unequal social relationship. The recipient might be more dominant or specially skilled, and hence can pay something back in a different currency (see Barrett & Henzi, 2001.; Barrett et al., 1999; Koyama et al., 2006; Noë et al., 1991; Noë & Hammerstein, 1995; Schino & Aureli, 2009; Stambach, 1988). Researchers have demonstrated that grooming is traded for itself (Barrett et al., 2000; Watts, 2002), traded for food (de Waal, 1997; Ventura et al., 2006; Watts, 2003), and several other commodities (review in Barrett & Henzi, 2001; Schino & Aureli, 2009). The receipt of grooming might bear some trading value because the act might increase the receiver's future inclination to repay the favour (in same or different currency).

Analyses in the biological markets framework carry the implicit assumption of costs and benefits. One way to model this conflict between the costs and benefits accruing to individuals, is as a social dilemma in the form of an evolutionary game. Nowak and Sigmund (2005) describe and analyse a simple model in which pairs of players are randomly chosen from a large population. The first player chooses an amount to invest in their partner, which can be positive (cooperation) or zero (defection), and their payoff is simply the negative of this donation. On the other hand, the second player receives a positive payoff which is some multiple greater than one of the donation by their partner. In repeated plays, players can benefit from positive donations provided that partners *reciprocate* on subsequent rounds of play. Thus in a small population the payoffs are analogous to the prisoner's dilemma in which there is a temptation to defect (Axelrod 1997). In repeated games, modeling shows that cooperation can be sustained by various forms of reciprocity. In small populations, *direct* reciprocity can be evolutionarily-stable under certain conditions (for a definition of an evolutionarily stable strategy, see Parker & Maynard Smith, 1990). Direct reciprocity entails tit-for-tat strategies in which players cooperate conditionally on whether a particular partner cooperated with them in previous rounds of play (cf. Dugatkin, 1997; Binmore, 2007). Applied to a primate group, this “I scratch your back, you scratch my back” behaviour can be thought of as an exchange of grooming for grooming.

Direct reciprocity has been invoked as an explanation of the symmetry observed in time-investments in grooming between pairs of individuals in primate societies. The implicit assumption is that there is a small fitness cost involved in giving grooming out, and a larger fitness benefit to receiving it. In other words, giving out is intrinsically less fitness-enhancing than receiving due to some fitness cost. In order to validate this assumption, ideally we would attempt to measure the ultimate costs and benefits of grooming interactions in terms of inclusive

fitness. Whilst there have been important studies of the fitness benefits of grooming (e.g. Silk et al., 2003), there has been relatively little attention paid to the costs. This is understandable given that by the very fact that we expect the costs to be small in relation to the benefits it would be difficult to quantify the marginal fitness benefits of a reduction in grooming effort *ceteris paribus*. In fact, if we were able to show that the proximate costs of grooming in terms of energy-expenditure or opportunity costs for other fitness-enhancing activities are negligible, then this would cast serious doubt on the existence of fitness costs for allogrooming, which in turn could possibly undermine a biological markets view of grooming interactions. If grooming were cost-free, then grooming exchanges would merely represent cases of commensalism, not true reciprocation (cf. Dugatkin, 1997, pp. 31-34). We discuss this issue later.

The specification of “costs” and “benefits” are integral in game-theoretic and optimality modelling (Binmore, 2007; Dugatkin, 1997; Parker & Maynard Smith, 1990). Accordingly, numerical values are assigned to behaviours in order to construct models that illustrate the way a system works in nature. Here, the numbers are only important for the internal validity of the model. For example, in the Hawk-Dove game (Dugatkin, 1997; Binmore, 2007), the specific numerical payoffs (“+2” for a dove who meets another dove, “0” for a dove who meets a hawk, “-5” for a hawk meeting another hawk) are only there because they illustrate the conditions of a game where different players will differentially benefit given specific conditions. Here, the numbers are not chosen to reflect real-world values. In fact, it is common practice in biological modelling to illustrate a general process using numbers which – although arbitrary – are meaningful insofar as the results of the model are meaningfully applicable to real biological phenomena (Parker & Maynard Smith, 1990). The issue of real-life quantifiability only emerges in studies which aim to model the behaviour of specific species in a given environment (*ibid.*).

Unfortunately, as Noë et al. (1991) say, “in practice, it is usually impossible to determine the budget of an interaction in more than general terms” (p. 98).

Note that the putative “trading” behaviour cited above is a functional rather than a proximate explanation (sensu Tinbergen, 1963; cf. Schino & Aureli, 2009, pp. 53-55). The trading system may somehow work adaptively, but the participants themselves – the primates – do not necessarily cogitate on their own behaviour and think rationally in terms of fairness (Bräuer & Hanus, 2012; Schino & Aureli, 2009). Indeed, some primatologists (e.g. Pugo-Gonzales et al., 2009), through computer modelling, have made efforts to show that cognitive sophistication is not necessary for allowing primate cooperation. Yet, it is clear that animals are highly responsive to their environments (Fraser et al., 2008; Krebs & Dawkins, 1984; Russell et al., 2008 Videan et al., 2005) and that grooming is a conspicuous (and sometimes ubiquitous) behaviour which cannot escape the attention of other members of the primate group (Russell, 2007). Primates unequivocally gain some subjective impression when they give and receive grooming – but what exactly are they feeling? Can we meaningfully place the proximate – subjective – feelings into the context of the functional implications of grooming?

In addition to the intellectual interest, there may be good logistical reasons for investigating the presence of proximate mechanisms. One reason is that it could simply be so much easier to measure a proximate than an ultimate costs and benefits. Studies of ultimate consequences need to be long-term (e.g. Silk et al., 2003), beyond the scope of what most studies can do. Towards this goal, here we ask whether we can find some objective way to quantify the *proximate* costs and benefits. In this paper, we take exploratory steps in this direction by reviewing literature which considers grooming as a physiological activity.

How do you measure pleasure?

Virtually everyone who writes about primate allogrooming construes it as beneficial to the recipient. Indeed, this idea forms the crux of numerous observational studies on primates where grooming is considered a form of “currency” – valuable to the recipient (grooming gained) and, presumably, incurring a cost to the giver (grooming given out). This is operationalised most concretely in studies using biological markets as described above. The obvious usable variable is “time”, by far the commonest measurement of value in grooming studies (Barrett et al., 2000; Dunbar, 1991; Dunbar et al., 2009; Grueter et al., 2013, Russell, 2010, and many others), Indices of grooming are always expressed in units of time. For example, in the grooming reciprocity index of Boesch and Boesch-Achermann (2000), time of grooming received is simply divided by time of grooming given out. The implicit value of time derives from its finiteness, which imposes a constraint on the time budget of animals (Dunbar, 1992; Dunbar et al., 2009). Time is obviously beneficial on the ultimate level (e.g. Dunbar, 1992), but animals cannot measure time and are (arguably) unaware of the concept of time and being patient (Roberts, 2002; Schino & Aureli, 2009).

Is it possible to establish an intrinsic value to the currency of grooming? What are the costs and benefits in physiological terms? Some authors (e.g. Dunbar, 2010; Barrett & Henzi, 2001) have pointed out, grooming is valuable because it confers hedonic pleasure onto the recipient. This is because grooming stimulates the release of β -endorphins in the recipient (Keverne et al., 1989; Dunbar, 2010). The same release of β -endorphins also occurs in humans whilst receiving therapeutic massage (Kaada & Torsteinbø, 1989). In humans, endorphins are known to activate opiate receptors, and therefore to create a pleasurable (analgesic) effect (Hawkes, 1992). It is the endogenous (naturally occurring in body) functional equivalent of

morphine (van Ree et al., 2000) and its desirable effect is known among a wide range of animals (ibid.) (although it is important to note is that β -endorphins do not exert their effects in physiological isolation, see Hawkes, 1992; van Ree et al., 2000). Grooming is likely a crucial instigator of pleasure among all monkeys and apes (review in Dunbar, 2010). This is probably true for all/most mammals, if we allow ourselves to reason inductively from evidence that grooming functions as a commodity in many other mammal species (see examples in Dugatkin, 1997). For example in rats, injections of β -endorphins have been found to intensify social tactile behaviour, including social grooming (van Ree & Niesink, 1983). Endorphins are not only a reward but also a motivator of social contact (van Ree et al., 2000; Graves et al., 2002). Allogrooming appears to function as a tension-reduction mechanism among primates (Schino et al., 1988; Fraser et al., 2008), creating an effect of relaxation. There is research to show that grooming causes a reduction in heart rate for rhesus macaques (Aureli et al., 1999), horses (Feh & de Mazières, 1993), and cows (Sato & Tarumizu, 1993). Similarly, another study of grooming on horses (i.e. humans grooming horses) showed that grooming created a “more relaxed, calm state in the horse” (McBride et al., 2004, p. 78) according to behavioural measures. For human recipients, massage is known to promote relaxation and pain relief (Goats, 1994), and to reduce blood pressure (Cady & Jones, 1997).

The intrinsic pleasure from the receipt of grooming does appear well supported by the evidence (Dunbar, 2010) – but how can we proceed to assign a value to it? Philosophers define intrinsic pleasure as a sensation pursued as a goal in itself (Feldman, 1997; cf. Higgins, 2006, on motivational force). The value of the intrinsic pleasure can be construed in three ways (Feldman, 1997): (1) reflecting the quantity of the pleasurable stimulus, (2) proportional to the intensity of desire to continue the sensation, and (3) intensity of pleasure derived from the knowledge that one is experiencing that sensation. Applied to primate data, option 1 is the only thing that can be

measured, as number of many minutes of grooming receipt occurred. Direct information about options 2 and 3 would be extraordinarily tricky information to obtain from non-linguistic animals, however in principle 2 could be operationalised using choice modeling experiments (Hensher & Johnson 1981) in which we calibrate a model of the animal's utility function against observations of empirically-observed pairwise preferences for receiving grooming over other activities.

Even if it were possible, we should ask whether it is enough to simply measure hedonic value. There must be a number of other benefits to consider. What are they? The most thorough cataloguing of possible benefits and costs of grooming were by Pérez and Veà (1998). After a literature review, they listed all conceivable benefits and costs of grooming to both actor (giver) and recipient. They subdivided the cost and benefits into 'immediate' and 'delayed' categories, and subdivided further into social and individual benefits. Their lists are summarized in table 1 (this information did not appear in table form in the original). Only seven of the cells display factors that the ape is likely to be cognitively aware of at the time. Only three of these concern *intrinsic* experiences (recipient gratification and relief of tension, tension relief for giver, and giver expending effort). The other four factors involve *extrinsic* pleasures – which is defined by philosophers as non-sensory pleasures that involve a pleasurable *attitude* towards an object or state of affairs (Feldman, 1997). Here the extrinsic pleasures concern affiliative preferences. Whilst socializing and sensory pleasure are closely intertwined (van Ree & Niesink, 1983), a feeling of affiliation is separate from (although associated with) sensory pleasure. Animals learn to associate specific (formerly neutral) events with sensory pleasure, and consequently learn to pursue the experiences that led to the pleasure on previous occasions (van Ree et al., 2000). This is surely how affiliations grow: a learned association between intrinsic pleasure and the interaction with a specific individual – leading to the pursuit of interacting with someone for its

own sake. This is conceivable as an ‘extrinsic’ pleasure (comprising an attitude towards an entity, Feldman, 1997), which could be derived from emotional responses that are specific to a particular relationship. Such emotions are an important ‘intervening variable’ in how an animal responds to others with whom a relationship has been established (Pérez & Veà, 1998); the emotional response will be the product of an accumulated history of interactions (ibid.; cf. Hinde, 1976).

Too much of a good thing?

An important question to ask is how *constant* this received pleasure would be. Will every minute of grooming receipt be perceived *equally* pleasurable? Would there be a dissipation in pleasure as the minutes of touching pass? It is true that people habituate to the sensation of touch if the mechanical stimulation occurs repeatedly on the same spot in the same way (e.g. see brainwave study by Angel et al., 1985, showing decrements in somatosensory evoked potentials in response to repetitive mechanical stimulation). But grooming is not necessarily a monotonous activity, because the to-be-removed objects (bugs, dust, etc.) appear at a variety of locations upon the recipient’s body. For example, chimpanzees frequently switch the area of the body that they are grooming (van Lawick-Goodall, 1968), and the recipient often encourages the switch by presenting a certain part of their body to the groomer. The pleasure of being touched would be renewed every time. A more pertinent question concerns the impact of the *endorphins*.

Exactly how long does the pleasurable effect last? That depends on the ‘dose’ received. Yaksh et al. (1982) injected rhesus monkeys with β -endorphins at four different doses (100, 250, 500, 750 μ g) and, unsurprisingly, found that the magnitude and duration of the effect (how long endorphins stay in system) is heavily dose-dependent. Even at the lowest dose, the β -endorphins

remained in the monkeys' systems for hours (as measured by pain tolerance thresholds in response to shock). The dose response curves indicated a slow increase leading to a blunt peak, followed by a gradual decline (peaks are flatter when the doses are smaller). However, the degree of subjective pleasure derived from a 'dose' will depend on the degree of tolerance that an individual has developed towards a particular opioid (van Ree et al., 2000). It is unclear whether we should refer to grooming as 'addictive', but some chimpanzee grooming sessions are certainly lengthy (e.g. Nishida, 1970, reported a three-male grooming episode lasting 105 minutes). Whether this reflects any form of 'drug tolerance' to grooming is unknown. How much does the receipt of grooming actually resemble a single dose of opiate administered during an experiment? The 'doses' received during grooming would be comparatively tiny but delivered continuously. It may have the same additive effect, judging from the aforementioned study of β -endorphins and massage (Kaada, & Torsteinbø, 1989). In that study, a massage lasting thirty minutes produced increases in recipient β -endorphins that were still present 60 minutes (but not 120 minutes) later. Massage would provide tiny 'doses' in the same continuous manner as grooming.

Endorphins appear to be a gift that keeps on giving (at least for a while). Moreover, its effects are likely to be felt early in the grooming session (Keverne et al. 1989, found their β -endorphin results within three minutes after the grooming event). However, it is a routine occurrence in primate groups (e.g. Russell, 2007) for the grooming recipient to choose to end the grooming session (e.g., by walking away). It is impossible to know whether a cessation occurred because the recipient had received an adequate 'fix' and needed nothing more, or because the giver was an incompetent groomer, or some other factor. As some authors pointed out, grooming may not be universally good. Dunbar (2010) mentions that being a grooming recipient might also be painful (based on a personal anecdote of being groomed by an animal himself!). Moreover,

Schino and Aureli (2009, pp. 60-61) expostulate on the issue of grooming benefit, noting that morphine (even endogenous) could actually cause social withdrawal – contrary to usual assumptions about benefits. Nonetheless, what is clear from injection studies (Yaksh et al., 1982) is that the hedonic benefit is *not* constant from one minute to the next. The diminishing of presumed hedonic effect surely follows the *law of diminishing marginal utility* in economics (Binmore, 2007), reflecting the well-documented process whereby habituation to a stimulus decreases the motivation to continue seeking it (McSweeney & Swindell, 1999). This kind of satiation should occur even though the focal patch on the recipient’s body is constantly shifting (e.g., Pérez & Veà, 2000). The desire to be groomed likely follows the same cyclical pattern of motivation and demotivation (following satiation and deprivation, respectively) as do other kinds of stimuli (McSweeney & Swindell, 1999).

What cost is lost?

How do we subtract a ‘cost’ incurred by the effort of the *giver*? Dunbar and Sharman (1984) argue that the small energetic cost of allogrooming is unlikely to impact on the groomer’s reproductive success overall. Even if there is some intrinsic pleasure in grooming someone else (see Table 1), it seems that the giver will not be as relaxed as the recipient simply because the act of grooming involves a form of ‘labor’. This is the actual removal of objects from their recipient’s fur (Hutchins & Barash, 1976; Nishida et al., 1999; Tanaka & Takefushi, 1993; Tanaka, 1998). Does laboriousness equate to a lack of pleasure for the giver? Suppose that it might even be mentally stimulating, rather than aversive, to the chimpanzee to fish for (possibly edible) objects in someone else’s fur (cf. Higgins, 2006, on “engagement”). Would it be fair to claim that grooming would produce a subjective experience less similar to pure relaxation and more similar to foraging?

It would not burn as many calories as foraging, but psychologically it might be similar in being a manual task that requires concentration, and hence the expenditure of *cognitive* resources (Naish, 2010) that might ultimately impact on fitness. Tanaka (1998) provided a detailed illustration of a grooming procedure within his study of how Japanese macaques remove louse eggs from each other's fur. It proceeds in four steps (ibid., p. 1231): (1) "the egg is gripped between the first finger and thumb", (2), "the adhesive ring of the egg is held precisely and the egg is drawn by the forefinger and thumb to the tip of the hair", (3) "the detached egg is carried to the mouth", and (4) "it is eaten". Doing this proficiently requires some practice. Apparently, Japanese macaques can learn from *each other* how to do this (ibid.). Grooming can therefore be characterized as an 'effort', but can it really be described as a 'cost'? Certainly, if a 'benefit' is relaxation (as mentioned earlier), then the 'cost' of grooming might be some *decrease* of relaxation. In fact, the structure of the task (find object, remove it) constitutes an 'anticipation-reaction' type of activity that perhaps keeps the groomer in a fairly alert mental state. If a scientist were to measure a groomer's brainwaves during the act of grooming, then likely the scientist would detect 'expectancy waves' similar to those found in humans (Walter et al., 1964). Also called 'contingent negative variation' (CNV), these phenomena are characterized as conspicuous and sustained increases in brainwave amplitude that occur when someone is anticipating a motor response to a stimulus (Touge et al., 2003). They have been measured in human research participants who have been given tasks where they must plan their own response in anticipation of a stimulus (Nagai et al., 2004; Touge et al., 2003; Walter et al., 1964). The most common paradigm is where the participant hears two sounds: (1) a tone that informs the participant to get ready to respond, and (2) an 'imperative' tone which is the cue for the response to occur, e.g. push a button (Nagai et al., 2004). The CNV occurs during the period between the first and the second sound, when the human is anticipating their own motor response (Nagai et

al., 2004; Walter et al., 1964). While the CNV is in progress, brain activation (measured as local blood deoxygenation) occurs in regions involved in planning of movements, anticipating tasks and rewards, and general arousal and awareness (ibid.). This should also apply for tasks with an element of unpredictability. For example, Touge et al. (2003) gave their participants a game where they needed to repeatedly deflect a ping-pong ball with their index fingers. CNV waves appeared during the anticipation period. Like grooming, this task involved skilled finger movements. Interestingly, the CNV waves decreased in amplitude if the participants were able to gain practice. Similarly, an experienced groomer might perceive the task as less effortful than an inexperienced groomer would. Even so, the degree of effort will vary. As Jane Goodall observed (van Lawick-Goodall, 1968), long grooming sessions alternated between “periods of intense concentration” and “periods of slow and lazy grooming when each chimpanzee sat with half closed eyes, idly running a forefinger through the hair of the other” (van Lawick-Goodall, 1968, p. 264). CNV waves show increased amplitude when an individual is devoting much attention to a task, compared to when an individual paying less attention (Kropp et al., 2001). For the groomer, high amounts of effort and attention will probably produce a better result for the recipient (both hygienically and hedonically); but it may also cause the groomer to be (at least somewhat) less relaxed than an individual who is receiving grooming but not giving.

On a hedonic level, however, the time-cost of grooming should be directly connected to the metabolic cost. One potential cost of grooming has been identified as the energy required to perform the task (see Pérez & Veà, 1998 and references therein). Veà et al. (1999) developed a cost/benefit model of grooming predicated on a formula that specifies the cost of grooming as roughly 24 calories per hour for a 5 kg animal (see references therein). A notional representation of the model is sketched in figure 1 (adapted from Veà et al., 1999, p. 250). The cost is represented as a linear function representing cost multiplied by time (ibid., function 3). The

benefit here refers to the groomer, not the recipient. It is represented by the formula: $\text{benefit} = a * t / b + t$; where a is the maximum benefit obtainable, b is the 'growing rate' for benefits, and t is time (ibid., function 4). The return on investment begins to diminish when the two lines meet: where cost exceeds benefit. The maximum benefit is obtainable earlier: where the benefit curve is flattening out. Veà et al. (1999) applied their model to observational data on white crowned mangabeys, with the 'cost' as energy expenditure, and the 'benefit' was aggression avoidance (measured as the proportion of successful versus unsuccessful grooming episodes where grooming succeeded in stopping aggression, or maintaining a non-aggressive situation). They found a significant correlation between mangabey age and efficiency of investment. Specifically, the older ones were more efficient in being able to groom long enough to approach maximum benefit, but not to exceed that point. Younger ones fell short of maximising their benefits. In other words, age and experience allow the mangabey to groom optimally (cf. Parker & Maynard Smith, 1990).

The analysis of Veà et al. (1999) described above shows that the costs and benefits *can* be operationalized in a way that produces meaningful results. Yet, they took two completely different currencies (grooming vs. aggression avoidance). Can we apply such a system to an analysis of grooming? We certainly can, but this is not the question we asked: can we use knowledge of *intrinsic* costs and benefits can somehow allow us to calculate a *natural* cost-benefit ratio? Above, the discussion was about how the 'pleasure' will dissipate over time; and also that individuals will vary in the manual effort they invest in a grooming episode. It does seem subjective to allow the construction of an index based on psychological experience. Moreover, even if the act of grooming is psychologically a form of 'micro-foraging', it is impossible to say that it bears a 'cost'. It might even be an enriching activity (intellectually stimulating) for a group of captive apes. Some psychologists (e.g. Higgins, 2006) aver that

focused concentration on a task is a cognitive reward in itself. The act of grooming would qualify for this kind of activity.

The Opportunity Costs of Grooming.

We might suppose that one of the most significant proximate costs to investing in allogrooming would be the opportunity cost of foregoing other activities - such as foraging, moving, and resting - during the time allocated to allogrooming (Dunbar et al., 2009; Dunbar & Sharman, 1984). On first consideration, these costs would seem considerable since we might view the animal's time budget as entirely “fungible”; i.e., time allocated to allogrooming could be spent equally on foraging, eating, child-rearing or any other activity that would ultimately enhance fitness. The famous Japanese primatologist Nishida (1970) described grooming as “friendly behaviour during rest” (p. 56) and argued that it probably does not supplant more important activities such as feeding (cf. Dunbar & Sharman, 1984). If anything, it will probably supplant other types of resting behaviour (Newton-Fisher, 1999; Dunbar et al., 2009). More serious time constraints are detectable from the point of view of an individual primate. Within a large group of primates, there simply isn't time for an individual to groom everyone in the social network (Dunbar, 1991): one of the most significant opportunity costs is foregoing the opportunity to groom another partner, and this cost in itself would bootstrap a biological market in which grooming could be exchanged for other goods and services.

However, the above discussion ignores the fact that the range of activities that can be engaged in *whilst being groomed* is severely restricted. For example, during field work with a captive group of chimpanzees at Chester Zoo, the first author observed that – when a chimpanzee was the recipient of a grooming event – there was a very limited choice of alternative activities.

Whilst sitting and being groomed, the recipient could either (i) reciprocate the grooming, (ii) engage in auto-grooming (Boccia, 1983), (iii) handling infants, and (iv) occasionally eating. For most other activities (e.g. defecating, socialising with others, etc.), it would be necessary to walk away from the grooming bout. Dunbar et al. (2009) partition an animal's time budget into four primary activities: feeding, travelling, resting, and social time; and they partitioned resting time into enforced rest (that which is necessary) and free rest (non-essential) (ibid.). Extending this idea, we might partition *sociality* the same way as resting, into "necessary" (assuming necessity of sociality, see Dunbar, 2010) and "free" (beyond that which is needed). In the free sociality, the opportunity cost is actually much higher than that of the necessary sociality, because the set of possible activities is much smaller. Thus, whilst a groomee in "free" grooming can do A, B, C, D, E, F, G, etc., a groomee in "necessary" grooming can only do A, B, and C. This has important implications for understanding grooming interactions as a biological market, or a form of altruism, since the opportunity costs for an individual reduce dramatically for the recipient of grooming. If opportunity costs constitute the majority of the total cost of grooming, then any underlying social dilemma is severely weakened; we might observe something that looks superficially like direct reciprocity or tit-for-tat like behaviour, but in fact this might simply reflect that there is a relatively little else to do whilst being groomed apart from to groom back.

Conclusion

Any deep understanding of primate social interaction is contingent on being able to explain grooming behaviour. Biological market theory attempts to explain grooming by appealing to its apparent fungibility and use as a medium of exchange for other goods and services, including grooming itself. However, such a biological market understanding of grooming can only really be made to work if we are able to understand the underlying costs and

benefits of grooming, *both* proximate and ultimate. As discussed above, measuring the precise costs and benefits of grooming is a formidable challenge (Dugatkin, 1997, pp. 116-119; Noë et al., 1991; Russell, 2007). Our short discussion has illustrated some of the inherent problems in viewing grooming as a medium of exchange.

There is a caloric cost (Veà et al., 1999), but a negligible one. There is an attentional ‘cost’ in the sense that it is consuming cognitive resources (for comparison, see Naish, 2010, about the ‘resource limitations’ on human attention), but this is likely not to a physiological ‘cost’. Instead, it might be more saliently viewed as an attentional opportunity cost, for example because of the fact that it might distract someone from noticing a danger in the environment (cf. Mooring & Hart, 1995, for an interesting example in impalas). Regardless of measurable cost, there is simply no commensurate benefit using the same currency: we cannot claim that receiving grooming has a caloric benefit. Flipping the comparison around, we also cannot find a cost in the same currency as the benefit. Grooming may induce pleasure in the participant (Keverne et al., 1989; Dunbar, 2010), but we cannot reasonably claim an equally proportional ‘pleasure debit’ for the giver of grooming. Currently, there is no evidence that grooming someone else is aversive, or that this activity is unpleasurable for the giver.

Game theorists often model hypothetical situations by quantifying the hypothesized benefits and then deciding how individuals would behave based on the relative payoffs (see examples in Binmore, 2007, Dugatkin, 1997; Parker & Maynard Smith, 1990). Inspired by such paradigms, the aim of this paper was to search for some kind of justification for determining a way to quantify costs and benefits in a way that can be adopted for primatological analyses of grooming. What the preceding discussion has revealed is that – although it is plausible that intrinsic costs and benefits of grooming do exist – we cannot map both costs and benefits of

grooming onto the same yardstick. However, this does not mean that we should give up on the idea of including some proximate measure of costs and benefits. In a way, our question parallels those of early economists who contemplated the cognitive underpinnings of revealed preference.

As Binmore (2007) wrote:

“Victorian economists thought of utility as measuring how much pleasure or pain a person feels. Nobody doubts that our feelings influence the decisions we make, but the time has long gone when anybody thought that a simple model of a mental utility generator is capable of capturing the complex mental process that swings into action when a human being makes a choice. The modern theory of utility has therefore abandoned the idea that a util can be interpreted as one unit more or less of pleasure or pain... One of these days, psychologists will doubtless come up with a workable theory of what goes on in our brains when we decide something. In the interim, economists get by with *no theory at all* of why people choose one thing rather than another. The modern theory of utility makes no attempt to *explain* choice behavior. It assumes that we already know what people choose in some situations and uses this data to deduce what they will choose in others — on the assumption that their behavior is consistent (pp. 111-112, italics original).

Binmore’s comments above are pertinent to our discussion of primate grooming costs and benefits. Proximate variables were ignored because there are too many unknowns, and researchers in biological markets do not need to know how the animal feels inside in order to produce meaningful data. However, that does not mean that we should give up on proximate mechanisms. Researchers in primatology do express an interest in understanding the proximate mechanisms that underlay prosociality. For example, Schino and Aureli (2009) propose that primates engage in a kind of emotional book-keeping which determines how their exchange

behaviour is governed. This implies a system of credits and debits. Yet, we still know little about the underlying mechanism to support this hypothesis (cf. Dunbar & Shultz, 2010).

Does it make sense to devise a hedonic scale of proximate benefits, measured as “+*n*” for grooming received, and “-*n*” for grooming given out? Judging from the data, the issue of *cost* is more contentious than benefit. This is an important issue, because the principle of reciprocal exchange in biological markets theory – as applied to grooming – would be rendered irrelevant if we conclusively decide that grooming has no cost. This would entail “+*n*” for grooming received, and “0” for grooming given out (commensalism). Alternately, if grooming really does provide positive mental stimulation and enjoyment, then it would be “+*n*” for grooming received, and “+*n*” for grooming given out. This would make it *byproduct mutualism* (Dugatkin, 1997) instead of trading. In fact, Schino and Aureli (2009) argue that this “low-cost altruism” (p. 48) is fairly common in the animal kingdom.

“Since costs are negligible anyway, there is little incentive for cheating (i.e., reaping the immediate benefits and failing to reciprocate later) and selection must have favored the maximization of received return benefits more than the minimization of immediate costs. Thus, we may expect selection to have favored the evolution of proximate mechanisms based on some form of partner choice (“groom most of the individuals who groom you most”) more than mechanisms aimed at the immediate detection of cheating” (Schino & Aureli, p. 48).

The presumption of “low-cost” needs should be empirically confirmed yet few have addressed the issue of cost (but see Pérez & Veà, 1998; Veà et al., 1999). In this review, we have not seen cogent empirical evidence of proximate cost, neither energetically nor cognitively. The issue of *opportunity cost* is more plausible than the others, but this will surely be highly context-

dependent depending on the overall time budget of the animal (see Dunbar et al., 2009). When judging opportunity cost, we can see that grooming will be far more “expensive” for a group of free-ranging primates with live in a poor-quality habitat where foraging is time consuming (e.g. Dunbar, 1992) than for a group of primates living in a zoo with ample food and comfort and much free time (e.g. Russell, 2007). Nonetheless, it may someday possible to get inside the head of the animals and find a way to measure relative costs and benefits. We have already mentioned the choice modelling paradigm (Hensher & Johnson, 1981) as one possible route. Alternately, we could gain insights from studying the brain directly (e.g. Dunbar, 2010). A third option might arise from computational psychology. This is a sub-discipline of cognitive psychology (see Gobet et al., 2011) where programmers simulate the cognitive architecture of humans and test these models against actual empirical results (e.g. Lane et al., 2008, on chess players). Such simulations could be done for the primate mind to test how internal variables can play out in terms of partner preference in grooming. This kind of modelling has already been done in economics to study the cognitive underpinnings of economic decision making (Busemeyer & Johnson, 2005), the models of which include continuous variables of emotion, knowledge, etc. This could also be done for primate decision making (cf. Puga-Gonzalez et al., 2009) incorporating emotion, different levels of costs and benefits (e.g. low cost, high benefit) and other factors in order to provide new levels of explanation for the social grooming behaviour of primates.

References

Angel, R. W., Quick, W. M., Boylls, C. C., Weinrich, M. & Rodnitzky, R. L. (1985). Decrement of somatosensory evoked potentials during repetitive stimulation. *Electroencephalography and Clinical Neuropsychology*, 60, 335-342.

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.

Axelrod, R. (1997). *The Complexity of Cooperation: Agent-based Models of Competition and Collaboration*. Princeton, NJ: Princeton University Press.

Barrett, L., & Henzi, S. P. (2001). The utility of grooming in baboon troops. In R. Noë, J. A. R. A. M. van Hooff, & P. Hammerstein (Eds.) *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets* (pp. 119-145). Cambridge: Cambridge University Press.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 266, 665-670.

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (2000). Female baboons do not raise the stakes but they give as good as they get. *Animal Behaviour*, 59, 763-770.

Binmore, K. (2007). *Playing for Real: A Text on Game Theory*. Oxford: Oxford University Press.

Boccia, M. L. (1983). A functional analysis of social grooming patterns through direct comparison with self-grooming in Rhesus Monkeys. *International Journal of Primatology*, 4, 399-418.

Boesch, C., & Boesch-Achermann, H. (2000). *Chimpanzees of the Tai Forest*. Oxford: Oxford University Press.

Bräuer, J. & Hanus, D. (2012). Fairness in non human primates? *Social Justice Research*, 25, 256-276.

Busemeyer, J. R., & Johnson, J. G. (2005). Micro-process models of decision making. In R. Sun (ed.). *Cambridge Handbook of Computational Psychology* (pp. 302-321). Cambridge: Cambridge University Press.

Cady, S. H., & Jones, G. E. (1997). Massage therapy as a workplace intervention for reduction of stress. *Perceptual and Motor Skills*, 84, 157-158.

de Waal, F. B. M. (1997). The chimpanzee's service economy: food for grooming. *Evolution and Human Behaviour*, 18, 375-386.

Dugatkin, L. A. (1997). *Cooperation Among Animals: An Evolutionary Perspective*. New York: Oxford University Press.

Dunbar, R. I. M. (1988). *Primate Social Systems*. London: Croon Helm.

Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. *Folia Primatologica*, 57, 121-131.

Dunbar, R. I. M. (1992). Time: A hidden constraint in the socioecology of baboons. *Behavioural Ecology and Sociobiology*, 31, 35-49.

Dunbar, R. I. M. (2010). The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. *Neuroscience and Biobehavioral Reviews*, 34, 260-268.

Dunbar, R. I. M., Korstjens, A. H., & Lehmann, J. (2009). Time as an ecological constraint. *Biological Reviews*, 84, 413-429.

Dunbar, R. I. M., & Sharman, M. (1984). Is social grooming altruistic? *Zeitschrift für Tierpsychologie*, 64, 163-173.

Dunbar, R. I. M., & Shultz, S. (2010). Bondedness and sociality. *Behaviour*, 147, 775-803.

Feh, C., & de Mazières, J. (1993). Grooming at a preferred site reduces heart rate in horses. *Animal Behaviour*, 46, 1191-1194.

Feldman, F. (1997). On the intrinsic value of pleasures. *Ethics*, 107, 448-466.

Fraser, O. N., Stahl, D., & Aureli, F. (2008). Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of the United States*, *105*, 8557-8562.

Goats, G. C. (1994). Massage - the scientific basis of an ancient art part 2. Physiological and therapeutic effects. *British Journal of Sports Medicine*, *28*, 153-156.

Gobet, F., Chassy, P., & Bilalić, M. (2011). *Foundations of cognitive psychology*. New York, NY: McGraw Hill.

Graves, F. C., Wallen, K. & Maestriperi, D. (2002). Opioids and attachment in rhesus macaques (*Macaca mulatta*) abusive mothers. *Behavioral Neuroscience*, *116*, 489-493.

Grueter, C. C., Bisonette, A., Isler, K., & van Schaik, C. P. (2013). Grooming and group cohesion in primates: implications for the evolution of language. *Evolution & Human Behaviour*, *34*, 61-68.

Hawkes, C. (1992). Endorphins: the basis of pleasure? *Journal of Neurology, Neurosurgery, & Psychiatry*, *55*, 247-250.

Hensher, D.A. & Johnson, L.W., (1981). *Applied Discrete-Choice Modelling*. London: Croon Helm.

Higgins, E. T. (2006). Value from hedonic experience and engagement. *Psychological Review*, *113*, 439-460.

Hinde, R. A. (1976). Interactions, relationships, and social structure. *Man, 11*, 1-17.

Hutchins, M., & Barash, D. P. (1976). Grooming in primates: implications for its utilitarian function. *Primates, 17*, 145-150.

Kaada, B., & Torsteinbø, O. (1989). Increase of plasma β -endorphins in connective tissue massage. *General Pharmacology, 20*, 487-489.

Keverne, E. B., Martensz, N. D., & Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology, 14*, 155-161.

Krebs, J. R., & Dawkins, R. (1984). Animal signals: mindreading and manipulation. In J. R. Krebs & N. B. Davies (Eds.). *Behavioural Ecology: An Evolutionary Approach* (2nd Ed.). Oxford: Blackwell.

Koyama, N. F., Caws, C., & Aureli, F. (2006). Interchange of grooming and agonistic support in chimpanzees. *International Journal of Primatology, 27*, 1293-1309.

Kropp, P., Linstedt, U., Niederberger, U., & Gerber, W. D. (2001). Contingent negative variation and attentional performance in humans. *Neurological Research, 23*, 647-650.

Lane, P. C. R., Gobet, F., & Smith, R. L. (2008). Attention mechanisms in the CHREST cognitive architecture. In L. Paletta & J. K. Tsotsos (eds.), *Proceedings of the 5th International Workshop on Attention in Cognitive Systems* (pp. 207-220). Graz: Joanneum Research.

McBride, S. D., Hemmings, A. & Robinson, K. (2004). A preliminary study on the effect of massage to reduce stress in the horse. *Journal of Equine Veterinary Science*, 24, 76-81.

McSweeney, F.K., & Swindell, S. (1999). General-process theories of motivation revisited: The role of habituation. *Psychological Bulletin*, 125, 437-457.

Mooring, M. S., & Hart, B. L. (1995). Costs of allogrooming in impala: distraction from vigilance. *Animal Behaviour*, 49, 1414-1416.

Nagai, Y., Critchley, H. D., Featherstone, E., Fenwick, P. B. C., Trimble, M. R., & Dolan, R. J. (2004). Brain activity relating to the contingent negative variation: an fMRI investigation. *NeuroImage*, 21, 1232-1241.

Naish, P. (2010). Attention. In H. Kaye (ed.). *Cognitive Psychology* (2nd ed.). Milton Keynes: The Open University.

Newton-Fisher, N. E. (1999). Association by male chimpanzees: a social tactic? *Behaviour*, 136, 705-730.

Nishida, T. (1970). Social behavior and relationship among wild chimpanzees of the Mahali mountains. *Primates*, 11, 47-87.

Nishida, T., Kano, T., Goodall, J., McGrew, W. C., & Nakamura, M. (1999). Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science*, *107*, 141-188.

Noë, R., & Hammerstein, P. (1995). Biological Markets. *Trends in Ecology and Evolution*, *10*, 336-339.

Noë, R., van Schaik, C. P., & van Hooff, J. A. R. A. M. (1991). The market effect: An explanation for payoff asymmetries among collaborating animals. *Ethology*, *87*, 97-118.

Nowak, A., & Sigmund, K. (2005). Evolution of indirect reciprocity. *Nature*, *437*, 1291–1298.

Parker, G.A., & Maynard Smith, J. (1990) Optimality theory in evolutionary biology. *Nature*, *348*, 27-33.

Pérez, A., & Vèa, J. J. (1998). Cost-benefit analysis of allogrooming behaviour in primates II. *Primate Report*, *50*, 15-37.

Pérez, A. P. & Veà, J. J. (2000). Allogrooming behavior in *Cercocebus torquatus*: The case for the hygienic functional hypothesis. *Primates*, *41*, 199-207.

Puga-Gonzalez, I., Hildenbrandt, H., Hemelrijk, C. K. (2009). Emergent patterns of social affiliation in primates, a model. *PLoS Computational Biology*, *5*. e1000630.

Roberts, W. A. (2002). Are animals stuck in time? *Psychological Bulletin*, *3*, 473-489.

Russell, Y. I. (2007). *Reputations and Polyadic Interactions Among Great Apes*. Ph.D. thesis, University of Liverpool.

Russell, Y. I. (2010). Third party grooming in a captive chimpanzee group. *Primates*, *51*, 79-82.

Russell, Y. I., Call, J., & Dunbar, R. I. M. (2008). Image scoring in great apes. *Behavioural Processes*, *78*, 108-111.

Sato, S., & Tarumizu, K. (1993). Heart rates before, during and after allo-grooming in cattle (*Bos taurus*). *Journal of Ethology*, *11*, 149-150.

Schino, G., & Aureli, F. (2009). Reciprocal altruism in primates: partner choice, cognition, and emotions. *Advances in the Study of Behaviour*, *39*, 45-69.

Schino, G., Scucchi, S., Maestripieri, D., & Turillazzi, P. G. (1988). Allogrooming as a tension reduction mechanism: A behavioral approach. *American Journal of Primatology*, *16*, 43-50.

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, *302*, 1231-1234.

Stammbach, E. (1988). Group responses to specially skilled individuals in a *Macaca fascicularis* group. *Behaviour*, *107*, 241-266.

Tanaka, I. (1998). Social diffusion of modified louse egg-handling techniques during grooming in free-ranging Japanese macaques. *Animal Behaviour*, *56*, 1229-1236.

Tanaka, I., & Takefushi, H. (1993). Elimination of external parasites (lice) is the primary function of grooming in free-ranging Japanese macaques. *Anthropological Science*, *101*, 187-193.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, *20*, 410-433.

Touge, T., Ikeguchi, M., Deguchi, K., Watanabe, S., Kuriyama, S., & Takeuchi, H. (2003). Effects of serial visuomotor tasks on contingent negative variation. *International Journal of Neuroscience*, *113*, 431-443.

van Lawick-Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, *1*, 161-311.

van Ree, J. M., & Niesink, R. J. M. (1983). Low doses of β -endorphin increase social contacts of rats tested in dyadic encounters. *Life Sciences*, *33*, S611-S614.

van Ree, J. M., Niesink, R. J. M., van Wolfswinkel, L., Ramsey, N. F., Kornet, M. L. M. W., van Furth, W. R., Vanderschuren, L. J. M. J., Gerrits, M. A. F. M., & van den Berg, C. L. (2000). Endogenous opioids and reward. *European Journal of Pharmacology*, *405*, 89-101.

Veà, J. J., Pérez, A. P., Baldellou, M., & Alea, V. (1999). Cost-benefit analysis of allogrooming behaviour in *Cercocebus torquatus lunulatus*. *Behaviour*, *136*, 243-256.

Ventura, R., Majolo, B., Koyama, N. F., Hardie, S., & Schino, G. (2006). Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology*, *68*, 1138-1149.

Videan, E. N., Fritz, J., Schwandt, M., & Howell, S. (2005). Neighbor effect: evidence of affiliative and agonistic social contagion in captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *66*, 131-144.

Walter, W. G., Cooper, R., Aldridge, V. J., McCallum, W. C., & Winter, A. L. (1964). Contingent negative variation: an electric sign of sensorimotor association and expectancy in the human brain. *Nature*, *203*, 380-384.

Watts, D. P. (2002). Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour*, *139*, 343-370.

Watts, D. P. (2003). Interchange of grooming and coalitionary support by wild male chimpanzees. *American Journal of Physical Anthropology*, *117*, S162.

Yaksh, T. L., Gross, K. E., & Li, C. H. (1982). Studies on the intrathecal effect of β -endorphin in primate. *Brain Research*, *241*, 261-269.

Figure 1. Cost-benefit model of grooming (according to Veà et al., 1999).

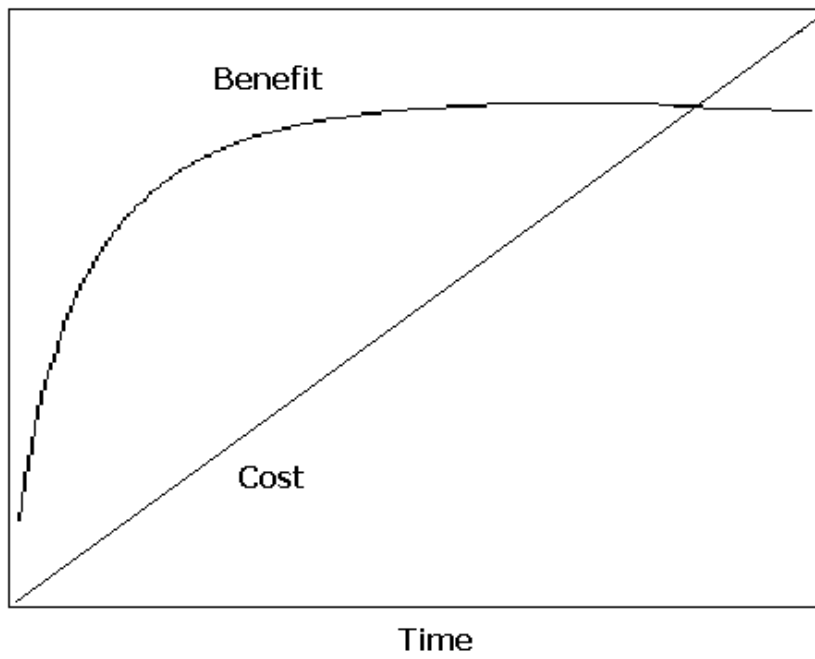


Table 1. Costs and benefits of grooming (summarized from Pérez & Veà, 1998).

			Actor (giver)	Recipient
Cost	Immediate	Social	Aggression from recipient or others	Aggression from giver or others
		Individual	Expend time, energy, saliva; inattention to possible predators	Consume time; inattention to possible predators
	Delayed	Social	-	Aggression from being associated with giver
		Individual	Catch illness from contagions in ectoparasites, open wounds ; get hair in mouth	-
Benefit	Immediate	Social	Express affiliative preferences; avoid aggression / reconcile; learn if recipient wants to interact; raise status	Express affiliative preferences; preserve status; avoid aggression
		Individual	Decrease of tension; body heat rise; access to nearby resources as result of grooming; eating tasty things picked out of fur	Subjective gratification (itch relief, pleasure from touch); relieve tension
	Delayed	Social	Express affiliative preferences; attain status; form alliances	Form/preserve affiliative bonds; overall group cohesion
		Individual	-	Keep skin/fur clean; remove ectoparasites; clean wounds.