An investigation into the hygienic function of allogrooming in capuchin monkeys (Cebus apella): grooming of different body regions in relation to surface area

Aspen, Robert E.

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Robert E. Aspden

An investigation into the hygienic function of allogrooming in capuchin monkeys (Cebus apella): grooming of different body regions in relation to surface area.

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Abstract

The evolutionary origin of allogrooming behaviour is generally accepted to be hygiene. In recent years this function has received little interest from scientific research while the relatively new social functions are repeatedly studied in a wide variety of species. The discussion of allogrooming having multiple functions (namely in primates) has been reviewed numerous times; however, hygiene is often ignored or is considered through implicit reference only. The aim of this investigation was to examine the importance of hygiene in the allogrooming behaviour of capuchin monkeys (Cebus apella). This species has never before been thoroughly studied for allogrooming in the context of hygiene.

Previous work by Pérez and Veà Baró (1999) examined the hygienic function of allogrooming in the white-crowned mangabey (*Cercocebus torquatus lunulatus*) and gave evidence supporting this function. Their analyses were marred by the use of percentages in a chi-square test. This investigation repeats the analysis of Pérez and Veà Baró (1999) with the intention of highlighting these errors and providing suitable alternative approaches to data analysis. In doing so the study provides significant data in support of grooming for hygiene. These results are based on a large sample size (5 focal females, 153 hours of observations) and show a high level of grooming activity. The focal females observed were involved in alloG bouts for 5.94% of observation time. The work by Pérez and Veà Baró (1999) and the current investigation support the evidence of Barton (1983a, b, 1985) and Hutchins and Barash (1976) for the importance of hygiene in primate allogrooming.

The study also shows that the support for the hygienic function does not discredit any of the alternative functions hypothesised. Indeed, the data suggest that other "more social" functions are in operation and can be seen in the variation between individuals and across observation periods. A discussion of the multiple functions of grooming and consideration of a "multiple functions" hypothesis will also be made in this investigation. It will also be discussed how allogrooming, in the context of hygiene, can benefit both the groomer and groomee without the need to invoke models such as reciprocal altruism or kin selection.

Declaration

The study here is to be considered for the qualification of Master of Science (Anthropology). All work in this thesis is that of the author, Robert Aspden. No quotation from this thesis should be published without prior permission of the author in written consent. Information derived from this thesis must be acknowledged appropriately.

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Index

Figures and Tables

Page

04 – *Method*

05 – *Results*

-1-

Introduction

In primates, no other behaviour has attained as much interest from scientific research as grooming, and more specifically grooming *between individuals*. Still, whilst this behaviour has been studied extensively, many questions have been overlooked or neglected without gathering sufficient data. One idea that has escaped attention in recent years is whether grooming between individuals (allogrooming) serves a hygienic function in primate systems. Allogrooming is a clear indicator of social relationships, both friendships and rivalries, playing a role in aspects of cooperation and competition. The interest in the "complex" and "human-like" phenomena of sociality may have contributed to the hygienic function of allogrooming being reduced in importance to implicit reference. It is the goal of this thesis to examine the hygienic function of grooming for its importance in a group of tufted capuchin monkeys (*Cebus apella*).

The erroneous neglect of hygiene as a function of allogrooming was a point first highlighted by Hutchins and Barash (1976). This effort produced some research on hygiene but this function still remains an implicit feature of allogrooming research rather than an explicit variable. After a decade of examining hygiene and tension reduction (including the proximate mechanism of hedonism) in the Eighties, research in the Nineties continued on the social complexity of the behaviour. A commonality seen in the literature is a variation on the statement that *the amount of allogrooming performed goes beyond that necessary to serve the hygienic function* (Sparks, 1967; Boccia, 1983; Dunbar, 1991; Pérez and Veà Baró, 1999). In more recent literature it appears that this statement has been falsely interpreted to mean that it no longer serves a hygienic function or serves "primarily" other social functions because the behaviour is too common, which is not what this statement actually says. In a more complete statement, it should be said that allogrooming *still* serves a hygienic function but the abundance and variation of the behaviour means it *also* serves another (or multiple other) function(s); as is stated by authors such as Dunbar (1991) and Di Bitteti (1997).

The support for a *"multiple function" hypothesis* for allogrooming is widespread in the literature (Sade, 1966; Sparks, 1967; Alexander, 1974; Doyle, 1974; Hutchins and Barash, 1976; Seyfarth, 1977, 1980; Barton, 1983b, 1985; Dunbar, 1984, 1991; Schino *et al.*, 1988; Boccia, 1989; Di Bitteti, 1997; Perez and Veá, 2000, Lazaro-Perea *et al.*, 2004). A number of authors, however, ignore the importance of hygiene as one of these multiple functions (for examples see Doyle, 1974; Boccia, 1989) acknowledging or emphasising only the social functions like aggression inhibition and tension reduction. Dunbar (1991) suggested that allogrooming served a more social role in catarrhines, while serving a more hygienic role in platyrrhines. The literature on catarrhines is almost exclusively social so no reference for hygiene can be made. Similarly, studies in platyrrhines have primarily investigated social functions so a statement that grooming still serves a hygienic function in platyrrhines is unsubstantiated. Furthermore at the time Dunbar made this statement the number of studies on platyrrhine species was few and consisted of few study subjects. Boccia (1983) used terms such as "primary" function, ranking the functions for importance, a procedure also unsubstantiated and argued to be invalid by Barton (1985).

For these reasons, to make the statement that allogrooming "still serves" a hygienic function in primates requires supporting evidence. Furthermore, the emphasis for hygiene in platyrrhines also needs investigating because of previous support for social functions in these species (Di Bitteti, 1997; Manson, 1999; Manson *et al.*, 1999). Capuchin monkeys have not been the subject of an investigation looking at the hygienic function except in the comparative analysis of Barton (1983a, b), which investigated multiple species obtaining only a small sample of data for capuchin monkeys. A recent study, by Pérez and Veà Baró (1999), showed that allogrooming still served a hygienic function in the catarrhine species, the white-crowned mangabey (*Cercocebus torquatus lunulatus*). The investigation in this thesis aims to repeat the analysis of the study by Pérez and Veà Baró (1999), for the platyrrhine species of tufted capuchin. In repeating this study I will also highlight some complexities of applying statistics in the way employed by Pérez and Veà Baró and go beyond the previous study to find alternative and more suitable statistical evidence.

The next two chapters discuss the scientific literature on the study of allogrooming and divide these studies into two topics. Chapter 2 is a review of the studies of grooming styles (methods) in different species, including primates and other mammals and also birds and insects. Furthermore, the chapter looks at how grooming terminology has developed through the years. It will look at studies of both allogrooming and autogrooming (grooming the self) in a variety of different species and how this has influenced scientific understanding of the intricacies of such behaviour. It will also discuss how these two similar behaviours are morphologically and functionally different. Chapter 3 reviews the functional explanations of allogrooming and also discusses how autogrooming may be socially mediated. How previous authors (cited above) have developed the idea that allogrooming serves multiple functions will also be discussed in Chapter 3. I will also argue that the proposed functions of allogrooming are not mutually exclusive and that support for one function does not discredit support for the others. This will include how various functions may interact with each other and how one or more functions may result as a direct outcome of other functional applications.

This investigation into grooming behaviour in capuchin monkeys is based on similar methodology to Barton (1983a), Boccia (1983) and Pérez and Veà Baró (1999). The behaviours of allogrooming and autogrooming will be investigated for distribution over the body surface. A specific grooming pattern said to be indicative of "hygienic allogrooming" is based on the idea that allogrooming should be more abundant on regions of the body that cannot be groomed easily whilst autogrooming (Hutchins and Barash, 1976; Barton, 1983a, b, 1985; Boccia, 1983; Pérez and Veà Baró, 1999; see Chapters 3 and 5). This generates specific test predictions for, firstly, allogrooming for hygiene and secondly, an inverse correlation for autogrooming and allogrooming together, which will be discussed in Chapter 3.

The statistical analysis performed in this thesis advances the work of Hutchins and Barash (1976), Barton (1983a, b, 1985) and Boccia (1983) and repeats that of Pérez and Veà Baró (1999) by distinguishing three body categories that have different levels of difficulty in terms of autogrooming and may as a result also receive differing levels of allogrooming. By repeating the work of Pérez and Veà Baró (1999) any result for the distribution of allogrooming in the capuchin will be comparable with that of the mangabey, subject of the previous study. However, due to a statistical weakness in the tests of the previous paper, further analysis is also performed with this capuchin data set to advance the theory and provide stronger supporting evidence. This will include using the duration data in more appropriate tests and also reformatting the data to repeat chi-square tests with frequency data instead of percentages. The statistical power of the test used in Pérez and Veà Baró (1999) is discussed in the method (chapter 4) and in the discussion (chapter 6). With the large volume of data collected in this thesis the results not only support the importance of the hygienic function for capuchin allogrooming, but also suggest that hygiene is not the only function in operation.

-2-

Grooming: A description for primates and other animals

The origins of grooming

In the fight for survival, organisms invest considerable effort in maintaining or improving their physical condition. Actively preventing or reducing the level of parasitic infestation and detritus forms one important part of this improvement. The immune system is involved in maintaining the internal state of organisms and eradicates the majority of internal fitness-reducing parasites and microbes. Part of the external protection involves chemical defence, a variety of secretions like oils and mucus. Cleaning behaviour removes infestation and dirt and can be an efficient way of maintaining good health. The behaviour of cleaning the body has developed in a variety of forms and is widespread throughout the animal kingdom (Goosen, 1987). The evolutionary origin of grooming in animals is generally accepted to be of a hygienic basis, i.e. that "grooming originally evolved for purely hygienic reasons" (Dunbar, 1991). A number of other functional hypotheses and circumstances to do with social relationships and social cohesion have also been developed, especially in primate species. The next chapter will discuss some of these scientific hypotheses, debating the function of grooming in primates. The aim of this chapter is to discuss the various forms (styles) of grooming between individuals in a number of species.

Much of the work investigating cleaning, particularly between individuals, comes from studies of avian species. Preening is the use of the beak to comb through, over or between the feathers. Cullen (1961) invoked use of the terms allopreening (alloP) and autopreening (autoP), cleaning of other individuals and cleaning oneself, respectively. He promoted the terms as more appropriate than terms in earlier literature, *hetero*preening not having an appropriate "root" to the word and *homo*preening, as the antonym, not being appropriate for the act of self-cleaning. The terms of alloP and autoP were utilised to indicate nothing more than the significant behavioural differences between the two acts and eliminate the implication of function, whilst acknowledging the complexity and intricacy of interactions with others. Terminology is an important consideration in the study of animal behaviour as it may lead to the suggestion of more than was originally implied. The difference between a functional and structural description of a specific type of behaviour may (even subconsciously) change the way that observers interpret behaviour (Martin and Bateson, 1993).

> "*The terms Social Preening or Sexual Preening have in the past been used widely to label* [*the act of one animal preening another*], *but neither of these is altogether satisfactory as it may be difficult to specify the relationship in this way.*"
>
> Cullen, 1963 (page 121)

> "[*Allogrooming*] *has been referred to under a variety of names, such as social, mutual or reciprocal grooming; 'flea catching', 'sham louse picking', or simply the 'picking reaction', have been used with reference to primate behaviour. A number of objections may be raised in connection with these terms, and a number of them are misleading; for example, mutual grooming should only apply to the behaviour when the participants are simultaneously grooming each other.*"
>
> Sparks, 1967 (page 148)

Sparks (1967), citing the publication of Cullen (1963), also used the roots allo- (*another*) and auto- (*self*) for *grooming* in mammals (specifically primates). In the interest of standardisation and the removal of implicit meanings the terms allogrooming (from here alloG) and autogrooming (from here autoG) will be used in this thesis, indicating nothing but the occurrence of (and distinguishing between) the acts themselves. The use of the term "*social* grooming" while possibly having originally meant the grooming of one individual by another can be suggestive of an established relationship between the two individuals involved. Through the use of this term in association with the study of social relationships, the two have almost become synonymous (Sparks, 1967). With many of the hypothesised functions directed at explaining alloG between selfish individuals, even agonistic rivals, the use of 'social' is misguiding in some cases. Mutual and reciprocal grooming are acceptable descriptions of instances when grooming is either simultaneous or continually swapping direction but are not appropriate for a structural description of the act itself.

Further terminology is also important to clarify. I use the term groomer here to identify the individual that carries out the behaviour of grooming, and groomee to indicate the individual being groomed. Other terms such as recipient and performer have been used in past literature for allogrooming, however I argue against using these terms. Firstly, sticking to the use of structural terminology, groomer and groomee both indicate the role in the interaction of each participant and the actual behaviour being performed. One further modification would be to incorporate the earlier terminology applicable in both alloG and autoG. Therefore, allogroomer and autogroomer define whether the animal is involved in an interaction or alone, this is important because "groomer" is applicable in both activities. The term 'groomee' is specific to alloG; in autoG the groomer and groomee are the same individual, this distinction is not necessary. For simplicity only, the terms groomer and groomee will be used from here.

I will also use the terminology that I have interpreted to be the standard way of describing grooming interactions. When individuals groom each other this can be done simultaneously or one after the other. Simultaneous grooming is normally known as mutual grooming. When grooming changes direction, where the groomer becomes the groomee and original groomee then becomes groomer, this is known as instantaneous reciprocity (see Krebs and Davies, 2000, page 280-289). In terms of alloG, bout will be used to describe one individual grooming another individual *once*, i.e. a unidirectional grooming interaction. When the first bout is instantaneously reciprocated with a change of grooming direction (with no intervening behaviour) or if both individuals mutually groom each other the whole interaction (all bouts) will then be called a grooming session. The pair of grooming individuals is normally referred to as a dyad, likewise, the term partner(s) is also applied to a dyad. AutoG can only involve a single individual grooming itself, once; therefore the term bout will be used to describe autoG events.

Grooming in primates

The act of grooming takes two main forms using two physical features of the body. In oral grooming animals use various parts of the mouth to comb the pelage or skin surface. The tongue is a highly dextrous muscle and both the lips and teeth can also be used. Oral grooming is the grooming style of the strepsirhines, both using the teeth to comb and using the tongue to lick. In anthropoid primates grooming comes mainly in the form of manual grooming. Meaning 'of or relating to the hand', *manual* is intended to suggest a more complex behaviour than simple scratching, the hand being used to comb, move, pick and manipulate the pelage. Anthropoid primates may still utilise oral grooming and combine it with manual grooming to move and separate the pelage thus gain access for oral licking of the skin surface. Scratching can be considered part of primate grooming as in most other mammals, this will be discussed later in this chapter.

AlloG behaviour is the most studied form of interaction between individuals in primate groups and, as an example, is reported to make up 95% of the "social time" of individuals in groups of baboons, genus *Papio* (Dunbar and Sharman, 1984, based on 40 field studies). Dunbar and Sharman (1984) further argued that this was a reserved measure as they were interpreting data from other publications. Watson (1908) described grooming in rhesus monkeys (*Macaca mulatta*) as "the most fundamental and basal form of social intercourse". The frequency of alloG in primates is not universal for the entire order. AlloG is not common in the strepsirhines occurring with varying degrees of rarity. Furthermore in this suborder of primates, instantaneous reciprocal grooming (groomer becomes groomee and vice versa) or mutual grooming (simultaneous grooming) are both also very rare (see Goosen, 1987), alloG normally consisting of unidirectional grooming bouts. In the haplorhines, alloG is much more abundant and interactions can vary from just a few seconds to many minutes; with grooming direction changing regularly and with grooming partners grooming each other simultaneously. From report to report, the abundance of grooming (alloG and autoG) in different species of primates varies greatly in description.

Grooming *"Partnerships"/"Relationships"*

It is important to note here that, without any suggestion of the functional reasons as to why, studies have shown primates possess clear preferences for specific individuals within groups with which they groom more than others. These "partnerships" exist in other animals besides primates, including fish, but the pattern of preferences for certain grooming partners is never clearer than in primates. In these so-called partnerships, grooming is often highly reciprocal changing directions instantaneously and producing long grooming sessions. Most authors argue reciprocal grooming increases the length of the interaction and the reciprocal nature of the grooming interaction maintains the partnership (Sade, 1966; Seyfarth, 1977; Boccia, 1983; Barton, 1985; Di Bitteti, 1997; Barrett *et al.*, 1999, 2000 see also Goosen, 1987 for a review). These partnerships show a complex combination of interactions that have intrigued and captivated researchers, producing several hypothetical models. The fundamental underlying principles of how these varying hypotheses function in grooming partnerships is still a matter of debate, furthermore the disregard for some functions while supporting others should be and still needs to be addressed.

Grooming patterns in a variety of studies have been shown to be affected by "kin-bias" (Chapais, 2001) and the dominance hierarchy (Seyfarth, 1977). The complexity of studying such correlations is that many other features of primate life history can produce the exact same pattern of behaviour or relationships. Dominance and kinship often correlate, in that family members often occupy the same rank with daughters (in female philopatric groups) acquiring a rank similar to their mother (Prud'homme and Chapais, 1993). Chapais (2001) argues that this "correlation between kinship and rank has led to an overestimation of the effect of kinship". Therefore if by either the theory of Kin Selection (Hamilton, 1964a, b; Maynard Smith, 1964) or by animals grooming closely ranked individuals (as in the grooming model predicted by Seyfarth, 1977), the resulting pattern of behaviour would be identical. It is important to emphasize the use of the term above, "kin-bias", because, as noted by Chapais (2001, page 204), primatologists have created "an implicit equation" between kin preference and the theory of kin selection, ignoring as he says "kin-biased mutualism" and "kin-biased reciprocity" both of which explain a kin preference but without the need to invoke the theory of kin selection.

Grooming style

The style, or the motor pattern, of grooming in primates has been discussed in many publications and reviews of both alloG and autoG (Sparks, 1967; see Goosen, 1987, for a review of alloG). Most oral groomers, specifically the strepsirhines, have a specialised toothcomb that is used to rake through the hair and brush the skin surface. In lemurs (lemuridae) it is suggested that this toothcomb serves no purpose for feeding and only serves a use in grooming behaviour (Barton, 1987, see also Sparks, 1967; Goosen, 1987). Barton (1987) suggested that oral groomers such as the strepsirhines normally engage in mutual grooming in symmetrical postures (see also Feh and de Mazières, 1993) while manual groomers normally form asymmetrical postures in either unidirectional grooming bouts or reciprocal grooming sessions. Manual grooming primates are less restricted than oral grooming primates in mutual grooming sessions. Manual groomers are capable of concentrating on different areas of the body to each other whilst grooming simultaneously. Barton (1983b) linked the fact that lemurs groom the lower back more than other areas to their mutual alloG style and highlighted that this region is most easily accessible to both individuals in a facing posture (see also Barton, 1985, 1987).

The physical dexterity of anthropoid primates with gripping hands; manipulative fingers and opposable thumbs, means manual grooming has many motor patterns. Sparks (1967) described four main forms of grooming: i. "*Drawing hair(s) through forefinger and thumb*", a few or even individual hairs are inspected by being drawn through the forefinger and the thumb (semi- or fully opposable in most species); ii. "*Raking/combing/smoothing*", a variety of behaviours when the hairs are spread or parted using either thumbs or fingers;

iii. "*Collecting/sheafing*", more prominent in species with long hair, the hairs are gathered in bunches or moved as a whole object; iv. "*Miscellaneous patterns*", all other behaviours not grouped under the other general titles. Note that these general titles contain various substyles each with a varying physical posture and action, for example the title of second group describes that there are at least three different forms in that group. Raking, combing and smoothing are morphologically very different and each is also able to vary depending upon whether the act is performed using the whole hand, just fingers or just thumbs. Furthermore, Sparks (1967) describes how these behaviours can alternate between one or two hands and that whilst in a grooming bout an animal may change which behaviour each hand is doing, one performing the manipulative act and the other searching or inspecting the hairs.

Sade (1966) also described four motor patterns for alloG in rhesus macaques: i. The "*slide*", a flat hand being used to spread the hairs; ii. The "*scrape*", the fingertips and nails raking through the hair like a comb; iii. The "*pick*", objects are removed using the forefinger and thumb to grip and pull out detritus, skin flakes, hair, etc; iv. The "*lick*", use of the tongue to lick the skin/pelage, may also use the lips/teeth. Boccia (1983) describes three forms: i. "S*troking*", a flat hand is drawn over the surface of the pelage, hairs are straightened but not pulled; ii. "*Picking*", in a variety of ways the hair is manipulated and intensively inspected; iii. "*Stroking and picking*", in a combination of the two forms both hands are employed to simultaneously stroke and pick at the pelage. Boccia (1983) argues that stroking is least efficient for grooming, in terms of removal of ectoparasites, so should occur less frequently than the other two. I would argue against this assumption because based on the general description given by Mooring *et al.* (1996), grooming is also important in terms of conditioning the pelage and removing excess oils in addition to controlling ectoparasites and detritus. Pérez and Veà Baró (1999) similarly describe the conditioning of the fur. The comment by Boccia (1983) also assumes that stroking does not remove surface detritus like leaf matter, insects and dead hair or maintain condition. I would argue that included in this conditioning of the fur would be a thermoregulatory and protective benefit in having all the hairs facing the same way. Another protective benefit of having neat and tidy hair is that there is a reduction in the ability for ectoparasites to attach to the skin and for dirt to get into the pelage. In support of this, many authors describe how the grooming direction often follows that of the direction of hair growth (Sparks, 1967; Doyle, 1974; Boccia, 1983; Pérez and Veà Baró, 1999).

Pérez and Veà Baró (1999) describe a variety of general grooming forms, however make specific distinctions between alloG and autoG based on what was observed in a study of white-crowned mangabeys (*Cercocebus torquatus lunulatus*). Categories observed *only* in autogrooming: i. "*Scratch*", rub or scrub repeatedly and rapidly, can use any of the feet or hands; ii. "*Graze*", subtle or light contact of the finger(-tips) to the skin surface, exclusively with the hands; iii. "*Direct hand-pick*", hair(s) are pulled selectively with the hand, and is not preceded by visual inspection. Categories observed in both autoG and alloG: i. "*Lick*", passing the tongue over a region of the body, this occurs without any associated behaviour, ii. "*Slide*" running of one or both hands over the body, "stroking or combing it". "*Slide*" squashes or flattens the hair, normally done in the direction of hair growth. Again, as in Sparks (1967) one hand can perform either activity of holding or combing the hair and the hands may change roles while grooming. iii. "*Superficial Grooming*", manual or tactile screening of part of the body, the action is described as messing it up, this differs from slide as superficial grooming is described as going "through" the hairs, slide goes "over" the hair; iv. "*Deep Grooming*", intense inspection of the hairs, slower and more methodical than the other forms, deep grooming differs further from superficial grooming as it involves independent movement of the fingers; superficial grooming utilising the hand like a blade.

It is possible to compare some of the descriptions given by the various authors, however it is apparent that some, for example Pérez and Veà Baró (1999), change the level of description between structural definitions and implicit or functional descriptions to make more general categories that may contain multiple forms described separately by other authors. Pérez and Veà Baró (1999) use the term *slide* as does Sade (1966) but the *slide* described in Pérez and Veà Baró includes some of the characteristics given for *scrape* in Sade's paper. Boccia (1983) gives three clear general categories that incorporate the various forms into simplistic categories. This might not be appropriate if intent or act is to be interpreted from the data. Other authors describe more detailed forms of grooming, including finger movement and hand placement. It may therefore become important for a collection of grooming descriptions to be produced, firmly embedded at the structural level. If these universally approved categories and morphological descriptions are applied in comparative tests then the functions or intentions behind a diverse form of behaviour such as grooming may be established (supported by Sade, 1966). The use of the same terminology to describe morphologically different types of the same behaviour as described in the literature above will not serve to benefit research in the long run.

Furthermore, if as argued by Schino (2001) approaches such as the meta-analysis are to be become more commonplace, it is important that the research is universally accurate at the base level.

Scratching

Scratching behaviour in animals varies greatly in description and importance. Continuing with the description for primates in Pérez and Veà Baró (1999), scratching only occurred as autoG behaviour. It was also exclusively with the hands, which is not the case for all primate species. Scratching, in Sade (1966), Sparks (1967), Barton (1983a, b, 1985) and Boccia, (1983), is described as a rapid movement using an open hand to mess or rake the hair with no apparent care; however, the description is applied to both alloG and autoG, occurs at a range of durations from a few seconds to a few minutes and may also involve the feet. Scratching may mean use of the fingertips (nails) to rapidly rake through the hair, while many of the descriptions, cited above, suggest only an open hand used like a blade. It is a standard practice in the majority of papers to de-emphasize scratching and it is often only included in data collection if it occurs for a long period of time. The usefulness of scratching at shorter durations may be minimal, however, disregarding it as unimportant is a false practice as it may serve to dislodge minor irritations such as loose soil or flies that land on the pelage.

Grooming in other mammals

A lot of work on grooming, examining the physiological and functional benefits and the altruistic and cooperative nature of alloG, is being performed in other animals besides primates. Some of these studies are producing similar data to that in many primate studies. Antelope are oral groomers and have a specialised grooming apparatus that appears to serve no function in grazing or browsing (Mooring *et al.* 1996). This apparatus is scraped or combed through the hair in the direction of the hair growth. In impala (*Aepyceros melampus*) the grooming apparatus is made up from the lateral incisors and canine teeth. Impala groom each other regularly and the behaviour is mostly reciprocal. Horses on the other hand often groom mutually, standing side-by-side (Feh and de Mazières, 1993) grooming each other symmetrically, as was seen in lemurs (Barton, 1985, 1987). Mooring *et al.* (1996) point out cattle, unlike other ungulates including antelope and cervids, groom with the tongue instead of the teeth (grooming apparatus).

Impala autoG has been described as operating by a "grooming clock"; grooming is "periodically activated independently of cutaneous stimulation" (Mooring *et al.*, 1996, page 966) and is regulated by the balance between maintaining a healthy body and the costs of regular grooming. Mooring *et al.* (1999) found that individuals that groomed the most had the least ticks and that smaller species had fewer ticks because they groomed more than larger species. This supported their assumption of this autonomic grooming model and also gave further support to the link between the grooming behaviour and condition of the skin/ pelage (hygiene). There is also a strong link between increased grooming rate and tick load. This was related to surface stimulation and blood contamination (through tick saliva) having an effect on grooming rates.

Horses often groom each other in a symmetrical position; therefore the reciprocal exchange of behaviour, as seen in the impala, is not common. The mutual nature of grooming in horses provides the benefit of the act to both horses simultaneously. This symmetrical pattern often reflects the grooming style of lemurs in that the two horses stand with identical postures and groom the same region of each other (see figure 1 in Feh and de Mazières, 1993). The two grooming partners receive an equal amount of grooming to what they provide; this mutual cooperation is much more stable between partners and is less susceptible to free-riders. Horses are oral groomers like most mammals, yet they differ from antelope (such as the impala) in that they use the upper incisors to scrape the pelage as opposed to the lower incisors (comparison between descriptions in Feh and de Mazières, 1993, and Hart *et al.*, 1992). This grooming action is also used in combination with grooming using the tongue, a technique similar to cattle.

Grooming and body region preference in other mammals

Hart *et al.* (1992) described how scratch grooming was preferentially directed towards the head and neck regions and acted as an alternative grooming style for not being able to oral groom this region. Scratch grooming appeared extremely accurate in most species and placement of the hooves of the rear legs was extremely precise (for examples see figure 1, pictures *c* and *d*, in Hart *et al.*, 1992, page 621). In impala, scratch grooming was significantly lower than in other antelope species and was attributed to the greater level of alloG in impala. The amount of alloG received to the head and neck in impala was half of what was given to the rest of the body when the head and neck made up only 20% of the entire body surface. This links the behaviours of autoG and alloG in these impala species.

Feh and de Mazières (1993) examined the site preference of alloG in horses, *Equus caballus*, and similarly found that the neck and head was a preferred site. They furthered this work to show that a specific site (the lower part of the dorsal region; see figure 2, Feh and de Mazières, 1993, page 1193) on the neck received more alloG than all other sites of the body including other parts of the neck. Over half of all alloG events were directed to this one site, which made up 1.2% of the entire body surface. Grooming received to this region caused a significant decrease in heart rate of animals tested, compared to base rates and control test grooming experiments.

Feh and de Mazières (1993) remain unsure of the connection between this region and control of the heart; however they hypothesise that, as this region is the location of the second largest ganglion found in horses, stimulation may affect heart rate through relaxation (a physiological hedonistic effect). This evidence indicates that it is the *behaviour itself* that is responsible for the reduction in heart rate as opposed to simply being in proximity to another horse. The method of the study supports this because grooming was simulated by an experimenter (not a horse) simply scratching the preferred region of the neck. Furthermore, because heart rate did not go down in the control test (scratching of another region) not only is the act itself important but the act in a specific localised region. If the effect of standing near another horse (or experimenter) could explain the reduction in heart rate this would have been seen in the control test. Similar heart rate reduction has also been studied in primates, the function of this occurrence forms part of the next chapter (see "Tension reduction" including hedonistic effect).

Vampire bats (*Desmodus rotundus*) are also oral groomers, combing the pelage and skin with the teeth. This species groom both mutually and reciprocally in roosting nests. It is known that in these small, enclosed spaces there is a greater correlation between affiliation (proximity) and alloG than between relatedness of roost-mates and alloG. This has led to the hypothesis that grooming in vampire bats is exchanged for grooming or interchanged (Hemelrijk, 1991) for other resources like food. Wilkinson (1984) showed vampire bats also *reciprocally* share their blood meals with each other. He was able to show that sharing was more likely to occur if the beggar had shared blood meals with the individual being begged from, on previous nights. The connection of grooming with food sharing, when food sharing is reciprocal in nature argues against the interchange idea. It may be that grooming has become a cue to trigger regurgitation from roost-mates or that it is not actually grooming being performed but a communicative act that resembles grooming behaviour. Such behaviour may serve two purposes in that it informs the other individual of a desire to receive a share of food and that it may serve as a way of inspecting another individual for feeding success, clues like the smell of the animals breath or stomach distension may be highly obvious in a species capable of eating its own weight in blood in a single feeding (Wilkinson, 1986).

Grooming in other classes

Many amphibians, reptiles, birds and insects are known to autogroom, many species also allogroom one another. In species of social insects, alloG, as well as autoG, may be an important and integral part a worker's everyday activity. Ants lick each other to clean important parts of the body such as the eyes (Wallis, 1962, cited in Sparks, 1967). It has been noticed that in honey bees (*Apis mellifera*) alloG occurs in the form of removal of pollen grains, dust and other particles from the body, limb joints and wings (Land and Seeley, 2004). Grooming of other workers at these points on the body surface is extremely important for two reasons, firstly the animal may suffer reduced movement if pollen/dust restricts flexibility and secondly, the insect is not able to groom itself at these points. It appears in social insects that the nature of alloG is strictly hygienic but there may also be some purpose in transmitting beneficial chemicals between workers, maintaining the efficiency (health and nutrition) of the colony, and possibly also a uniform 'signalling' chemical; a group signature (Land and Seeley, 2004).

Interestingly, similar to the occurrence of the waggle dance (the dance that communicates the location, direction and abundance of food sources), honey bees appear to have another dance that communicates the need to be groomed. Land and Seeley (2004) showed an association with alloG initiated specifically after the dance motion was performed. The grooming dance was intermittently interrupted with bouts of autoG performed by the dancer. These autoG bouts were very short and "more frenetic" than normal autoG bouts. The origin of this dance is thought to be associated with autoG due to its similarity to frantic autoG and the connection with inspection behaviour by workers (Land and Steeley, 2004, citing Bozic & Valentincic, 1995). This association suggests two things. Firstly, that the behaviour of soliciting alloG is partially ritualized, in that this dance appears to have assimilated an exaggerated version of autoG behaviour. Secondly, the idea that this exaggerated autoG behaviour is a trigger of alloG, links normal autoG and alloG behaviours together, suggesting that they serve the same function and that alloG is required as a more effective cleaning procedure at the regions of the body were autoG is ineffective.

The form and style of alloP has been studied extensively, even before Cullen (1963) coined the terminology of allo- and autopreening. Birds can be described as oral groomers using the beak as the main tool for stroking, combing and manipulating the feathers. Birds may also use the feet in autoP, to scratch areas that cannot be reached using the beak. Much of the early work on bird preening was attributed to sexual interactions, females grooming males or vice versa; as described by the term hetero-preening from Miller and Miller (1958). The root *hetero* was supposed to be indicative of one sex preening another (Miller and Miller, 1958). Furthermore Miller and Miller (1958) made the association of heteropreening being a parent-offspring interaction. Miller and Miller's description of autopreening (or "homo-preening") is quite accurate and provides a useful structural interpretation. "The [bird] may arrange its feathers and their parts with the bill, each feather being passed between the mandibles in turn. A [bird] cannot reach its own head and many of the neck feathers for preening." (Miller and Miller, 1958, page 7). The number of apparent motor patterns for autoP and alloP do not appear to be as diverse as autoG and alloG and the majority of these preening styles are the same throughout bird species (Harrison, 1963).

Restriction of autogrooming

Because different species have different grooming styles, the restrictions suffered by these species, whilst autoG, are dependent on their specific grooming style. Oral groomers by definition can only use the mouth so any region out of reach to the mouth is impossible to groom. This would include a large majority of the body, unless animals were capable of extreme twisting. Areas such as the back of the head, the face, dorsal side of the neck and the shoulders are inaccessible even when an animal twists to extremes. Manual groomers are likely to have a greater range of movement for reaching all parts of the body (Doyle, 1974; Hart *et al.*, 1992) but then are incapable of seeing regions if the eyes cannot be turned to view them.

AutoG in manual-grooming primates, regardless of any function, cannot cover the entire body surface equally because the animal is restricted both in *accessibility* and *visibility*. An animal needs to bend its arms to reach dorsally and must twist its neck if it needs to observe an area in order to groom it. Doyle (1974) argued that, in autoG, primates can reach all parts of the body. This may in fact be true and primates could be able to reach all areas but they cannot do so to an equal level of efficiency for all parts of the body. Most non-homonoid primates have less rotation at the shoulder joint compared to hominoid primates so are restricted in reaching dorsally (discussed in chapter 4). This limitation varies the ability to access different parts of the body. The effect of any autoG restriction would be the production of a *gradient effect* of body parts that could be groomed easily, those it is more difficult and then those that may be harder or even impossible to autogroom with any significant efficiency.

Due to the hygienic function that autoG serves, any region of the body that suffers a restriction through accessibility, or visibility, whilst being autogroomed, may furthermore suffer from a greater susceptibility to infestation, etc. The "gradient" of cleaning ability over the body surface would similarly produce a "gradient" of clean, semi-clean and unclean regions due to this higher susceptibility of certain parts. It may benefit the individual, therefore, to receive the essential cleaning from other group members and more importantly that this received grooming be to those regions of the body where autoG has little or no efficiency in cleaning. This produces a further "gradient"; a scale of regions requiring alloG from others, which could be called a *grooming pattern.* The grooming pattern of alloG should be inversely proportional to the grooming pattern of autoG seen over the entire body should the two behaviours serve the same function. This is the basis for observing the hygienic function of alloG, to be discussed in chapter 3.

Costs of allogrooming

Any cost of alloG is dependent upon the functional context and which of the grooming partners is being considered. For example alloG in a hygienic context must be described as improving the quality of the groomee rather than the groomer, because it is the groomee having the parasite or detritus removed. Following the suggestion that the groomee is the beneficiary of alloG in a hygienic context, the benefit to the groomer is harder to define (however see "the selfish groomer" idea in the discussion). Because benefit to the groomer is unclear, research has focused on the cooperative nature of alloG to explain any groomer benefit. This has led to alloG being studied under the guise of altruism. The dilemma with altruistic behaviour is that based on its definition there is a "net loss in direct fitness for the donor [(in this case the groomer)] and a net gain in direct fitness for the recipient [(groomee)]" (Brown, 1983). In this light the groomer must incur a cost if hygiene is the only function considered. The biological question is: Why do altruistic acts (such as alloG) persist if it is detrimental to the animal performing the act? Theories like kin selection (Hamilton, 1964a, b; Maynard-Smith, 1964) and reciprocal altruism (Trivers, 1971) amongst others have been formulated to explain how altruistic behaviour may indirectly benefit individuals performing these acts. AlloG has been repeatedly used as a model behaviour for such explanations and many advancements to such theories are made based on grooming studies (for examples see: Noë *et al.*, 1991, "Biological Markets"; O'Connor, 1995, "Parcelling model of reciprocity"; de Waal, 1997, "Service economy", Roberts and Sherratt, 1998, "Raise the stakes", Barrett *et al.*, 1999, "Time-matching").

Interestingly, Dunbar and Sharman (1984) have argued that the classification of alloG as a costly behaviour is probably misappropriated. They, amongst others, emphasise that the true definition of altruism describes a *net* cost in the act and that some acts classified as being altruistic may become beneficial when considered in conjunction with other behaviours. When animals reciprocally perform behaviours they cannot do to themselves there is a clear benefit compared to not receiving the behaviour at all. Therefore, calling alloG altruistic is not valid. Dunbar and Sharman (1984) based this assessment on collated data from multiple studies (n = 40) in populations of baboons (*Papio* genus). They showed that the amount of alloG in groups remained constant when food abundance or foraging time differed. This suggested an alternative to a point previously argued in the literature, that alloG affected an animal's foraging time. Whatever the function of alloG, it is clear that it is highly important and of little cost to both (all) participants, or the benefits significantly outweigh any costs.

One interesting cost that has been put forward in the vampire bat is that time spent in alloG is costly due to time away from autoG (Wilkinson, 1986). This cost highlights the difference in benefits to the groomer and groomee. During autoG, the groomer is also the groomee thus reaps the benefits of its own behaviour; when alloG another individual, the benefits are with this other individual and the groomer incurs the cost of performing the act and then not grooming itself. Even if the two behaviours serve the same hygienic function because the benefit of alloG is not with the groomer a cost is still incurred. However, in considering the evidence of the reciprocal nature of alloG in vampire bats (Wilkinson, 1986; and similarly in primates), if alloG serves a hygienic function it would provide the same benefit as autoG, therefore time away from autoG is countered by time spent receiving alloG (see also Sparks ,1967). If alloG served a different function to that of autoG, a social function for example, then it would have a significant cost. The time away from autoG is not cancelled out through reciprocity of alloG because the behaviours no longer serve the same function. However, time spent searching for food could be interpreted as a cost by being viewed as time away from autoG, yet the benefit of eating significantly outweighs the cost of not grooming oneself. From this, if alloG did serve a social function the benefit of this other social function must outweigh the cost of not autoG for the behaviour to persist.

Costs specific to oral groomers, highlighted by O'Connor (1995), are the physiological detriments. He highlights tooth wear caused by the scraping action and also water and electrolyte loss from use of, or loss of, saliva. This, in addition to the energy expended in the action of moving the jaw and neck repeatedly, Dunbar and Sharman (1984) argued that to use 'energy loss' as an explanatory cost would "trivialise the concept of altruism" as little significant energy is used. Saliva may be significant if it could be shown that the level of water loss were high enough to affect the animal's body. In the case of tooth wear, this point is likely to be insignificant as many oral groomers, like antelope and lemurs, have the specially modified toothcombs that appear to serve only a grooming function. This wear may affect the quality of future oral grooming but it would have no detrimental affect on feeding ability. The abundance and distribution of oral grooming in primates, bats, equine, ungulates and other species, suggest that these costs are significantly outweighed by any benefits.

The main universal detriment to all grooming species that could be a significant cost to a groomer in an alloG bout is reduced vigilance. Animals need to remain vigilant for predator detection and furthermore intra- and intergroup aggression. AlloG is a distraction from vigilance as the eyes are normally used to inspect the skin surface being groomed. Oral groomers have a greater problem than manual groomers because the eyes are extremely close to the body surface (being located near the mouth) so have a greater reduction in line-of-sight and are unable to turn their head to observe around them while grooming. Manual groomers may be able to observe around them whilst grooming but this then reduces the efficiency of the grooming act. Intragroup competition is a contributing factor to levels of vigilance as both dominant and subordinate individuals maintain and update the knowledge of rivals and affiliates and their current temperaments (Chalmeau *et al.*, 1998; Hirsch, 2002). In impala it has been shown that territorial males with a harem sacrifice received alloG and autoG to levels below what is sufficient for hygiene, in order to maintain vigilance over their territory for possible invasion from bachelors (Mooring and Hart, 1995).

Sade (1966) claims the majority of grooming bouts or sessions, in his study group of rhesus macaques (*Macaca mulatta*), ended as a result of agonistic conflict within the group or some other kind of intragroup disturbance. The most common of all was the avoidance of an approaching group member. If animals are aware of approach whilst in alloG bouts then vigilance may not be hampered significantly. A further report (Cowlishaw *et al.*, 2004) suggests that animals do not suffer heavily from loss of anti-predator vigilance due to, in part, the "many-eyes" principle (Pulliam, 1973) whereby only some members of the group maintain vigilance and those non-vigilant group members are warned of danger. Cowlishaw *et al.* (2004) argue that animals should limit vigilance as much as possible because it interferes with other activities (such as grooming and feeding). If this statement holds true, vigilance can be eliminated as a possible factor affecting grooming.

Most of the evidence, then, supports the claim of Dunbar and Sharman (1984) in that the costs of alloG are arguably minimal. With the possibility of limited, small associated costs and large benefits, grooming behaviour has become widespread in the animal kingdom. Any costs of grooming, whether of alloG or autoG, can only be determined by applying a functional explanation of the behaviour because each function may have different costs and benefits to either groomer or groomee. The possibility of multiple functions of alloG has been neglected in recent years and a clearly defined explanation of what these functions are is also undetermined. However, without such clear functional explanations, authors still consider and debate the costs and benefits of grooming behaviour. What these multiple functions are will be discussed in the next chapter.

- 3 -

Grooming: Function and context

The functional divide

Hutchins and Barash (1976) highlighted the growing trend of applying social aspects to the research on alloG (since Watson, 1908). They made reference to a paper by Doyle (1974) in which the "Functions of Allogrooming" (pages 318-320) were identified as "being exclusively social, with no reference to the hygienic role" (Hutchins and Barash, 1976, page 145). The Doyle paper, in fact, does make a reference to the hygienic function of alloG but this is an insignificant reference that appears to dismiss the importance of alloG in terms of hygiene; an increasingly common interpretation in much of the primate literature. It must be said, however, that it is unclear in such papers whether this neglect or ignorance toward the hygienic function is intentional or simply that the point was not made explicit.

A vast array of functions have been formulated and attributed to the behaviour of alloG. Suitable evidence supports the functions, which will be discussed below. This discussion will show how the support for one function does not necessarily disregard the other functions. Furthermore, it is the aim of this chapter to show how different functions maybe prerequisites for other functions of the same behaviour. Hygiene, tension reduction, aggression inhibition, reconciliation, sexual consort and coalition formation will all be discussed. It can be argued that the major distinction between the 'social' functions and hygiene is that only hygiene appears not to benefit the groomer. If alloG serves to improve the external condition, only the groomee can benefit. After discussing each individual proposed function, a "*multiple functions*" hypothesis will be introduced. The lack of mutually exclusive hypotheses considering the various functions of alloG warrants expansion of this complex hypothesis. Hygiene as the evolutionary origin of the behaviour may warrant a place in this "multiple functions" hypothesis but lacks the emphasis in the literature directed to other functions.

Tension reduction

The hypothesis of tension reduction as a result of alloG was first put forward by Terry (1970). Tension is described by most authors as a reflection of an animal's internal state. Schino *et al.* (1988) specify precisely that this internal state of tension be derived from a conflict situation. Authors investigating the emotional attributes of animal behaviours call this internal state anxiety (Aureli and Schaffner, 2002a). Anxiety and tension may occur as a result of approach from dominant or highly aggressive individuals without confrontation or conflict (Castles *et al.*, 1999; Aureli and Schaffner, 2002a) so Schino *et al.*'s (1988) definition may be too specific. Manson and Perry (2000) correlated higher levels of self-directed behaviour (SDB), which is thought to be an indicator of anxiety, with proximity to others in a group of white-faced capuchins (*Cebus capucinus*) irrespective of rank (see "*AutoG as SDB*" below). *Tension reduction* (or distension) may simply include any situation where the social cohesion of a group is returned to norm. Aggression suppression and reconciliation are instances of social unrest (as described by Schino *et al.*, 1988) but will be considered separately to the tension reduction hypothesis because these instances do not necessarily have to involve tension and anxiety. Tension will henceforth be described as the outward expression of anxiety in one individual caused by the proximity of another or its environment.

Using biotelemetry, Aureli *et al.* (1999) were able to collect data on heart rates of rhesus macaques, using data recorders implanted subcutaneously. These data showed that heart rates increased in association with tension-inducing situations. This included proximity to, or approach from unfamiliar or dominant individuals. These results were compared to the effects that anxiogenic (anxiety causing) and anxiolytic (anxiety reducing) drugs produced because it is necessary to link emotional (internal) states to behavioural (external) responses. AlloG had the opposite effect on heart rates; heart rates slowed when the animals received grooming (Aureli *et al.*, 1999; Schino *et al.*, 1988; see also Feh and de Mazières, 1993 and literature cited in Aureli and Schaffner, 2002a).

The physiological effect of alloG that leads to reduced tension may be controlled by one of two things. It may be either a reduction in anxiety-causing hormones or a release of endorphins. These two mechanisms of tension reduction would have very different outcomes whilst both leading to tension reduction. The release of endorphins would produce to a state of satiation which is often referred to as hedonistic; the idea that the animal is receiving pleasure from being groomed and is therefore directly opposed to anxiety and tension. Alternatively, the reduction in levels of anxiety-inducing hormones simply implies that the animal returns to an internal state of normality. The distinction is that hedonism suggests relaxation to a point beyond that of normality. The hedonistic effect of alloG has been associated with tension reduction since its conceptualisation by Terry (1970); however, it is not necessary that an animal enjoys the act of grooming to reduce tension. To allogroom individuals must be in close proximity. If proximity is maintained without aggression or threats then this passive proximity may be enough to ease tension. Tension reduction has been long associated with alloG but this function does not explain every case of alloG recorded nor can it be said that every tense situation is calmed by one individual grooming another. It is important to say, therefore, that while evidence suggests that alloG can be used to reduce tension, this is unlikely to be its sole function.

Aggression inhibition

If aggression is "a tool of competition and negotiation" (de Waal, 2000a, page 586) can alloG be seen as an alternative "tool" of negotiation, used as an answer to this aggression? It has often been cited that in certain cases of primate interaction there appears to be anticipation of aggressive confrontation, "monkeys seem to anticipate aggression and forestall it by grooming the potential aggressor" (Sade, 1966, page 8). In this instance it is possible to say that the "answer" of alloG is given before the question of aggression can be asked, which is a strong strategy; it is more beneficial (or at least less costly) to prevent aggression than deal with its consequences. Subordinates often groom dominants upon being approached (Sade, 1966, Sparks, 1967) and may use alloG as a form of communication leading to pacification. AlloG along with (or as part of) submission displays may acknowledge the more superior status of the dominant individual and serve to calm the more powerful individual, thus avoiding confrontation. If behaviour is used as a form of communication (Dunbar, 1991) then grooming accurately conveys intent for peaceful interaction.

It may be difficult to analyse a correlation between aggression and alloG because they are strictly incompatible with one another. Aggression is described as an anti-social behaviour while alloG is considered a social behaviour. By assessing the amount of aggression between two individuals compared to the amount of alloG performed by these individuals, a false association may be found. If aggression is incompatible with alloG then as soon as two individuals engage in a grooming session aggression would, by default, decline.

However, this is not saying that the individuals are grooming each other in order to reduce aggression between them. If, for example, hygiene was the function of alloG then it serves a groomee not to attack those who clean it in alloG sessions. Furthermore, if resources are plentiful levels of aggression would decline as individuals benefit from reduced competition and conversely individuals would be able to engage in more reciprocal alloG sessions because foraging time is lower (for example see Barrett *et al.*, 2002). AlloG is seen prior to and after conflict situations. This suggests it is not a foolproof mechanism for reducing aggression but it does appear to serve some degree of aggression inhibition. Post-conflict alloG would suggest a strong link to reconciliation behaviour.

Reconciliation

As stated by de Waal (2000a), the vast majority of aggression involves familiar individuals, thus its "antisocial" nature carries a highly significant impact on the cohesion of these relationships and also third-party relationships. Reconciliation allows for current rivals who may have a history of peaceful interaction to repair damage to their relationship and restore the social cohesion. Non-friendly rivals may use reconciliation as appeasement to reduce future aggression and restore the social relationships of the entire group. Reconciliation can be defined as "a friendly reunion between former opponents not long after an aggressive confrontation" (de Waal, 2000a, page 586). Individuals who are highly related and/or interact regularly in peaceful behaviours have the greatest to lose from breaks in relations so have the most to gain from reconciling quickly after disputes (Castles *et al.*, 1999; de Waal, 2000a). This reconciliation often comes in the form of grooming and, in some species, other types of ritualised displays (Aureli *et al.*, 2002). The potential function of tension reduction and the proximate mechanism of hedonism may play a role in appeasing an aggressive individual and reaffirming a stable relationship.

The nature of alloG as a peaceful interaction (incompatible with aggression) may be enough to reconcile the relationship without invoking tension reduction or hedonism, but I include these here as plausible considerations. I would argue that reconciliation is different to aggression inhibition because the initiation of reconciliation following agonistic behaviour is often punctuated with a period of non-aggressive behaviour. If the alloG bout were serving to inhibit the present aggressive situation it should be initiated either before the aggression starts (Sade, 1966) or immediately after cessation of the conflict. If it is to be argued that this aggression inhibition is supposed to mean reducing future aggression, then that is part of the result of reconciliation.

One reason for suggesting that *act* of grooming, alone, is the tool for reconciliation is the common appearance in the literature that postconflict grooming is performed with "exaggerated movements and at a rapid rate" (Sade, 1966, page 8). This style of grooming would lose any effectual property for other functions such as hygiene (Sparks, 1967; Terry, 1970; Boccia, 1983). Erratic movements are unlikely to be hygienic or hedonistic but may serve to calm an excited situation back to normality through ritualised communication; demonstrating a desire to repair the relationship. Separating the tension reduction hypothesis is extremely difficult to explain because aggressive encounters normally result in anxiety-like responses; however I follow suit with authors like Aureli and Schaffner (2002a) and argue the benefit of listing all the functions discussed as separate features of grooming, each with the potential to affect the others. Grooming in some cases may appease aggression but the animals involved remain uncertain and tense about the relationship and fear further renewed aggression. Employing the idea of emotional mediation (Aureli and Schaffner, 2002a) it could be that anxiety and fear are the emotions that mediate or trigger initiation of reconciliation between individuals but are not controlled or affected by it. This further justifies listing all associated functions separately.

There is evidence that postconflict reunions not only repair the relationship and reduce aggression but also remove this "uncertainty" between individuals ("uncertainty-reduction hypothesis", Aureli *et al.*, 2002, citing Aureli and van Schaik, 1991). Both the subordinate and dominant individuals in the relationship exhibit lower levels of SDB (a sign of anxiety, see "AutoG as SDB" below) if reconciliation occurs quickly after the initial conflict (Castles, *et al.*, 1999; de Waal, 2000a; Aureli and Schaffner, 2002a; Aureli *et al.*, 2002). Peaceful postconflict contact or interaction between the former opponents is essential to reduce uncertainty (anxiety) and in cases where reconciliation does not occur, avoidance and anxiety related behaviours such as SDB persist much longer after the initial confrontation (de Waal, 2000a). Aureli *et al.* (2002) showed that repeat attacks following an initial conflict are higher for individuals who are not reconciled than for those that are reconciled quickly. This was shown to be universal for 3 primate species and the spotted hyena studied. Rates of SDB (Aureli *et al.*, 2002) are also higher in those postconflict periods that remain unreconciled. In some cases, interaction with third-parties reduces aggression but levels of anxiety and SDB remain unaffected if the two opponents of the original conflict remain unreconciled (Aureli *et al.*, 2002, de Waal, 2000a), further reasoning to keep aggression and anxiety separate, thus also keep reconciliation and tension reduction as separate functions of alloG.

Coalition formation

Individuals may benefit from soliciting support from friendly individuals in a coalition against aggressors and rivals. Such coalitions may raise the dominance status of a subordinate individual above that of a physically dominant individual (Welker *et al.*, 1983). This implies a social rank order as opposed to a physical rank (Nishida, 1983) in which individuals may benefit from reduced aggression (Seyfarth, 1980; Hemelrijk and Luteijn, 1998; Palombit *et al.*, 2001) and which may serve to reinforce the natural dominance hierarchy (Silk *et al.*, 2004). It is possible that grooming may be traded for this social support from dominant (or third-party) individuals; this forms part of Seyfarth's suggestion as to why dominant individuals are so attractive as grooming partners (Seyfarth, 1977, 1980).

While grooming for coalition is supported, the number of coalitions compared to the total number of conflicts is low (Silk *et al.*, 2004), suggesting that grooming does not necessarily guarantee a coalition from a grooming partner. With the abundance of alloG, coalition formation is not a suitable explanation for the majority of grooming recorded (supported by Henzi *et al.*, 2003). An interesting feature of the pattern of coalitions that might help explain this is that higher-ranking individuals formed more coalitions, possibly as they would have the most to gain from supporting each other (Silk *et al.*, 2004) and likewise they also received the most grooming. Henzi *et al.* (2003) suggest that coalition formation and access to grooming partners occurred in baboons irrespective of rank and was based more on levels of group competition. The evidence linking alloG and coalitions is well based but more research is needed to differentiate between demographic characteristics such as rank and kinship. The question of sociality is a likely clue in this search. Do animals prefer family or friends (Chapais, 2001) and when are they more valuable/preferable? Furthermore, are individuals behaving friendly because they are spatially close or does their "social" behaviour make them increasingly close?

Sexual consorts

One of the original titles or classifications of the behaviour of alloG was as a sexual behaviour (also the case for allopreening, Miller and Miller, 1958). It was suggested that male primates used grooming to calm and consort females and females use grooming to accept copulation or entice males into copulating (females may communicate the onset of oestrus by increasing grooming; Rosenblum *et al.*, 1966). In general, males, particularly dominant males, do less alloG than other group members (Sparks, 1967). AlloP males in bird species often mount the females immediately after finishing the preening bout (Sparks, 1967). Sparks (1967) does however, emphasise that this connection to consort behaviour is only a feature of alloG as "there seems little doubt that allogrooming is very important in pair behaviour in primates although it is unlikely to be sexual in its motivation." The association of alloG and sexual behaviour may also have come about due to the prominent sexual dimorphism in the behaviour with females performing considerably more than males (Rosenblum *et al.*, 1966) and the fact that males generally reserve their small amount of alloG to the "consort period" (Sparks, 1967). I take the same view as Sparks (1967) in that alloG seems important for pair bonding but is not sexual in intent. There is however some evidence that alloG is used to secure mates (for example see Lazaro-Perea *et al.*, 2004). For a review of grooming interaction and the association of sexual consort behaviour see Goosen (1987).

Hygiene

The hygienic function of alloG and alloP is thought to be (and is accepted as) the evolutionary origin of the behaviour. Its similarity in motor pattern to that of autoG(P), which serves for hygiene, is a good indication that the conditioning and maintenance of the hair(feathers) and skin of another is a main function of the behaviour. In fact, Pulliam (1973) argued that alloP itself originated as a by-product of autoP whilst in proximity to other birds. There is an abundance of evidence in primates (more so in catarrhine species) to suggest a utilitarian, hygienic function of alloG based on the fact that alloG appears preferentially directed to those regions of the body unreachable to an animal whilst autoG (Sade, 1966; Sparks, 1967; Hutchins and Barash, 1976; Barton, 1983a, b, 1985; Pérez and Veà Baró, 1999). Tanaka and Takefushi (1993) were able to show that alloG did indeed target the removal of ticks, lice and parasite eggs as well as other detritus. It is interesting that in contrast to this abundance of evidence, researchers are investigating alternative hypotheses without complete information or conclusion on the basic and original hygiene function. Indeed, Tanaka and Takefushi (1993) even went so far as to recommend that more investigation of hygiene and alloG was essential before further progress could be made.

Hutchins and Barash (1976) discuss an interaction between autoG and alloG that would maximise the efficiency of the grooming act. Morphologically animals are incapable of grooming their own body with equal attention to all parts because it is not possible to see or reach the entire body surface equally. Therefore to maximise ones own health, receiving grooming to those regions that cannot be autogroomed will remove any ectoparasites or detritus or anything that cannot be detected. It is possible to allogroom another animal on any part of the body as either animal can move into a position to allow access to the body surface. Sparks (1967) goes as far to say that "most of the skin care requirements of a member of a monkey troop are provided by a companion or grooming partner". As described in the previous chapter grooming takes on many styles known as motor patterns. AlloG is often highly manipulative with the groomer moving hair and/or raising limbs or other extremities, even to a point of twisting or rolling the groomee into a position that allows the groomer to access the region of interest. Similarly groomees often occupy a position of complete relaxation turning over to receive grooming (personal observation, see also Sade, 1966, Sparks, 1967, Barton, 1983a).

Barton (1983a, b, 1985) provided more evidence to advance the interpretation put forward by Hutchins and Barash (1976) examining patterns of alloG and autoG in a number of primate species at Jersey Zoo and found that they groomed to a predictable pattern over the body surface area that could be considered an indicator of hygienic grooming. The pattern was predicted on the basis that animals should receive alloG to those regions that cannot be seen or reached easily while autoG. Boccia (1983) argued that the divisions for "accessible" and "inaccessible" regions of the body did not make an accurate test because the areas that were classified as "accessible" and "inaccessible" were not proportional in size and therefore even if grooming were distributed evenly over the body surface one category would, by default, receive more grooming. However, when Barton (1983b) considered the variation in size of surface area between his two categories of accessible and inaccessible, the result became *more* significant. The amount of alloG directed to those sites categorised as inaccessible was statistically significantly greater compared to regions that were seen as accessible. Furthermore, by comparing alloG with autoG it could be argued that this eliminates the effect of this size difference. If alloG in one area is compared to autoG in the same area the size is irrelevant because it is the same for both behaviours, only when examining the difference over the body surface for either behaviour does the surface area of each category become important.

Hutchins and Barash (1976) support the hygienic function with anecdotal evidence from other authors who suggest troops of monkeys occupying the same area as wild dogs and cattle were tick free as a result of engaging in more alloG as well as autoG, whilst these sympatric species were heavily infested in ectoparasites (Hutchins and Barash, 1976, citing Washburn and De Vore, 1961). This is a significant fact in that as highlighted by Hart *et al.*

(1992) the ticks that infest many of the animals living in the African savannahs are not species-specific and are thus capable of feeding from and transferring to multiple species. Similarly, Hutchins and Barash (1976) made reference to reports by Ruch (1959, baboons) and Struhsaker (1967, vervets) in which bachelor males living solitary lives outside groups were reported to be heavily infested with ectoparasites and upon joining or returning to a group would receive intensive alloG and thereupon the parasitic infestation would be eradicated. As discussed before (chapter 2) impala males in charge of a harem sacrifice receipt of alloG to maintain vigilance and territorial defence against roaming bachelor males and as correspondingly suffer from increased tick infestation (Hart *et al.*, 1992; Mooring and Hart, 1995). This may have significant consequences if the infestation reduces the fitness of the male beyond the capability of being able to defend both a territory and the harem he has already secured.

General body size (as opposed to surface area) is another significant factor in terms of hygiene. The loss of blood from ectoparasites feeding on a small animal is likely to have a much greater effect than on a larger host. Hart *et al.* (1992) found that small antelopes would groom (alloG and autoG) more frequently than other larger antelope species. They also describe a significant effect on developing individuals, as young are seriously affected by the chemicals in ectoparasite saliva, an effect that can result in stunted growth. This has significant economic effects for farming of cattle hence the importance of studying this feature in African savannahs where cattle and wild animals often graze the same environment. These factors led Hart *et al.* (1992) to the suggestion that grooming in general should be balanced between the benefits and costs of the behaviour based on "species-typical vulnerability to ectoparasites and the costs of engaging in grooming".

All the other functions except hygiene have clear affects on social relationships, either affecting individual relationships, or entire group dynamics. Some functions can affect individuals and as a result in turn affect the entire group structure. Only in the case of hygiene is there no clear association with having an affect of group dynamics. This is because the benefit of hygienic alloG as mentioned above is directed towards the groomee as it is their surface being cleaned. It is perhaps for this reason that evolutionists, looking for reasons benefiting the groomer have moved towards the other more complex functions of the behaviour. After highlighting all these various functions it is clear that they are not mutually exclusive. Because an animal is trying to form or enhance social relationships it does not necessarily mean that grooming for hygiene does not accomplish this or alternatively that both functions can be achieved simultaneously.

"Multiple functions" hypothesis

Grooming may convey more than one of the functions described above. The communicative value of grooming and the abundance of supporting evidence indicate the behaviour to be one that is extremely flexible and adaptive, capable of being hygienically beneficial and socially organising (Sade, 1966; Sparks, 1967; Alexander, 1974; Hutchins and Barash, 1976; Seyfarth, 1977, 1980; Dunbar and Sharman, 1984; Schino *et al.*, 1988; Dunbar, 1991; Di Bitteti, 1997; Perez and Veá, 2000; Manson *et al.*, 2004). Boccia (1983) claims the "primary" function of allogrooming in primates is social while it still serves (an under-emphasised) hygienic function. Later, Boccia *et al.* (1989) inferred a "multiple functions" hypothesis but ignored hygiene as one of these potential functions. Barton (1985) argued against using the term "primary function" and suggests that when one function is supported by any available evidence this is not to say that others should be rejected or de-emphasised. Similarly Schino *et al.* (1988) stated that in no way are the social functions and hygiene incompatible. Whilst there is an abundance of literature supporting a "multiple functions" hypothesis it was not possible to find an explicit rejection of this idea.

> *"The fact that social parameters influence allogrooming methods is seen as evidence that social functions are more important. However, even if social constraints do compromise efficiency, this does not mean that the skin-care aspect is insignificant. It is probably not useful to focus discussion on a hard and fast dichotomy between social and utilitarian functions; it cannot be inferred that if one function is important, then the other must be unimportant... Because, in any interaction, the interests of individuals are likely to differ, it is not possible validly to rank particular functions in order of overall importance. In this context, then, such terms as "primary function" have little meaning."*
>
> Barton, 1985, (page 530)

The idea of a dichotomy between hygiene and the social functions is, for sure, a false division. The abundance of literature supporting the different individual functions of alloG make it a certain chance that alloG has developed or evolved to serve more than its original utilitarian function but this does not necessarily mean the hygienic function is now redundant. While I would collectively group "aggression inhibition", "tension reduction", "reconciliation", "coalition formation" and "sexual consort" under a single category of 'sociality' (social functions), hygiene (on current evidence) cannot be classified as social (however see discussion in chapter 6). It may be that proximate mechanisms by which each of these functions operates blurs the "Functional divide" and means these functions are not mutually exclusive. For example, the mechanism that causes a *hedonistic effect* is likely to be the same internal physiological change that *reduces tension* and *suppresses aggression*;

however, this state of being pleasured may result from being hygienically groomed if the knowledge of being clean is in itself pleasurable.

Two further facts may support the "multiple functions" hypothesis. Firstly, the variation in grooming style. Boccia (1983) argued that the erratic grooming style often seen in aggressive situations would hold no hygienic value. However, Sade (1966) highlighted that this erratic grooming style only occurred in aggressive situations, or when dominant individuals approached, and that normally grooming produced a peaceful situation were the groomer would be transfixed on the area being groomed (see also Sparks, 1967). Sade (1966) suggested that the variation in grooming style might give insight into the nature or intent of each grooming bout/session. Likewise, Boccia *et al.* (1989) state that the grooming method (or motor pattern) subserves the function i.e. indicates intent. For example, physical manipulation of the groomee's body, by the groomer, would indicate the intention to alter the external (and possibly internal) status of the groomee, which is not a practice necessary for (or likely to enhance) a social function. Disturbing the groomee by rolling is unlikely to be hedonistic or socially motivated. Similarly, erratic grooming is unlikely to serve for hygiene but communicates desire or unease, in testing of relationships or reconciliation. As stated by Schino *et al.* (1988), if hedonism produces a calm relaxed state in the groomee then the groomer is able to remove a greater number of ectoparasites and detritus with a greater level of efficiency, yet conversely the removal of disease causing parasites and low levels of aggression may lead to reduced anxiety and a hedonistic effect.

The second fact for support is the timescale over which these functions may act varies greatly. Some social functions may have an immediate effect while others make differences to the social organisation over a longer period of time. Social functions like coalition formation and reconciliation must operate on both a short-term and a long-term timescale to serve their functions; conflict being best reconciled immediately (de Waal, 2000a). However, it must have the capacity to affect future interactions to prevent aggression reoccurring. Coalition formation could not operate on a short-term timescale because conflict itself cannot be predicted, unless the coalition is intending on starting the confrontation which requires mutual understanding of a future event. Animals are repeatedly getting dirty thus the hygienic function is likely to serve only a short-term benefit. The effect of hedonism, like hygiene, would only serve a short-term benefit because the physiological state of individuals is constantly changing (Barton, 1985; Schino *et al.*, 1988). However, if it plays a role in tension reduction, aggression inhibition and/or reconciliation it may contribute to other long-term effects and thus be maintained. The lack of mutually exclusive functional hypotheses can be seen in their effect over time, as noted by Schino *et al.* (1988) who argued that, even on a short-term timescale, the immediate social benefits of grooming are not contradictory to the immediate benefits of other functions such as hygiene.

A model developed in the early nineties has recently received much interest in primatology and especially in the context of grooming and grooming relationships. The Biological Market Principle (Noë *et al.*, 1991) describes how the resource value of a behaviour operates with a market effect and can be traded for return of like resources (reciprocity, Trivers, 1971) and alternatively for different resources (interchange, Hemelrijk and Ek, 1991). Not only has the Market Principle been applied to primate grooming behaviour but also many of its fundamental ideas have been developed and advanced due to research on primate grooming (Hemelrijk and Ek, 1991; Noë and Hammerstein, 1995; de Waal, 1997; Hemelriejk and Luteijn, 1998; Barrett *et al.*, 1999; Henzi and Barrett, 2002, Henzi *et al.*, 2003). The Market Principle is a suitable model for analysing alloG because it considers the resource in terms of benefit to the groomee which is then traded for benefits to the groomer and also that it allows for multiple functions to result from the same behaviour. As a result it has been described as a more suitable predictor of interactions compared to Seyfarth's original model (1977) for females in a female-bonded society.

Whatever the function(s) of alloG, its diversity and abundance with respect to the array of grooming styles and the support for the various functions discussed, indicates both its importance in the early evolution of the primate behavioural repertoire and the probable evolution of the behaviour from a single original function to a multiple-functioning behaviour. Based on the evidence I have presented above, the fact that these functions are not mutually exclusive and the intricacy and diversity of primate alloG, support of the "multiple functions" hypothesis warrants clarification or definition of this hypothesis. The lack of explicit support for hygiene as an individual function and as part of the "multiple functions" hypothesis, in the current literature beyond that of Barton and Pérez and Veà Baró (cited above), has led to this investigation in capuchin monkeys for an examination of the importance of hygiene as a function of alloG. By investigating the hygienic function of alloG this thesis aims to establish whether the evolutionary origin of the behaviour (the removal of ectoparasites and detritus) still has importance in grooming behaviour. An interaction between individuals, such as alloG, has obvious social implications because it involves two individual organisms with differing motivations and states. AutoG, however, is an individualistic behaviour but has recently been investigated for how it may have influence on or may be influenced by other animals in the social group.

Autogrooming: a social context

It is accepted that autoG arose to serve and still serves a hygienic function in animals; hence its direct comparison with alloG for hygiene. However, it is worth noting a recent development of investigating the social context in which autoG is performed. This suggestion considers how autoG can be socially mediated and may give indications to the social structure and relationship status of differing individuals. The main study of autoG in social context is as SDB (self-directed behaviour), which has been thought to be an indicator of anxiety and therefore tension (Maestripieri *et al.*, 1992). Evidence provided by Castles *et al.* (1999) did not support solitary autoG or, interestingly, autoG for purely hygienic reasons.

Castles *et al.* (1999) found a link between rates of SDB and anxiety triggered by proximity to dominant females, in female olive baboons. They did not relate this to 'rank distance' but were able to simply correlate it with dominance. The strongest result was found when the conspecific of the anxious individual was dominant *and* without a 'secure' relationship, i.e. individuals who did not interact regularly. Subjects were more anxious and exhibited high levels of SDB when in close proximity to non-friendly dominant individuals. High levels of alloG should in this context result in lower levels of autoG because it is reducing heart rate (Schino *et al.*, 1988; Boccia *et al.*, 1989, Aureli *et al.*, 1999), anxiety (Castles *et al.*, 1999; Manson and Perry, 2000) and rates of SDB (Schino *et al*, 1988; Castles *et al.*, 1999; Manson and Perry, 2000). However, this is unlikely to affect the pattern of grooming over the body surface for either alloG or autoG.

Studies of grooming in New World primates

Since the review study by Dunbar (1991) there has been a presumed difference between catarrhines (Old World) and platyrrhines (New World) in the function of alloG. Dunbar (1991) showed that catarrhines had a more social basis for their alloG distribution whereas the platyrrhine species included in the study, had a pattern reflective of being more hygienic in orientation. One point of note is that Dunbar was careful not exclude the other functions in his discussion and emphasised that it appeared more hygienic or more social in each species. The study by Dunbar also served to highlight the bias in primate studies for focusing on catarrhine species (see also comments in Schino, 2001). The sample size for platyrrhines in Dunbar (1991) totalled 11 species out of 44.

Whilst the literature may be biased towards catarrhines, efforts are now being made to collect the qualitative and quantitative data for platyrrhines. A common aspect of the literature is that alloG "is less frequent among New World than Old World monkeys" (Schino 2001; see also Dunbar, 1991; Ahumada, 1992; Di Bitteti, 1997; Lazaro-Perea *et al.*, 2004). Species differences are likely to make this fact have a wide range of figures. Differences in habitat type, habitat use and social dynamics are likely to contribute to this variation between platyrrhine species. Current studies are beginning to show a range of social influences on alloG allocation and abundance. Even species like spider monkeys (*Ateles* spp.) have some degree of social interaction and show correlations between alloG and social interactions; where individuals engaging in more alloG, engage in more social interactions and more sharing (Pastor-Nieto, 2001).

Sánchez-Villagra *et al.* (1998) showed that in troops of red Howler monkeys (*Alouatta seniculus*) alloG was highly varied between individuals, females groomed more than males and data supported both grooming for hygiene and social relationships (including males grooming females for sexual consort). Interestingly, the study by Sánchez-Villagra *et al.* (1998) showed similar results to catarrhine species in Dunbar (1991) in that social structure was a better predictor of alloG pattern (abundance) than was body size. Similar results, supporting social functions of alloG are being shown in other South American species such as spider monkeys (*Ateles geoffroyi*; Ahumada, 1992), moustached tamarins (*Saguinus mystax*: Heymann, 1996) and common marmosets (Callithrix jacchus; Lazaro-Perea *et al.*, 2004). One genus of platyrrhines receiving a lot of interest and producing a lot of conflicting evidence is capuchin monkeys (*Cebus* spp.). These monkeys live in complex social groups, have large brains relative to body size and are considered to be highly adaptive and flexible animals (Izawa, 1980; Freese and Oppenheimer, 1981; Fragaszy, *et al.* 1990; Fedigan, 1990).

Grooming studies in *Cebus*

Studies of grooming function in capuchin monkeys have mostly focused on the social complexities as opposed to the hygienic function of either alloG or autoG. The importance of strong social bonds in capuchin species has perhaps dictated or predisposed that studies into alloG and autoG should focus on these behaviours as indicators of social status. This may be seen as contradictory to the fact that Dunbar (1991) suggested the pattern of alloG in South American (platyrrhines) primate species serves a hygienic function, whereas the catarrhines groomed for social reasons. It may also be that Dunbar's conclusion on platyrrhine alloG has sparked the interest in establishing whether platyrrhines groom socially or not; especially when his original paper suffered from a small sample size of research papers on the platyrrhines. As a result, there is no study of capuchin alloG in the context of hygiene, except as a subset of data presented in Barton (1983a, b).

AlloG and sociality in Cebus

Grooming relationships in *Cebus* species are important for group members and intricate in structure (Di Bitteti, 1997). Grooming can last a few seconds or many minutes and comprise single bouts and reciprocal sessions. Reciprocal grooming sessions have been shown to last longer than unreciprocated bouts and this suggests some form of participatory commitment (Di Bitteti, 1997; Manson *et al.*, 2004; as found in catarrhines: Barrett *et al.*, 1999, 2000). Manson *et al.* (1999) found that grooming relationships were highly stable over long periods of time and that the general trend of grooming followed the pattern outlined by Seyfarth (1977). The idea of grooming for coalitionary aid (part of Seyfarth's model) was supported by data from one observation group but not the other.

AlloG and dominance in Cebus

AlloG in research on dominance relationships has produced mixed results. Most *C. capucinus* groups in a study by Manson *et al.* (1999) groomed up the hierarchy as predicted by Seyfarth's grooming model (1977), matching results in *C. apella* groups (Di Bitteti, 1997). In studies on *C. olivaceus* (O'Brien, 1993) and *C. apella* (Parr *et al.*, 1997) grooming was found to be directed down the hierarchy. In one group at the Santa Rosa research site (see Manson *et al.*, 1999) alloG was directed down the hierarchy, although this result was not significant. In the same study, other groups directed alloG down the hierarchy during differing study periods although again these results were never significant. This was explained by the presence of infants and the data showed no variation based on rank once the data set controlled for females with infants. AlloG directed down the hierarchy in Santa Rosa was attributed to two females being in constant rivalry for the alpha position. It was interpreted that these females may have been trading for support from coalitions and this dramatically altered grooming distribution and direction. Unlike the results seen in catarrhine species there seems to be no exclusion of subordinates from access to highest ranked grooming partners. Manson *et al.* (1999) saw very little agonistic disputes or supplants over access to other grooming partners.

SDB in Cebus

In the only study of SDB in platyrrhines, Manson and Perry (2000) tested levels (and patterns) of autoG in *C. capucinus* to determine if autoG is a form of tension-induced SDB. The results of this investigation did not match those of the catarrhine species tested previously. Females engaged in more SDB in proximity than when alone, this was regardless of the relative rank position of neighbours. It was also found to be high immediately before and after bouts of alloG, irrespective of whether the focal animal (the animal observed for SDB) was the groomer or the groomee. This second result supports an alternative to hygiene as a proximate cause for some cases of autoG, but the lack of a clear association with dominance does not support the anxiety hypothesis. Manson and Perry (2000) proposed two alternative interpretations.

Firstly they argued that capuchins do not exhibit anxiety through the same kinds of SDB as those catarrhine species previously tested. Support for this is seen in the fact that there was no correlation between rates of SDB and aggression rate or fear of aggression. There was also no correlation for SDB with rank. Alternatively, as a highly social species, the social contexts that elicit anxiety in capuchins may differ from those of the other species studied. For example, a desire to "service" (Manson and Perry, 2000, quoting Dunbar, 1991) social relationships by alloG may trigger anxiety while in proximity to social partners. This is supported by the apparent fickle nature of capuchin relationships (Manson and Perry, 2000; Nishida, 1983; see also Manson *et al.*, 1999, for nature of female social relationships in *C. capucinus*). This was linked to the observation that autoG occurred frequently before and after alloG sessions.

AlloG and hygiene in Cebus

In *Cebus*, the majority of studies investigating social functions or socially mediated factors acknowledge hygiene as the evolutionary origins of alloG (Di, Bitteti, 1997; Parr *et al.*, 1997; Manson *et al.*, 2004) but research into the importance of hygiene for capuchins does not exist. Some papers looking at social organisation never consider hygiene (O'Brien, 1993; Manson *et al.*, 1999). For example, O'Brien (1993) considers alloG to serve two social functions (coalition formation and tension reduction) and never offers other ideas for consideration. Because of the lack of alloG research in platyrrhine species for investigation of hygiene and the suggestion by Tanaka and Takefushi (1993) that this function is in need of further research, this investigation will look at grooming for hygiene in Cebus apella.

Hypotheses and Predictions

Although an animal may be able to reach any part of its body whilst autoG, it is unlikely that this animal will be able to access all regions with the same efficiency. This should produce two opposable hypotheses of grooming directed to different body regions and as a result produces opposing patterns of autoG over the body surface. Firstly, if regions are difficult to groom they will require more attention (longer durations) during autoG to completely remove the ectoparasites and detritus from the pelage. The grooming pattern here is those regions which cannot be reached easily will show longer autoG time than regions easily reached. Alternatively, autoG should be preferentially directed at regions that are easy to access and received alloG should be directed towards those regions that cannot be groomed effectively by autoG. The pattern here (for autoG only) should show a high amount of autoG to regions that are easily reached in autoG and difficult or impossible regions should receive very little attention. For this second hypothesis to stand, the pattern of received alloG should be inversely proportional to that of autoG; being preferentially received to regions impossible to autogroom effectively. The first hypothesis does not account for the effect that alloG would have if it served the same function as autoG.

The restriction in autoG to a manual groomer is twofold: *accessibility* (reaching the surface with the hands) and *visibility* (ability to see the surface of interest). Each body region is likely to differ for whether it can be reached or seen, both or not none at all. Due to the "gradient" of grooming efficiency and assuming that grooming serves a hygienic function, an animal would benefit from receiving more alloG to those regions it cannot groom itself, than to other regions. Therefore the pattern of alloG over the body surface could be an indicator of the hygienic function. There are three categories of efficiency (of autoG) that any one region could be placed under. ***Easy*** regions can be autogroomed with high efficiency. ***Difficult*** regions can either be seen or physically reached but not both so the efficiency of autoG is reduced. ***Impossible*** regions cannot be reached or seen easily so the efficiency (if any) is minimal. A full description of how the body regions were categorised in this investigation is given in the method (chapter 4).

In this thesis I will test the second of these conflicting hypotheses; that autoG will be directed to those regions easiest to autogroom, with the unattended regions being cleaned during alloG. The pattern of alloG over the body surface will be investigated to test whether alloG still serves a hygienic benefit to capuchin monkeys. The approach of Pérez and Veà Baró (1999) will be repeated so any result in this thesis will be comparable to that of the white-crowned mangabey. The null hypothesis in this case is that there is no variation over the body surface, so 1% of the body surface receives 1% of the total grooming (alloG or autoG). It is not the case, however, that the null hypothesis predicts that the three categories of body region types, easy, difficult and impossible, received 33.3% of grooming. This is because the three categories do not each make up 33.3% of the body surface area. As a result of this, the body surface area will be used as a correction for each of the three categories (as suggested by Boccia, 1983; Barton, 1983a, b; Pérez and Veà Baró, 1999).

Two clear predictions can be formed from the information above:

P1: AutoG will be preferentially directed to those regions that are easy to autogroom effectively.

P2: AlloG will be more abundant at body regions that cannot be autogroomed efficiently.

-4-

Method

Study species

This investigation will examine grooming behaviour in a group of capuchin monkeys (*Cebus apella*). Due to confusion and incomplete paternal records no distinction beyond this older classification (as presented in Rowe, 1999) can be made.

Cebus species form linear dominance hierarchies in both males and females. Individually, males are normally dominant to all females; however, the alpha-female can sometimes be dominant to the lowest ranked males (Freese and Oppenheimer, 1981; Hall and Fedigan, 1997; Manson *et al.*, 1999). All capuchins live in multimale-multifemale groups, and show female philopatry.

Age classification

Age categories used in this study replicate, primarily, data in Freese and Oppenheimer (1983, page 364-365, citing Gilmore, 1943) and secondly data from Izawa (1980), Welker *et al.* (1987, 1990a) and Di Bitteti (1997). Table 4.1 shows the classification of Freese and Oppenheimer (1983) and then the adjusted age classification used in this study (right hand column). Names of age categories in this study are as Freese and Oppenheimer (1981).

Category	Age range, F & R (1981)	This study
Infant I [fully dependent]	0 to 8 months – Incomplete deciduous dentition.	0-6 months
Infant II [relative independence]	6 to 18 months – Complete, deciduous dentition.	6 –12
Juvenile	14 to 40 months - Mixed deciduous and permanent dentition	12> <60
Sub-adult	36 to 42 months – Incomplete, permanent dentition.	N/A
Adult	36 months – Unworn, permanent dentition.	60+
Old Adult	8 years plus – Worn Permanent dentition.	N/A

▲ **Table 4.1** – ***Age Classification*** – The data presented in this table is taken from Freese and Oppenheimer (F & R, 1981, pages 364-365) citing Gilmore (1943). The categories are assigned based on data working from dentition. For simplicity in this study precise figures were given on age categories, which are given in the far right hand column. No distinction was made for "Sub-adult" or "Old Adult"; all animals classified as "Adult" after 60 months (5 years).

Grooming motor patterns in Cebus

Opposable thumbs and dextrous fingers mean capuchins are capable of accurate manipulation. Objects can be gripped, turned, probed, carried, caught and thrown under control (Adams-Curtis, 1997). As well as being able to control features of their environment this high degree of manipulation means capuchin alloG and autoG makes use of many of the different motor patterns discussed in chapter 2, including stroking, combing, picking, raking, spreading, licking, mouthing and scratching. *Cebus* species utilise a combination of oral and manual grooming techniques in both alloG and autoG. Capuchins do not possess a modified toothcomb like lemurs, so oral grooming is not as specialised but incorporates the use of the tongue and lips.

Study subjects

The capuchin group is housed in the primate park, *La Vallée des Singes* (LVDS), Romagne, France. At the beginning of the study, the park had housed the group for four and a half years following transfer from the behavioural research laboratory of the *Institut für Zoologie und Vergleichende Anatomie*, Universität Kassel, Germany (from here "Kassel") in March of 1998. All members of the group that were transferred to the park were born in captivity in Kassel. Throughout the study the group numbered 24, no members left the group and no new members were added (note: Falla was reintroduced to the group after a long absence through injury during the first study period). Group composition during the study was 2 adult males, 6 adult females, 10 juveniles (9 female, 1 male) and 6 infants (2 female, 4 male). Ages in the group ranged from the oldest female, Sarah, aged 23 years, 4 months in September, to the latest born infant, born 15th September 2002, during the habituation phase of the current study. The group number is similar to that considered typical of wild capuchin groups. All individuals are captive born and the maternal relatedness for all individuals is known. A matrilineal pedigree for all current individuals is shown in Appendix 4.1 and table 4.2 shows details of all current group members. Appendix 4.1 includes a complete matrilineal history for the "Sarah" and "Justus" lineages from Kassel along with information about the history of the founding group (from Welker *et al.*, 1983, 1987). The two adult males were kept separate during the daytime (visiting hours) because it was considered potentially dangerous to have males and visitors in close proximity. These two males were kept on a separate island to the females and had access to the building (housing).

Name	ID No.	Sex	D.O.B.	Age (S'02)	Age (A'03)	Mother
Sarah	133	F	22/05/1979	**23**,3,24	**23**,10,11	Sylvia (K)
Justus	134	M	25/09/1982	**20**,11,21	**21**,6,8	Teufel (K)
Silke	137	F	18/06/1686	**16**,2,28	**16**,9,15	Sarah (K)
Franziska	141	F	10/07/1989	**13**,2,5	**13**,8,23	Sarah (K)
Sunny	143	F	02/06/1992	**10**,3,13	**10**,10,0	Sarah (K)
Sita	145	F	04/08/1995	**7**,1,11	**7**,7,29	Franziska (K)
Falla	146	F	26/08/1995	**7**,0,20	**7**,7,7	Sarah (K)
Persimon	152	M	17/04/1997	**5**,4,29	**5**,11,15	Paula (K)
Eldorado	232	F	29/03/1999	**3**,5,17	**4**,0,4	Silke
Manaus	236	F	09/04/1999	**3**,5,6	**3**,11,24	Franziska
Salvador	251	F	29/07/1999	**3**,1,17	**3**,8,4	Sarah
Manatie	296	F	12/04/2000	**2**,5,3	**2**,11,21	Franziska
Sitty	315	F	28/06/2000	**2**,2,18	**2**,9,5	Silke
Maya	369	F	30/04/2001	**1**,4,15	**1**,11,2	Franziska
Felize	371	M	08/05/2001	**1**,4,7	**1**,10,25	Sita
Inca	376	F	09/06/2001	**1**,3,6	**1**,9,24	Sunny
Sascha	393	F	09/08/2001	**1**,1,6	**1**,7,24	Sarah
Nube	398	F	24/08/2001	**1**,0,22	**1**,7,9	Silke
Diabolo	452	F	03/06/2002	**0**,3,12	**0**,9,30	Franziska
Borakimo	458	F	09/07/2002	**0**,2,6	**0**,8,24	Sita
Cuca	459	M	17/07/2002	**0**,1,29	**0**,8,15	Falla
Loma	460	M	12/08/2002	**0**,1,3	**0**,7,21	Sarah
Quitu	461	M	14/08/2002	**0**,1,1	**0**,7,19	Sunny
Chimu	466	M	15/09/2002	**0**,0,1	**0**,6,18	Silke

▲ **Table 4.2** – *Group List* – This table gives information on each group member over the period of study (September 2002 to April 2003). **Age (S'02)** is the individual's age on September 15th 2002. **Age (A'03)** is the individual's age on April 2nd 2003. Ages are given as the number of **Years,**Months,Days after the date of birth (D.O.B.). "**(K)**" after the individuals' mother's name indicates the individual was born in the research laboratory in Kassel University before transport to LVDS; all other births occurred at LVDS.

All individuals are identified in the zoo using names and an ID number. To distinguish between individuals in discussion the names will be used. The females selected for focal sampling were Sarah (ID: 133), Silke (137), Franziska (140), Sunny (143) and Sita (145; see Appendix 4.2). Adult female, Falla (146), was not present in the group at the start of September 2002 so was not used as a focal subject in this study. Each female gave birth to a single infant before the study began. In this group the infants began independent movement (i.e. moving alone) and began feeding on solid food at about 3-6 months of age. Thus after six months, infants are classified as independent in this study, after this time they suckled very rarely and found their own provisioned food. This classification means that each adult female had a dependent infant during September 2002 and a relatively independent infant in April 2003 (following classification shown in table 4.1).

Identification of individuals was achieved through identifiable natural markings and any morphological differences. After the first week of habituation (02nd to 09th September 2002) each female could be identified accurately at distances over 20 metres. Size, shape and characteristic movements, for each female, made identification possible without the use of coloured tagging or other such artificial aids. Before the observations began, all group members could be identified accurately.

Study site

La Vallée des Singes (from here LVDS) is a modern zoological park specialising in the care of and breeding of primate species. Enclosures consist of large islands separated by canals of water and sleeping houses. Walkways allow access for researchers directly onto the island. The level of animal habituation to human presence is high and therefore allows for quality data collection in close proximity, sometimes less than 3 metres. The open environment means obscured vision is limited while observing the animals. The weather over the course of the study in the park was typical of European seasonality. No accurate measures were taken for climate with only one temperature measure taken daily between 12:00 and 12:30. Average temperatures were 25°C for both observation periods, however, the day often began very cold before becoming warm in mid to late afternoon; late afternoons being normally very mild. Rainfall was low during the study, although no measurements were taken.

The capuchin enclosure

The enclosure of the capuchins is divided into three sections (see Appendix 4.3 for map of the enclosure and surroundings). The females spent the entire observation period (08:45 – 18:00) on the main island (from here "Female Island", FI). The other two sections consisted of a second island and a building (night quarters) that was the only connection between the two islands. The building was used by all individuals to feed and sleep between 18:00 and 08:45 the following morning, but was closed to the females during the day. Access to the second island (from here "Male Island", MI) was maintained when in the night quarters. Two neighbouring islands housed further platyrrhine species; one island for a group of white-bellied spider monkeys (*Ateles belzebuth*), the other for a group of woolly monkeys.

FI was estimated to be about 1200m^2 with various mini-habitats of open grass, shrub and bush, and tall trees (up to 40 metres) of varying species. Feeding would take place on five feeding stations separated by a minimum of 5-6 metres. Daily feedings took place at set times during the day and provided a mixture of vegetables, fruit, nuts and artificial feeds. On certain days, grapes, bananas, and some other fruits, or nuts would be distributed (thrown) in the enclosure to vary the feeding habits of the group and encourage more natural foraging behaviour.

Study length

The study was divided into two study periods, September 2002 (18 days of observations; over a total of 30 days) and April 2003 (22 days of observations; over a total of 32 days). From here September 2002 will be referred to as S'02 and April 2003 will be referred to as A'03. Before observations began in either period the animals were habituated to the presence of the researcher (S'02 = 15 days of habituation, A'03 = 9 days). Although the animals were use to close interaction with visitors, habituation was seen as necessary because on occasion the researcher had to leave the visitor walkway to maintain sight of focal animals. Leaving the path was avoided when unnecessary, during observations, to limit disturbance to other animals not being observed as well as the focal animal. The prolonged presence of the researcher in the territory could potentially disturb the animals so the period of habituation was used to eliminate this problem. It was also useful time to make detailed descriptions of behaviours in an ethogram and, similarly, characterise each individual by facial features, bodily characteristics and physical movements for identification purposes.

Observation technique

Sampling method

Observations were made of the five females using *focal animal* sampling, recording continuous behaviour over a focal time of 30 minutes (following methods described in Martin and Bateson, 1993, pages 84-85, as previously described by Altmann, 1974). Focal animal sampling was chosen for two reasons. Firstly, it allows for accurate duration times to be recorded for all target behaviours. Secondly, it best suits the collection of social data, i.e. when it is interactions between individuals being recorded (Martin and Bateson, 1993, page 85) *Behaviour sampling* and *scan sampling* are more difficult for recording social behaviour and are also susceptible to group bias if all individuals are not active equally.

Observations of focal sampling were made at distances between 1 and 15 metres. For the purposes of observation the day was divided up into 17 time slots (30 minutes each starting on the hour or half past) from 09:00 to 17:30 (last recording starts at 17:00). Focal data were

Female	S'02	A'03	TOTAL
Sarah	13.5	17	30.5
Silke	13	17.5	30.5
Franziska	14	18	32
Sunny	14	16.5	30.5
Sita	13	16.5	29.5
TOTAL:	67.5	85.5	153.0

▲ **Table 4.3** – ***Hours of Data*** – Focal sampling durations for each female over both time periods (S'02 = September 2002, A'03 = April 2003).

recorded for each female at least once in each of the 17 time slots (mean sample = 2 per slot per individual, range 1-3). The total time of focal data collected is 153.0 hours (table 4.2 shows the breakdown of hours per female for both S'02 and A'03. 36 focal samples (18 hours) from S'02 were rejected before analysis because the data collection method changed in the field. These data all pre-date September 18th; all observations after this date are used in this analysis, no observations from A'03 were removed from analysis. If samples were taken in rain conditions a further sample was collected on a later date. Nevertheless, data collected in rain were still used in the analysis.

Conspicuous behaviours recorded include allogrooming and autogrooming (definitions and restrictions follow). Further behaviours of interest were recorded if time allowed whilst recording the main subject data. If behaviour involved interaction with other individuals, identities of all conspecifics were recorded. Behaviour was recorded by noting the start time and timing duration to the nearest second using a stopwatch. The behaviour had to continue for four seconds before it was recorded and the behaviour was recorded as having ended if it stopped for more than five seconds or was interrupted by another conspicuous behaviour or by another member of the group. When the animals were obscured from view, the total time of the animal remained obscured was recorded as "*out of sight*" (OoS). If the focal female was in view but her grooming partner was obscured this was eliminated from data collection.

- *Allogrooming and Autogrooming*

The identity of the conspecific(s) (in allogrooming) was noted along with the duration of each bout. When grooming direction changed (i.e. animal A groomed B then B groomed A) the two bouts were recorded separately, as the position of the focal female changed from receiver to groomer or vice versa. When the data were inputted into the computer a note was made of instantaneous reciprocity. Body regions were divided up and placed into specific categories assigned according to autogrooming efficiency (see descriptions to follow and Table 6.4). The duration of grooming in each category was recorded separately. Data were recorded per category without distinguishing body regions individually. It was not always clear which individual initiated or terminated a bout; if observed it was recorded. No analysis, therefore, will be done with these limited and possibly inaccurate data. It was my interpretation that allogrooming was generally initiated by the groomer rather than the groomee. Initiation through solicitation was witnessed numerous times in the group and will form part of the discussion.

Allogrooming is defined here as the manipulation or separation of body hair of one individual by another, using the hands and/or mouth.

Autogrooming is defined here as the manipulation or separation of own body hair, using the hands and/or mouth.

Body category assignment

As in the descriptions from Barton (1983a, b, 1985), and Pérez and Veà Baró (1999), the body surface was divided up into a number of distinct regions. The 18 regions used here, were classified as belonging to one of three categories depending upon the interpretation of how easily a capuchin could autogroom the specific region. The category classification followed previous approaches, based on the two variables, ***accessibility*** and ***visibility*** (Boccia, 1983). Accessibility in previous research considered how easy the hand could be orientated and moved to the region for grooming. Accessibility, in this thesis, also considered whether a region could be orally groomed based on capuchin grooming style, (as discussed in Chapter 2 and above). Visibility describes how easy the animal could see the region during grooming, which is important for controlled hand-eye coordination and better detection of parasites and detritus.

The body divisions in this paper were assessed while in the field so are specific to this paper, however the divisions used reflect those of Barton (1983a, b, 1985), and Pérez and Veà Baró (1999). By reaching to body regions and trying to look upon each region myself, a basic body map was designed for which regions could be reached or seen easily and which were restricted by either a lack of reach or lack of sight. A further consideration for rotation in reaching was made because manual grooming non-homonoid primate species have reduced shoulder rotation compared to humans because of the position of the shoulder joint. The scapulohumeral articulation in non-homonoid primates is restricted compared to species like humans (Ankel-Simmons (2000). The third consideration for how to classify each region was done by observing the capuchins themselves for rotation of the arms in reaching over the body, whilst in motion etc and further for observing the twisting of the body for both reach and visibility.

There is one clear distinction in the division of body regions between this thesis and Barton (1983a, b). The upper arm, or brachium, was divided in two in this investigation, to highlight the higher degree of difficulty autoG the dorsal side compared to the ventral side. While only being able to groom the entire brachium with one hand it is more difficult to see the dorsal side. On this description the dorsal side of the brachium was categorised as "difficult" to groom and the ventral side was categorised as easy (see table 4.4 for classification guide). Oral grooming also accounted for a difference in grooming of the ventral and dorsal sides of this part of the arm.

Classification	Description
Accessible/Visible	Can be seen visually and groomed using both hands
Inaccessible/Visible	The site can be reached only by one hand and the mouth, but is visible for controlled grooming.
Accessible/Non-visible	The site cannot be seen but both hands can be employed to groom the region.
Inaccessible/Non-visible	The region can only be groomed using one arm at most (and with little efficiency) and the site is not visible, or the site requires excessive body twisting to increase access.

▲ **Table 4.4** – ***Autogrooming Categories*** – The body surface was made up of four different categories of body regions based on the efficiency of an animal autogrooming.

The combination of possibilities of accessible, inaccessible and/or visible, non-visible produced four classifications for body region type (given in table 4.4). The two categories of Inaccessible/Visible and Accessible/Non-visible were collectively grouped together to make data recording easier. This produced three categories in which each body region was placed (see table 4.5). The category names were based on how ***efficiently*** an autogrooming animal could groom the regions in that category not whether the animal could or could not groom the region at all. All data for body regions under the same category was grouped to make data collection easier in the field, so no data for an individual body region can be presented. The definitions for the three body region types are as follows:

1. ***Easy*** – "*E*" – Grooming efficiency is high. Use of both hands in combination with possible oral grooming, whilst also visible, means autogrooming this region is not demanding. Contained regions classified as *Accessible/Visible.*

2. ***Difficult*** – "*D*" – Grooming efficiency is reduced either because the animal is unable to see or unable to reach the specific site. Contained regions classified as either *Accessible/Non-visible* or *Inaccessible/Visible.*

3. ***Impossible*** – "*I*" – Efficiency is extremely poor as the animal cannot see or effectively reach the location. This site would be reduced to single hand grooming or possibly only scratching. Contained regions classified as *Inaccessible/Non-visible.*

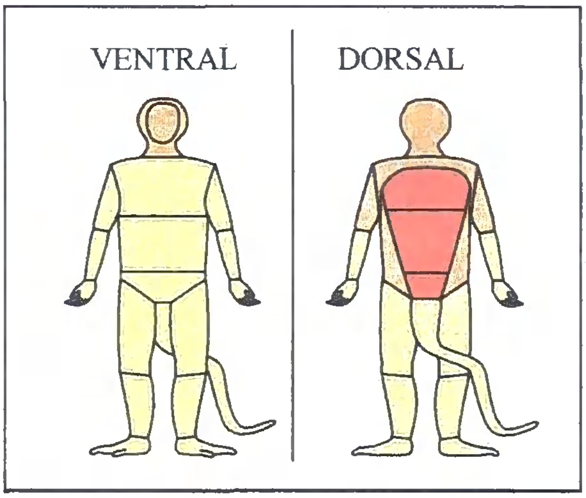
Body Site	Contains	Accessible	Visible	Category
Face	The area around the eyes, nose, mouth and cheeks, white and black area of the face.	Both hands	No	D
Scalp	Rest of the head, including the ears, not including the neck.	Both hands	No	D
Throat	Front of the neck, under the chin joining to the chest.	Both hands	No	D
Shoulders	Back and top part of the including the back of the neck, includes shoulder joint.	Both hands	No	D
Front	Includes the chest and abdomen from beneath the neck to the groin and hips.	Both hands	Yes	E
Stomach	The abdomen, runs from below the chest to the groin and from both sides.	Both hands	Yes	E
Upper, Middle and Lower Back	The 3 sections of the body that make up the back. Central region of the dorsal side running from the base of the neck to the base of the tail.	One hand only, & twisting	No	I
Groin	The region running between the thighs, front of the pelvic region not including the hips.	Both hands	Yes	I
L and R Flank	Both flank regions of the torso running from the armpits to the hip region, includes the armpits.	One hand	Yes	D
Tail	Entire length of the tail from the base to the apex.	Both hands, oral grooming (apex)	Yes	E
Ventral side of L and R arm (Brachium)	The forward-facing section of the upper arm not including the shoulder joint, running down to and including the elbow.	One hand, Oral grooming	Yes	E
Dorsal side of the L and R arm (Brachium)	The rear side of the upper arm not including the shoulders running to and including the elbow.	One hand	No	D
L and R Leg	The entire leg, includes the hip, thigh and lower leg.	Both hands, oral grooming of leg	Yes	E
L and R Hand	Back of the hands and digits, including the fingernails.	One hand, oral grooming	Yes	E
L and R Foot	Includes the ankle and the backs of the foot and toes including the toenails.	Both hands, oral grooming	Yes	E
Anosexual region	Region below the base of the tail surrounding the anus	Both hands	No	D

▲ **Table 4.5** – *Body Regions* – Each region of the body, a description of the area contained in each region (body part including joints etc). The level of accessibility and visibility for an autogrooming capuchin monkey and the category assigned is given for each of the body regions. Descriptions are linked to figure 4.i regarding the dorsal and ventral view. L = Left, R = Right. Region E = Easy, D = Difficult, I = Impossible.

Correcting for surface area

Based on body region type, the body surface area (BSA) was not divided into three equal portions. The surface areas for the categories used in this investigation were calculated from data provided in Barton (1983a) and Pérez and Veà Baró (1999). Other literature (*Macaca mulatta*: Lee and Fox, 1933 (called *Macaca rhesus* in the previous paper); Liu and Higbee, 1976; *Saimiri sciureus*: Stitt, *et al*., 1971; *Macaca fuscata*: Hori *et al*., 1972; *Macaca cyclopis*: Lin, 1976) did not provide data in a suitable format for use in this study. The surface area data used from previous studies was selected based on physical similarity with the capuchin species (body length, tail length, intermembral index). The physical characteristics of all species in both publications are presented in Appendix 4.4.

Because Barton (1983a) and Pérez and Veà Baró (1999) used joints and physical features as dividing lines if body parts had been categorised differently in this paper, data could be recalculated based on these simple dividing lines. The most significant change was to the upper arm (Brachium), which was separated in to two portions based on ventral and dorsal sides (not done in either previous study; see figure 4.i and table 4.5). To produce a value for both sides the value for the total upper arm in either Barton (1983a) or Pérez and Veà Baró (1999) was divided in two. The complete set of data used is presented in Appendix 4.5. Figures for the representative monkey from Barton (1983a) and Pérez and Veà Baró (1999) are shown in Appendix 4.6. The data in both publications are presented as percentages of the total body surface area of the animal; table 4.6 presents the average of all four sample animals used in this thesis. A small correction for error was necessary after calculating the average of the data from Barton (1983a) and Pérez and Veà Baró (1999). This is because the total did not add up to 100% as a result of the original data in the two publications being rounded to one decimal point. The difference between the summed percentage and 100 was divided by three and added equally to each category. The percentage of the BSA taken up by each category is shown in table 4.6. As can be seen



▲ **Figure 4.i** – ***Body Region Design*** – The dorsal and ventral view of a representative primate. The colours represent the three categories of body site used, cream = Easy; orange = Difficult; red = Impossible; this is based on the efficiency of an animal grooming itself.

from this table, the majority of the body surface is taken up by the easy category and very little being taken up by the impossible regions.

Body Category	Percentage of BSA
Easy	67.85
Difficult	21.10
Impossible	11.05
Total	100.00

▲ **Table 4.6** – ***BSA per Category*** – Shows the surface area of the body taken up by each of the three categories. These figures are calculated from data shown in Appendix 4.5

Data analysis

Three separate analyses were performed on either raw or transformed data. Data was edited on computer using *SPSS for windows* (version 12.0) and *Excel*. All statistical tests were two-tailed and were set at a level of significance of $P<0.05$. In all tests, degrees of freedom are 2 as all tests are looking for difference between the three body region categories. Each of the three statistical tests is described below including whether any transformations and refinements of data were necessary.

Analysis 1 – Chi-squared test

The test described in analysis 1 is the same as that for Pérez and Veà Baró (1999, page 231) entitled "Accessibility of autogrooming and "overall" distribution of allogrooming over the body surface". This analysis applies the chi-squared test to calculate an approximate P-value from percentage data. As stated by Pérez and Veà Baró (1999) this use of percentages carries a statistical error in "infringing on certain distributional assumptions" (page 231). There are two faults in the use of percentages, one more serious than the other. The less serious error results from the chi-squared test inferring a level of statistical power. In the case of percentages, this can only be accurate when the sample size equals 100 (percent ≈ frequency ≈ 100). If the sample size used is over 100 the calculated *P*-value, using percentages, will be less significant than the true *P*-value calculated using frequencies, and if the dataset is smaller than 100 samples, the *P*-value will be more significant than the real value.

The greatest infringement on statistical power in the chi-square test is of independence. When using percentages, data cannot be interpreted to be independent. Percentage data must by definition total 100. Therefore if the percentage of grooming in one of the categories changed (went up or down in total) one or more of the other categories must adjust accordingly so that the overall total still equals 100. By this rule, percentage data cannot be considered to be independent and is therefore not strictly suitable for use in this chi-square test. Statistical infringements will be discussed further in chapter 6. The use of percentages in a chi-square is repeated here for comparison with the results of Pérez and

Veà Baró (1999). Because of these statistical infringements, it is essential to retest the data with more appropriate tests (described in analysis 2 and 3).

The data were analysed by hand after refining the dataset using *Excel* and *SPSS*. The expected value of the chi-square test is based on the null hypothesis, which predicts that grooming will be distributed evenly over the body surface. The expected value for each category, therefore, is the percentage of BSA taken up by that category (as shown in table 4.6.) By using surface area as the expected value, the test automatically corrects for the differences between the BSA of each category. The results presented in Chapter 5 include the complete dataset in the analysis; therefore all grooming dyads are used. The dataset is refined again in further analyses to firstly eliminate variation within bouts and then also to examine whether individual variation may have affected the result. This was done by removal of specific data subsets if it was deemed there were invalid. The data subsets that were removed are identified in the results section.

Analysis 2 – Chi-squared test, frequency data

Because the chi-squared test is more suited to frequency data, the raw duration data was recalculated as point-sampling data, post-collection. The data collection method of recording exact start times and complete durations to the nearest second allows for the data to be recalculated into point-samples similar to if it had been done in the field (for a description of standard point-sampling see Martin and Bateson, 1993). Using a point-sampling interval of 15 seconds, the data was transformed into frequencies. To obtain an accurate representation of the duration data, 15 second intervals were marked on the minute (0:00) the quarter (0:15) the half (0:30) the three quarter (0:45) and back to the minute (1:00).

IDfc	IDp	ST	E	D	I
133	141	12:22:48	25	73	210
			64	25	50
				27	69
				15	

▲**Table 4.7a** – ***Raw duration data*** – This table shows an example of the raw data as it was collected, measured in seconds for each of the three body categories

IDfc	IDp	ST	E	D	I
133	141	12:22:48	|	𝍸	𝍸𝍸 ||||
			𝍸	|	||||
				|	𝍸
				|	
Totals			6	8	18

▲ **Table 4.7b** – ***Point-sample data*** – This table shows how duration data (table4.7a) is converted to frequency data using point-sampling at 15 second intervals

The data was converted by hand (an example of the conversion procedure is shown in table 4.7). From the start time, the duration of the top left hand cell (easy column) is added and the number of quarter-minutes (points) is sampled as frequencies. The remaining time is added onto the next column (difficult) on the same row and the process is repeated. Any left over time from the impossible column is then added to the easy column on the row below and continued until the maximum number of point-samples has been recorded. The frequency data will then be applied in the chi-square test in the same way as that for percentage analysis. Using the BSA of each body category type, SPSS will be able to calculate an expected frequency for all individual grooming bouts.

It has been argued that statistical infringements are being made in ethology even when using frequency data in the chi-square test. This is due to a lack of independence between samples when data was collected, not in the application of the test itself. If samples are made too close together the observations cannot be classed as independent because an animal being observed has not been given a likely time period to change activity. The accuracy of the test is lost if data is continuous, which is often the case in behavioural data collection. If there were a lack of independence between observations this would result in an altered chi-square value and either false acceptance or false rejection of the null hypothesis (Kramer and Schmidhammer, 1992). This ignorance is a notable infringement in this study, as individuals groomed multiple regions in one grooming bout. Kramer and Schmidhammer (1992) therefore recommend that ANOVA-style tests should be applied in such cases, as the non-parametric one-way ANOVA and associated tests have fewer assumptions and are more easily satisfied. By this justification, the data will also be analysed using the Friedman's test.

Analysis 3 – Friedman's test

Known as the Friedman's two-way analysis of variance by ranks, this non-parametric test applies a rank system to dependent data in k matched samples. The value k stands for the number of categories (variables) being compared across the rows (samples) of data (Siegel and Castellan, 1988). By comparing across rows, this test will analyse whether the data for each of the three variables, Easy, Difficult and Impossible, are the same or vary beyond that of chance. The Null Hypothesis of the test states that there will be no difference in the distribution of the ranks assigned to each category (i.e. that E, D and I will each have a similar distribution of the rank scores, in this case 1, 2 or 3). Post-hoc analysis is also necessary to interpret the difference between individual pairs of values. This post-hoc analysis will suggest between which of the variables the differences occur. The procedures for post-hoc analysis are described on pages 180-181 of Siegel and Castellan (1988).

-5-

Results

Descriptive statistics

Two statistical tests are performed in this analysis. The raw data are presented in table 5.1 showing the alloG and autoG durations for each adult female. Data are presented as totals for each season (S'02 and A'03). Data for alloG are presented as given and received grooming for each focal female. No data have been removed from this table, so it includes grooming bouts and sessions for adult-adult dyads, adult-juvenile dyads and adult-infant dyads and completed and incomplete bouts (for focal female only dyads see appendix 5.1). As males were never present on the Female Island, no adult-female-adult-male dyads were recorded. This table does not identify grooming partners of the focal female.

S'02	AlloG Given (seconds)				AlloG Received (seconds)				AutoG (seconds)			
	E	D	I	Total	E	D	I	Total	E	D	I	Total
Sarah	635	933	823	2391	896	992	953	2841	12	0	0	12
Silke	0	168	117	285	88	489	475	1052	0	0	0	0
Franziska	1312	2134	1717	5163	156	301	492	949	11	0	0	11
Sunny	12	108	29	149	96	453	536	1085	166	0	0	166
Sita	167	493	247	907	28	152	162	342	278	0	0	278
	2126	3836	2933	**8895**	1264	2387	2618	**6269**	467	0	0	**467**

A'03	AlloG Given				AlloG Received				AutoG			
	E	D	I	Total	E	D	I	Total	E	D	I	Total
Sarah	320	915	889	2124	333	1419	2225	3977	293	281	26	600
Silke	77	191	116	384	0	108	43	151	82	28	0	110
Franziska	631	1398	917	2946	27	112	244	383	140	36	0	176
Sunny	0	46	0	46	75	548	1347	1970	17	71	0	88
Sita	46	634	644	1324	106	442	160	708	86	0	0	86
	1074	3184	2566	**6824**	541	2629	4019	**7189**	618	416	26	**1060**

▲ **Table 5.1** – ***Observed duration data*** – Data collected for alloG and autoG of the five females. Data are presented as given and received grooming for each female and are categorized by body region type: E = *Easy*, D = *Difficult*, and I = *Impossible*

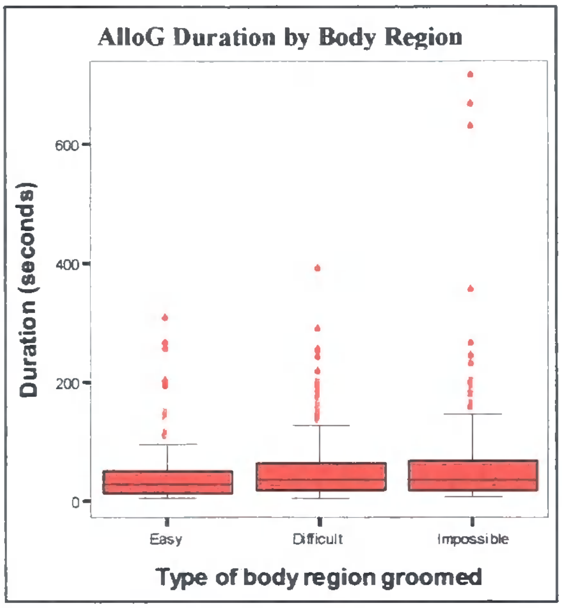
Groomers, non-groomers and groomees

There were a total of 392 grooming bouts recorded in the 153 hours of observations. This breaks down into 344 bouts of alloG (180 in 67.5 hours during S'02, 164 in 85.5 hours during A'03) and 48 bouts of autoG (8 during S'02, 40 during A'03). As a combined total the focal female spent a total of 14.08 hours out of sight (OoS); an average of 2.81 hours per female over both study periods. Correcting for this OoS data, 30704s of grooming (alloG and autoG) were recorded in 147.42 hours of observations. This means 5.79% of observation time was spent with the focal female engaged in some form of grooming behaviour. Table 5.2 shows the breakdown of observation times for each female and the respective grooming rate (GR, *measured in grooming seconds per hour*). GR varied between females and between time periods. The highest GR was from Franziska in S'02; grooming 538.50 seconds (8.98 minutes) every hour. The lowest GR was Silke in A'03; grooming for 37.96 seconds (0.63 minutes) every hour. *Note* that this does not consider when the adult females were involved in alloG sessions when other females were the focal subject. For example, the longest grooming bout in A'03 (735 seconds) was performed by Silke but when the female Sunny was the focal subject; this one grooming bout is almost 5 times greater than the entire amount of alloG performed by Silke when she was the focal female.

Individual	S'02				A'03				Total			
	OT (hr)	OoS (hr)	TR (hr)	GR (gs/hr)	OT	OoS	TR	GR	OT	OoS	TR	GR
Sarah	13.50	0.20	13.30	393.38	17.00	0.29	16.71	365.11	30.50	0.49	30.01	377.64
Silke	13.00	1.39	11.61	115.16	17.50	0.51	16.99	37.96	30.50	1.90	28.60	65.45
Franziska	14.00	2.65	11.35	538.50	18.00	0.50	17.50	200.29	32.00	3.15	28.85	327.24
Sunny	14.00	3.74	10.26	120.27	16.50	0.80	15.70	134.01	30.50	4.54	25.96	125.19
Sita	13.00	3.01	9.99	125.03	16.50	0.99	15.51	136.56	29.50	4.00	25.50	128.67
Average	13.50	2.20	11.30	**258.47**	17.10	0.61	16.49	**174.79**	30.60	2.82	27.78	**204.84**

▲ **Table 5.2** – ***Focal Grooming Rate*** – Shows number of hours of observations for each female (OT), the time the female spent out of sight (OoS), the time remaining (OT – OoS = TR) and grooming rate (GR) calculated by dividing the total number of seconds spent in grooming bouts (alloG+autoG) by TR. Units for GR are "grooming seconds per hour" (gs/hr). "Total" for each female is S'02+A'03. Number of grooming seconds is taken from table 5.1.

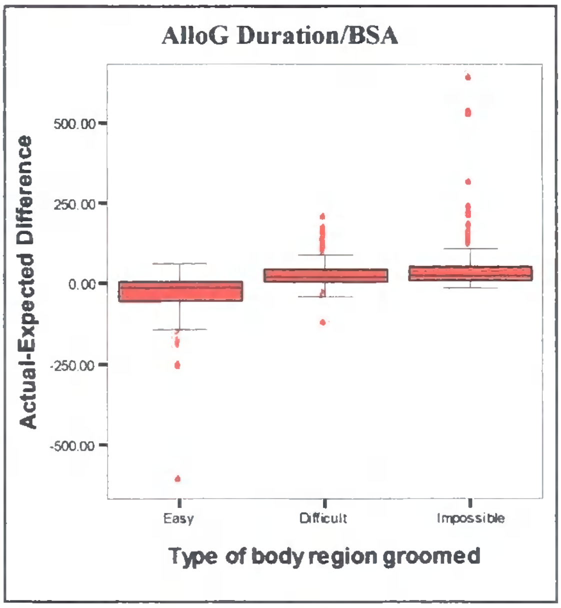
All individuals present on FI during the study period were involved in at least one single grooming bout with a focal female. Females, Sitty and Nube, were involved in fewest bouts (N=2 each). All individuals took part in grooming as either groomer or groomee, except for female juvenile, Sitty, and juvenile male, Felize, neither of which groomed any of the focal females. There was no recorded instance of an infant grooming an adult or juvenile, even in *ad libitum* sampling. In total, autoG was a fraction of the total grooming recorded, being only 12.2% of the number of grooming bouts recorded and making up only 5% of the total duration of grooming time. In S'02, the female Silke performed no autoG at all and the females Sarah and Franziska performed only 12 seconds and 11 seconds of autoG, respectively. If the complete dataset is considered for groomer and groomee as opposed to focal female and grooming partner, 48.2% of the total amount of alloG performed was performed by the female Franziska. Likewise 43.1% of the total alloG received was with Sarah as groomee.



▲ **Figure 5.i** – ***Duration data boxplot*** – The graphs shows the duration data for each of the three categories of body regions. The graph excludes zero values.

Boxplots

The boxplots presented represent the duration data separated by the three categories of body region type. Figure 5.i shows duration data (seconds) for each of the three category types and suggests little variation between different categories. Figure 5.ii shows the same dataset corrected for differences in BSA between the three categories, easy, difficult and impossible. When the data has been corrected for BSA, the graph shows that the easy regions receive less than expected (negative mean) and the difficult and impossible regions receive more than expected (positive mean). Likewise the interquartile ranges for difficult and impossible are positive, while easy is mostly negative. The error bars for each category suggest a lot of variation within categories, possibly caused by the very high/low outliers and extreme values.



▲ **Figure 5.ii** – ***Duration/BSA data boxplot*** – The graphs shows duration data corrected by the BSA separated body region category. Units are in seconds. The graph excludes zero values.

Chi-squared tests

The data for autoG were not suitable for analysis in the chi-square test due to a small sample size. The first set of calculations repeat the approach of Pérez and Veà Baró (1999) calculating chi-square from percentage data. The data in table 5.3 is presented as percentages for the amount of grooming directed to each category of body region types (easy, difficult and impossible) for each focal female, separated by grooming given and received for each period of observations. The data presented in this table is for completed bouts only. The raw data from table 5.1, for the entire dataset, is shown as percentages in appendix 5.1 and corresponds to the chi-squared calculation shown in table 5.4.

The first stage of analysis was the chi-squared test on the entire dataset (table 5.4) with no correction for any statistical inaccuracies or refinement of the raw data. All results for the initial chi-squared tests are highly significant (beyond a 0.001 threshold level for significance). If the assumption is followed that alloG may follow a set pattern of grooming over the body surface, from initiation to termination the use of incomplete bouts is invalid. The data was then corrected for incomplete bouts due to sampling procedures. All bouts that did not start and finish in the half hour focal sample were eliminated and the chi-square was repeated for the data of completed bouts only (percentages shown in table 5.3; chi-square calculation shown in table 5.5). Again, all results are significant beyond the 0.001 threshold. From here on, unless otherwise stated, only completed bouts will be used in all analyses.

S'02	AlloG Given (%)				AlloG Received (%)				AutoG (%)			
	E	D	I	Total	E	D	I	Total	E	D	I	Total
Sarah	27.64	41.93	30.43	100.00	30.77	36.47	32.76	100.00	100.00	0.00	0.00	100.00
Silke	0.00	58.95	41.05	100.00	8.99	42.49	48.52	100.00	-	-	-	-
Franziska	35.10	37.20	27.71	100.00	16.44	31.72	51.84	100.00	100.00	0.00	0.00	100.00
Sunny	8.05	72.48	19.46	100.00	8.85	41.75	49.40	100.00	100.00	0.00	0.00	100.00
Sita	21.44	46.85	31.71	100.00	3.04	42.23	54.73	100.00	100.00	0.00	0.00	100.00
	29.16	41.44	29.39	100.00	19.58	37.95	42.48	100.00	100.00	0.00	0.00	100.00

A'03	AlloG Given				AlloG Received				AutoG			
	E	D	I	Total	E	D	I	Total	E	D	I	Total
Sarah	15.60	37.94	46.46	100.00	8.89	35.26	55.85	100.00	42.94	52.23	4.83	100.00
Silke	12.33	67.40	20.26	100.00	0.00	71.52	28.48	100.00	74.55	25.45	0.00	100.00
Franziska	20.95	50.11	28.94	100.00	40.30	56.72	2.99	100.00	79.55	20.45	0.00	100.00
Sunny	0.00	100.00	0.00	100.00	3.81	27.82	68.38	100.00	19.32	80.68	0.00	100.00
Sita	1.45	49.18	49.37	100.00	14.97	62.43	22.60	100.00	100.00	0.00	0.00	100.00
	15.32	47.33	37.36	100.00	8.15	36.99	54.86	100.00	58.30	39.25	2.45	100.00

▲ **Table 5.3** – ***Percentage data (Complete bouts)*** – The duration data of completed bouts only, for each female, for each body region, is shown as percentages of total grooming. Data are presented as given and received grooming and are separated by season (S'02 and A'03). Note: Silke-S'02-AutoG: Silke did not autogroom at all in S'02

	Percentages				
	E	D	I	χ^2 Value	*P*-value
Grand T	17.15	41.25	41.59	141.43	<0.001
S'02 (g+r)	22.36	41.04	36.61	108.45	<0.001
A'03 (g+r)	11.53	41.48	46.99	183.36	<0.001
S'02 Giv	23.90	43.13	32.97	94.91	<0.001
S'02 Rec	20.16	38.08	41.76	132.53	<0.001
A'03 Giv	15.74	46.66	37.60	134.79	<0.001
A'03 Rec	7.53	36.57	55.90	247.05	<0.001

◄ **Table 5.4** – ***Chi-squared calculation –Whole dataset*** – No raw data has been eliminated in this chi-square analysis Giv = Allogrooming given, Rec = Allogrooming received. Degrees of freedom for all test is 2.

	Percentages				
	E	D	I	χ^2 Value	*P*-value
Grand T	18.24	40.79	40.97	133.08	<0.001
S'02 (g+r)	24.73	39.83	35.44	97.86	<0.001
A'03 (g+r)	11.48	41.79	46.73	182.36	<0.001
S'02 Giv	29.16	41.44	29.39	67.38	<0.001
S'02 Rec	19.58	37.95	42.48	131.19	<0.001
A'03 Giv	15.32	47.33	37.36	135.90	<0.001
A'03 Rec	8.15	36.99	54.86	238.22	<0.001

◄ **Table 5.5** – ***Chi-squared calculation – Completed bouts*** – Any bout where the entire bout was not recorded during the focal sample has been eliminated. Degrees of freedom for all tests are 2.

	Percentages				
	E	D	I	χ^2 Value	*P*-value
Grand T	20.93	40.92	38.16	117.56	<0.001
S'02 (g+r)	25.82	39.33	34.85	118.33	<0.001
A'03 (g+r)	14.30	43.07	42.63	155.38	<0.001
S'02 Giv	30.41	40.69	28.90	67.68	<0.001
S'02 Rec	20.44	37.72	41.84	132.03	<0.001
A'03 Giv	18.53	46.40	35.07	118.40	<0.001
A'03 Rec	9.86	39.58	50.56	207.04	<0.001

◄ **Table 5.6** – ***Chi-squared calculation – Valid females***– If any of the three regions for any female totalled less than 5% of her overall total for either given or received alloG this data was eliminated from the analysis. There were 8 data subsets eliminated. Degrees of freedom for all tests are 2.

	Percentages				
	E	D	I	χ^2 Value	*P*-value
S'02 Giv-	21.81	45.61	32.58	101.66	<0.001
Fran S'02 Given AlloG	35.10	37.20	27.21	51.72	<0.001

◄ **Table 5.7** – ***Chi-squared calculation – S'02 Given minus*** – Silke is eliminated from the analysis of S'02 given alloG because her dataset is invalid. Franziska's total for given grooming in S'02 totals more than 58% of all focal female given grooming, so is eliminated to test whether her dataset is biasing the result. The calculation for Franziska alone is also shown. Degrees of freedom for all tests are 2.

A further refinement of the dataset was used to test whether subsets of the data biased the results. Firstly, any female that significantly ignored any category (S'02/A'03, given/received) was identified as this would exaggerate the result and can be confounded by small sample size. If any individual female had one category (E, D or I) that fell below 5% of her total alloG for either given or received grooming in either season this subset of data was eliminated (see results in table 5.6). All results remained significant (<0.001) when only valid datasets were used. In all cases there was little effect in removing the invalid data subsets. Those datasets that were eliminated included:

- *Silke – S'02 – Given Grooming*
- *Sita – S'02 – Received Grooming*
- *Sunny – A'03 – Given Grooming*
- *Sita – A'03 – Given Grooming*
- *Franziska – A'03 – Received Grooming*
- *Silke – A'03 – Received Grooming*
- *Sunny – A'03 – Received Grooming*

When data was corrected for only completed bouts and invalid subsets were removed the data for *S'02 given grooming* was dominated by the female Franziska. In total, just over 58% of the grooming performed by focal females, when considering valid data, was made up of alloG by Franziska. When considering all females this specific subset of data was a significant proportion of the total grooming in that observation period. For this reason her dataset was eliminated from the total of *S'02 given grooming* and the chi-square was reanalysed separately for S'02 given grooming minus Franziska. The results are presented in table 5.7 and both show significance beyond the 0.001 threshold. The chi-squared test was also applied to the Franziska data subset to produce a P-value for the individual female as a comparison (also shown in table 5.7). Whilst both results are highly significant the only affect that the Franziska data subset has on the overall S'02 given grooming analysis is to reduce the level of significance as opposed to making it more significant. The results shown in table 5.6 and 5.7 suggest that the elimination of data for alloG in either study period is unwarranted in analysis 2 and 3 (below).

In all tests the resulting P-value has been presented as being more or less significant than the 0.001 threshold level. As an example of significance, the lowest chi-squared value is the result for Fran-S'02-Given AlloG in table 5.7 (chi-squared value is 51.72). The P-value calculated from the chi-squared distribution is 0.000000000005877 (5.877×10^{-12}). All test results are significant; supporting the idea that alloG is not directed evenly over the entire body surface and therefore rejects the null hypothesis. It is not possible from the chi-squared test to suggest which areas are preferred or neglected because the analysis only tests whether there is a significant difference between the observed and the expected values. From figure 5.ii, however, it can be inferred that this difference favours difficult and impossible regions, easy regions are neglected. This can be used in combination with the significant results of the chi-squared analysis.

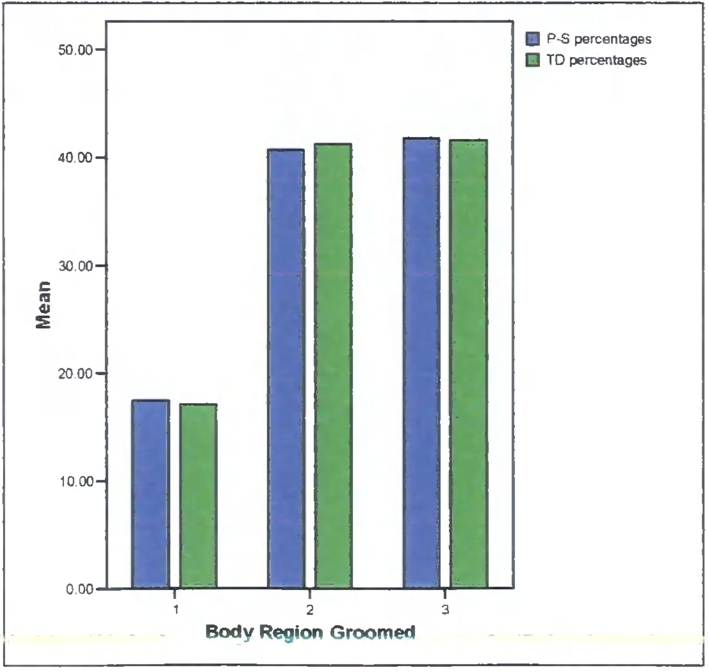
Frequencies

Although the test for chi-squared using percentages showed a clear result, the flouting of statistical assumptions, essential to the test, warrants retesting of the result to verify its significance. Converting the data to point-samples eliminates these errors by converting the timed durations to frequency data. Before applying the converted point sampling data in the chi-square test, the total frequency of each body region type was calculated as a percentage of the overall total and was compared to the percentages calculated from the duration data to see if the conversion had made any significant error (table 5.8); this was not found to be the case (figure 5.iii). This shows that the conversion of duration data to point-sample data is accurate, only if exact initiation times and duration times are recorded. The data presented in table 5.9 shows the results for completed bouts only. Expected frequencies are calculated based on the BSA of each body region category. By using the body surface areas as the expected values, each test calculates its own expected frequencies from the total of all categories combined. The expected frequencies and totals for each test are presented in the table. As stated above for the percentage-based chi-squared test, the lack of notable

	E	D	I	Total
Total Durations (s)	5005	12036	12136	29177
Percentages (TD)	17.15	41.25	41.59	100.00
Point-samples (f)	337	783	806	1926
Percentages (P-S)	17.50	40.70	41.80	100.00

▲ **Table 5.8** – ***Percentage comparison*** – Shows total data for both total durations (TD) of grooming time (seconds) and the converted point-sampling (P-S) data (frequencies). The percentages for the three body categories for both durations and frequencies are also given.

▼ **Figure 5.iii** – ***Percentage comparison graph*** –shows the mean percentages calculated from duration data compared to the mean percentages from point-sampling data for the three body categories.



	Observed (frequencies)			Expected (Frequencies)				Test results	
	E	D	I	E^E	D^E	I^E	Total	χ^2 Value	*P*-value
Grand T	291	681	693	1129.7	351.3	184.0	1665	2340.33	<0.001
S'02	192	333	305	563.2	175.1	91.7	830	882.92	<0.001
A'03	99	348	388	566.5	176.2	92.3	835	1501.27	<0.001
S'02 Giv	111	182	139	293.1	91.2	47.7	432	378.18	<0.001
S'02 Rec	81	151	166	270.0	84.0	44.0	398	524.38	<0.001
A'03 Giv	63	191	145	270.7	84.2	44.1	399	525.85	<0.001
A'03 Rec	36	157	243	295.8	92.0	48.2	436	1061.96	<0.001

▲ **Table 5.9** – ***Chi-squared calculation – Frequencies*** – Data for chi-squared using recalculated point sampling data. Only completed bouts are used in analysis. Data are presented as frequencies for each body category E, D and I. E^E, D^E and I^E are the expected frequencies based on BSA for each category type. Degrees of freedom for all tests are 2.

difference between each complimentary test from table 5.5 and 5.6 suggests any further refinement of the dataset is unwarranted. Therefore the only exclusion in frequency analysis is of the incomplete bouts. Table 5.9 shows that the observed frequencies are significantly different from the expected values in all tests. Again, referring to figure 5.ii this difference supports alloG directed to regions that cannot be autogroomed easily and neglect of regions that can be easily autogroomed.

If data from percentage-based chi-squared tests and frequency-based chi-squared tests are compared, both tests support alloG for hygiene with significance beyond the 0.001 threshold. What is worthy of note is that whilst percentages are supposed to be an inaccurate method of analysis it is the frequency data that produces results with the highest level of significance (the P-value calculated in *Excel* for a χ^2 value of 2340.33; df = 2, is given as 0; no similarity at all). Therefore if because the differing categories of percentage data are, by default, not independent any effect in this test as a result of using percentages was a reduction in significance and not to give a false positive; as suggested by Pérez and Veà Baró (1999).

Friedman's test analysis

Because the Friedman's test assumes the data is dependent a significant result (moving away from the null hypothesis) will support the argument that these data are different from one another due to factors other than their association or disassociation. The scores for ranks and level of significance are presented for each test in table 5.10. As with the chi-squared analysis the data have been edited for completed bouts and shown by observation period. Tests for raw, unedited data, completed bouts and corrected data are all presented in the table.

The result for data corrected by surface area, completed bouts only, shown on row Cc T (table 5.10) is highly significant beyond the level of 0.001. As can be seen from the rank scores and the chi-squared number, correcting for surface area has made the result found more significant. By separating the data into observation periods, both the rank scores and chi-squared values suggest there is little variation between grooming distributions over the body surface from one time period to another. The easy areas are always neglected (being closest to 1) and both the difficult and impossible regions have values over 2, so are preferred.

		Mean rank of categories			Test results	
	N	E	D	I	χ^2 Value	P-value
Grand T	344	1.65	2.27	2.08	79.716	<0.001
S'02	180	1.66	2.27	2.07	39.615	<0.001
A'03	164	1.64	2.26	2.09	40.303	<0.001
Com T	318	1.65	2.28	2.07	76.278	<0.001
Com S'02	165	1.65	2.28	2.08	39.112	<0.001
Com A'03	153	1.65	2.28	2.07	37.209	<0.001
Cc T	318	1.55	2.27	2.18	113.804	<0.001
Cc S'02	165	1.52	2.24	2.24	63.748	<0.001
Cc A'03	153	1.58	2.30	2.12	51.698	<0.001

▲ **Table 5.10** – ***Friedman's Test*** – Results of the Friedman test. Grand T is the total raw, unedited data; S'02 and A'03 are the same data separated by observation period; Com T is the total completed bouts only; Com S'02 and Com A'03 are the respective observation periods; Cc is completed bouts only corrected by the proportion of surface area for that category; Cc S'02 and Cc A'03 are the respective observation periods. N is the number of observations.

The Friedman's test does not, however, indicate that when there is a difference, between which pairs or groups of *k* variables the differences actually are. Using a further calculation (pages 180-181, Siegel and Castellan, 1988) post-hoc analysis can provide further information as to differences between the groups of data. The results of this post-hoc analysis are shown in table 5.11. Post-hoc analysis was performed for data in table 5.10. Calculations used total sum of ranked scores to calculate a critical difference, i.e. any pair showing a difference in rank scores greater than the critical difference can be said to be statistically different from each other beyond that of chance.

	Sum of Rank Scores				Difference between Rank Scores		
	E	D	I	*cd*	D-E	I-E	D-I
Grand T	567.5	781.0	715.5	62.79	213.5	148.0	65.5
S'02	299.0	408.5	372.5	45.42	109.5	73.5	36.0
A'03	269.0	371.0	344.0	43.36	102.0	75.0	27.0
Com T	524.5	725.0	658.5	60.37	200.5	134.0	66.5
Com S'02	271.5	375.5	343.0	43.49	104.0	71.5	32.5
Com A'03	252.5	349.0	316.5	41.88	96.5	64.0	32.5
Cc T	493.0	722.0	693.0	60.37	229.0	200.0	29.0
Cc S'02	251.0	369.5	369.5	43.49	118.5	118.5	0.0
Cc A'03	241.5	352.0	324.5	41.88	110.5	83.0	27.5

▲ **Table 5.11** – ***Post-hoc Analysis*** – Results for post-hoc calculations. The rows correspond to those used in table 5.10. Red boxes show differences between variables greater than the critical limit, blue shows those below the critical limit. Any rank difference above the critical limit can be considered to be statistically different. *cd* is the critical difference for each row

Table 5.11 shows that in all cases the difference between difficult and easy regions and that of impossible and easy regions are statistical different, with preference for difficult or impossible over easy regions. In most cases the results for difficult versus impossible show that there is no statistical difference for the distribution of ranks (and therefore grooming) given to these regions of the body. Two interesting points can be noted from this table. Firstly, in S'02, when the data is corrected for differences in body surface area, there is exactly zero difference between the two category variables. The most interesting result shown in table 5.11 is the effect of including body surface area as a correction in the calculation. When the grand total of either raw data or completed bouts is tested there is a statistically significant difference between the impossible and difficult regions with a preference for difficult regions. However, when the data is corrected for differences in BSA this result disappears. This result suggests that, overall, difficult and impossible regions receive the same amount of grooming per unit of surface area.

This result differs from that of the chi-squared tests because the calculation only examines the order of size for each variable and assigns a rank; no attention is paid to the magnitude of the variable. The chi-squared result increases in significance when the magnitudes of the test variables differ significantly. This has already been highlighted as a problem of the chi-squared test in this thesis because when one of the variables here increases in percentage by default one (or both of the others) must get smaller; thus exaggerating the difference, thus exaggerating the significance of the result. The following data and graphs are calculated to make each of the three variables more comparable. The amount of allogrooming for each body region category is corrected by the area of that specific category to present data for an equivalent unit of body surface (1%).

Grooming over the body surface

By correcting for differences in body surface area in both the chi-square test and the Friedman's tests, allogrooming has been shown to follow the pattern predicted by the hygienic function. The boxplots above show this pattern to be in favour of difficult and impossible regions while neglecting easy regions. It is important to reiterate that the categories easy, difficult and impossible were selected based on autoG capabilities. It

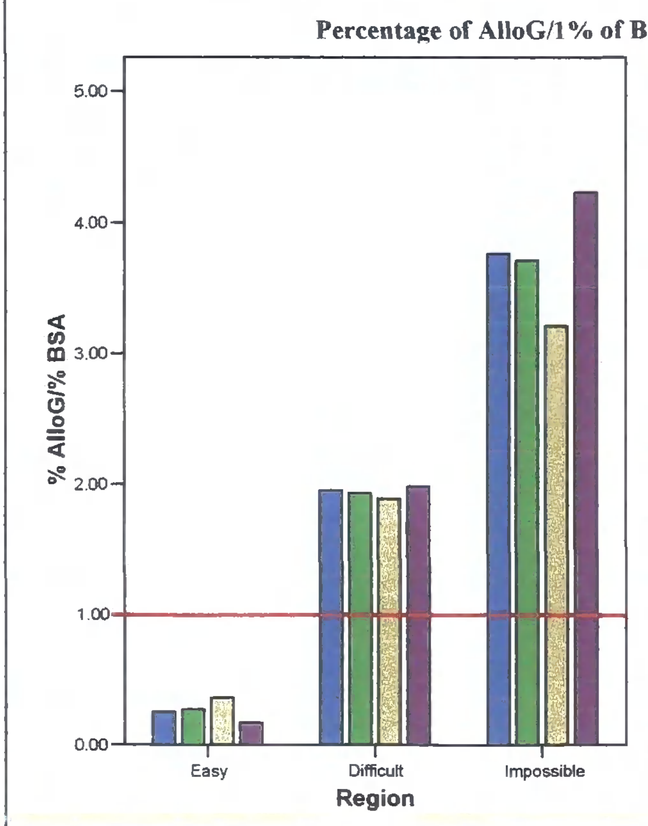
	Body Regions (%alloG/%BSA)		
Dataset	E	D	I
Grand T	0.25	1.95	3.76
Complete	0.27	1.93	3.71
S'02	0.36	1.89	3.21
A'03	0.17	1.98	4.23

▲ **Table 5.12** – ***% AlloG per 1% area*** – The percentage of alloG to a body category divided by the percentage of the BSA taken up by that category. By reducing the area to 1% of BSA in each category the values can be directly compared across rows. "Grand T" is all data with no editing. "Complete" shows the result for complete bouts only. S'02 and A'03 show separate results for complete bouts only separated by the two observation periods.

is important because it can be argued that for an animal to alloG another all regions are equally easy to get at (see and reach). Therefore if alloG was determined solely by regions accessible to alloG there should be no arguable difference. The pattern observed, therefore, directly supports alloG for hygiene and importantly links alloG and autoG.

As further support to these results, a figure can be calculated to show the proportion of the total amount of alloG directed to 1% of the body surface for each of the three body categories. The calculation is done by dividing the percentage of alloG to each body category by the percentage of body surface area taken up by that category. If grooming were distributed evenly (thus supporting the null hypothesis) then 1% of alloG should be directed to 1% of the BSA. If any value is less than 1 this region is relatively neglected and a value higher than 1 suggests that the region receives more attention than is necessary. The result is a value that can be directly compared between the body categories because the area over which each value is supposedly spread is the same in all cases. Data for different analyses (grand total, completed bouts, etc) are likewise comparable because data are presented as percentages. Table 5.12 shows data for the grand total (all data), completed bouts only and the completed bouts separated by season (S'02 and A'03).

The results of this calculation support the observation that alloG is preferentially directed



◄ **Figure 5.iv** – *% AlloG/% BSA* – The bars show the trend of increasing amounts of alloG from easy regions to difficult to impossible regions. It can be seen from the graph that easy regions are neglected in alloG and both difficult and more so impossible regions receive more than is predicted in the null hypothesis. The red line shows the level at which grooming is distributed evenly over the body as predicted by the null hypothesis (1% of grooming directed to 1% of BSA). The four different colours represent the different datasets as presented in table 5.12

to difficult and impossible regions, whilst easy regions are neglected but it also gives us more information. Firstly, as there are three categories it gives us clear directionality, in that, alloG is directed to impossible regions more than to difficult regions, with easy regions being neglected. Figure 5.ix uses clustered bars to show the increase in alloG from easy regions to difficult to impossible in all cases. The blue bars (Entire dataset) and green bars (Completed bouts only) show that there is little difference between using completed bouts only and the entire dataset. The red line shows the null hypothesis, i.e. the point at which grooming is equal to surface area for each category.

-6-

Discussion and Conclusion: Allogrooming and Hygiene

Allogrooming, autogrooming and hygiene

With only implicit reference or total ignorance seemingly the trend in current literature on allogrooming in primates, the purpose of this study was to test the significance of the hygienic function of alloG in capuchin monkeys. It was believed that because autoG cannot be distributed evenly nor with the same efficiency over the body surface, alloG, should it serve a hygienic function, would be primarily directed to those regions of the body that cannot be autogroomed. This produced two general ideas for the patterns of alloG and autoG. Firstly, alloG and autoG (considered separately) should not be distributed evenly over the body surface and secondly, alloG should be directed to those regions that are not easily groomed during autoG sessions. These ideas resulted in the two hypotheses of this investigation (chapter 3). The hypotheses considered were 1. that autoG should be directed preferentially towards regions easy to autogroom, 2. that alloG will be more abundant at regions of the body difficult to autogroom.

These two hypotheses, should they be supported in the results, would show that the functions of alloG and autoG are the same and as highlighted in chapter 3, are therefore hygienic in nature. When considering the different functions of alloG, only hygienic alloG should produce the pattern of alloG predicted in this thesis. Therefore any significant results should be in support of the hygienic function of alloG. Due to a small sample size for data of autoG, it is not possible to answer both the hypotheses stated in chapter 3. The sample size for autoG was too small to analyse statistically. It is worth noting that, of the little autoG recorded, just over 71% was directed at the easy regions (68% BSA), 27% to the difficult regions (21% BSA) and 2% to the impossible regions (11% BSA). Whilst this is not a valid or testable data source, there is an apparent neglect of autoG for the impossible regions compared to the other regions.

Because limited data was collected, the results section shows only analyses for alloG. This is no great loss however. Hypothesis 2 (alloG pattern) was formulated as a result of the idea behind hypothesis 1 (autoG pattern). Therefore any support for hypothesis 2 supports, overall, a link between alloG and autoG because of hygiene. This fact, coupled with the idea that only hygiene would link alloG and autoG in the pattern described, gives support to the data presented. Whilst implying a link between alloG and autoG, a positive result for hypothesis 2 does not, however, infer any result for hypothesis 1. It is clear to see that from the results shown in chapter 5, there is very strong support for the hygienic function of alloG in this group of capuchin monkeys.

In all tests, including chi-square (frequency and percentage-based) tests and the Friedman's analysis, alloG is preferentially directed to regions difficult or impossible to autogroom effectively. The same interpretation is supported by the graphs shown in chapter 5. The level of significance in almost all tests is highly significant with all P-values lower than the 0.001 threshold level. This is a strong result with a large sample size of data. AlloG sample size totalled 344 alloG bouts over the entire study (autoG sample size totalled 48 bouts). It was stated in the results that, excluding OoS time, the focal females spent 30704 seconds (8.53 hours) of 147.42 observation hours in grooming behaviour (5.79% of study time). Further to this, 29177 seconds (8.10 hours) of this grooming time was alloG; meaning the adult female capuchins spent 5.49% of the study time involved in alloG as either groomer or groomee. These figures should not be interpreted as the amount of their daily activity spent alloG, because observations only lasted whilst females were outside on FI (09:00 to 17:30hrs).

AlloG is abundant in this group of capuchin monkeys and shows clear preference over the body surface. This result significantly supports the hypothesis that alloG still serves a hygienic function in capuchin monkeys. Whether other functions are also supported has not been rejected and it is not the opinion of the author to do so. The sole aim of this thesis was to establish the current position of hygiene due to its acceptance as the evolutionary origin of the behaviour. Following contrasting research by other authors on alloG in capuchins (O'Brien, 1993; Di Bitteti, 1997; Parr, 1997; Manson *et al.*, 1999) and autoG (Mason and Perry, 2000) further analyses and research are recommended to test functional hypotheses for the "more social" elements of grooming behaviour. The next part of this discussion highlights some of the considerations made during this study that may prove to be very important in further studies. The discussion will then finish with comparison between this thesis and other research on grooming in primates with respect to functional hypotheses. Also considered are some of the author's personal points and ideas.

Statistical analysis

> *"Although the χ^2 test is more suitable to analyze frequency distributions than percentage distributions of accumulated time, we chose to apply it (though we were aware of infringing on certain statistical assumptions) because working with percentages, instead of frequencies, is associated with a reduction in the probability of obtaining significant differences [Barton, 1985]. This implies an increase in test power and thus, in the event that statistically significant differences were found, there would be no reason to question their value."*
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> Pérez and Veà Baró, 1999 (page 231)

The decision to repeat methods of Pérez and Veà Baró (1999) was made because of their own recommendation in favour of using percentages in a chi-squared test. After further research it has become clear that their interpretation of Barton (1985) was incorrect. The quotation they used from Barton (1985) states "the apparent violation of distributional assumptions underlying chi-square and t tests, through the use of percentage values – a procedure also likely to reduce the probability of obtaining significant values." Pérez and Veà Baró (1999) appear to have focused upon the tag-line in this statement as opposed to the warning being issued. Their interpretation took the fact that the procedure is likely to reduce obtaining significant values to mean a reduced likelihood of obtaining a false positive (a type two statistical error).

In the context of the original paper, Barton (1985) was actually suggesting a statistical weakness in the use of percentages and was emphasising the infringements on associated statistical assumptions of the chi-squared test more so than the reduction in significance. The reduced significance comes from the fact that, as stated in the method (Chapter 4), if the actual number of samples is greater than 100 any calculations are automatically transformed when using percentages (which by default total 100). The same effect would occur if using proportional data, which again would produce different results to a chi-square of either frequency or percentages. The infringements on assumptions however are more important.

The statistical error in using percentages is much more serious than a presumed benefit of reduced significance. The chi-squared test assumes that data follow a normal distribution and each category of data is independent. This assumption cannot possibly be met using either proportional data or percentages. As a result of this, it is the opinion of this author that chi-square tests should not be performed using percentage data (or proportional data). More appropriate tests should be used in cases when duration data is being rested instead of converting to percentages. For example, the Kruskall-Wallace analysis (recommended by Kramer and Schmidhammer, 1992) or the test used here, the Friedman's test (Siegel and Castellan, 1988). Alternatively it has been shown here that recalculating the data into frequencies after data collection produces little error in the data and still produces similar levels of significance in the results. An obvious alternative is to collect data differently in the first place. This would include collecting data as frequencies and distinguishing between all body regions during collection and then pooling data during analysis.

Surface structures

While examining the variation of alloG over the body surface, this investigation assumed that all body regions contain the same surface structure. The test hypothesis assumes that any preference or neglect to any body part is caused by an interaction with autoG behaviour. No consideration is made to variation over the body surface for differences in complexity of the surface. The body of a primate is not uniformly smooth; external structures and appendages are morphologically complex and distinct and other features like joints are complex because they create folds between two smooth parts of the body. Two main morphological differences in surface structures that differ between regions are hair length and anatomical differences.

▲ **Figure 6.i – Hair length** – The length of hair varies over the body surface. The coloured circles indicate regions with longest hair. Red=Tufts (adults only); Green=Flanks.

Hair growth is uneven over the body surface of most primate and mammalian species and there are also likely to be species-specific differences. *Cebus apella*, the tufted capuchin, gets its common name due to the long hair that grows either side of the forehead that produces two straight, "punk-like" tufts (ringed in red, figure 6.i). Other regions of the body (for example the lower flanks, ringed green in figure 6.i) also have distinctly longer hair growth while the remaining majority has short, neater hair. Different hair length for different regions could explain different durations of attention spent on each region. The suggestion here is that there is also a scale of difficulty for alloG as opposed to autoG. A contradictory argument is that long hair may inhibit the ability of parasites to become engorged or for debris to build up. This would produce a pattern of alloG the opposite to that hypothesised by long hair making it harder/longer to alloG. Because these theories contradict a simple observation and analysis would exclude either or both ideas.

As an example of anatomical variation, consider the head as one distinct part of the body. For the 'representative' monkey, used to calculate the percentage area for each body region, the head made up 5.63% of the total BSA. The head consists of the scalp (2.97% of total BSA) and the face (2.66% total BSA). The scalp is a smooth flat surface with little anatomical variation other than the ears. However, the face is a complex unit consisting of the majority of sensory organs. Eyes, nose and mouth are important morphological considerations, which may have an effect on grooming in two ways. Firstly, they are complex, so may be more difficult to groom and secondly, grooming of the important sensory organs may be slower than grooming over smoother skin surfaces because any damage to these organs would be detrimental to the groomee. Harrison (1963) for example, noted that alloP in birds was slower and more controlled around the eye of another bird compared to when preening other regions.

Posture

The test hypothesis of this thesis assumes that alloG can be directed with equal ease to all regions of another animal's body; this may not be strictly correct. When an animal grooms another, the areas of the groomee's body that are easiest to see and/or reach, for the groomer, are those parts that are closest. The posture of both groomer and groomee and the interaction thereof, are important factors in determining the regions that are easiest to allogroom. Barton (1983b) showed evidence of the importance of posture for grooming in primates. He showed alloG preferentially directed to the back region was also correlated with a dyad posture of "dorsal:ventral" (groomee:groomer). It is important to consider both groomer and groomee posture and then also how these postures interact with each other. It is likely that posture is species-specific, depending on species sociality (for example aversion to eye contact), method of locomotion, grooming style and/or habitat medium. Capuchins are quadrupedal, arboreal monkeys who groom manually with some oral grooming. This means that when dyads meet they are perching on branches and the groomee resting posture is lying longitudinally (normally on the ventral side).

On thin branches the position of groomee and groomer in relation to each other would most likely be ventral:ventral or dorsal:ventral as a result of the groomee lying longitudinally along the branches. The groomer would therefore be restricted in the regions of the groomee that can be reached. It was observed, however, in many alloG bouts that the groomer was able (and willing) to move around the body of the resting groomee to get to regions that could not be accessed from the original position. Animals often groomed at intersections of structures or at the point where the branch met the trunk. This allowed the groomer to sit side on to the groomee (flank:ventral) and also allowed the groomee to roll over or be rolled and manipulated; a behaviour seen often in the capuchin group.

The resting posture of the groomee (lying down) could possibly affect grooming pattern. A resting animal will have some of the body surface obscured by contact with the resting surface. The resting posture would result in the front (categorised easy) being inaccessible to alloG. This pattern of alloG over the body surface would, *de facto*, neglect the easy front region because the groomer would not be able to get at it. However, two points may reduce the importance of this effect. Firstly, the groomee was often seen to occupy relaxed postures, rolling over onto the flank or dorsal side of the body and exposing regions of the body for grooming. Secondly, as already mentioned, the groomer was often seen to manipulate limbs and to twist the groomee into alternative postures, to possibly access different regions of the body.

While posture could affect grooming pattern, it is equally likely that the reverse is also true, in that grooming pattern predicts posture. If grooming specific areas of the body has significant consequences, for whatever functional purpose, animals would benefit from assuming postures that allow easiest access to these specific regions. For example, in the case of allogrooming in horses (Feh and de Mazières, 1993), there is a clear link between a preferred grooming site, of the groomee's lower, dorsal neck region, and the physiological effect of reduced heart rate. Coupling this fact with the mutual nature of alloG in horses the result would be that the dyad should assume a posture that means both partners can access this important region of the neck easily and simultaneously (see figure 1 of Feh and de Mazières, 1993). If, in primates, alloG to the back region is important, as detailed by the hypothesis for the hygienic function for example, then the interaction of groomer and groomee posture should produce a formation that allows easiest access to this region, which may be "dorsal:ventral", as was found in Barton (1983b), or "flank:ventral" as was often observed (*ad libitum*) in this study.

Approach

Posture may affect grooming interaction, but first animals must come into contact to initiate grooming. Approach may therefore predict posture if animals, coming into proximity, must do so in a specific way. For example, in many species of primates it may be threatening to make eye-to-eye contact or approach an individual from the front. This would mean approaching from behind would predominate and result in contact (including grooming) being made in the "dorsal:ventral" position. Alternatively, when an individual approaches another and solicits grooming, unless the animal turns away after solicitation, grooming would be predominantly directed towards the face; because the animals are positioned "ventral:ventral".

In this capuchin group, there was no visible aversion from eye-to-eye contact and approach did not appear to be restricted. This may coincide with the interpretation that the strictness of dominance hierarchies in capuchins is less pronounced because of the importance of the complex interdependency of the social system (Izawa, 1980; Freese and Oppenheimer, 1981; Manson, 1999). It may also be a side effect of the captive situation, as competition is often considered to be lower in captivity (but see Aureli and de Waal, 1997). Based on the behaviour of the capuchin group observed, the idea of approach being a predictor of alloG pattern does not receive much emphasis or support here. Furthermore, as was argued against the importance of posture, once in grooming bouts, animals may turn, be turned or manipulated and the groomer is seen to move around the resting groomee. Hence, even if approach is restricted, this does not preclude a flexible grooming pattern.

Comparison with other platyrrhine studies

AlloG in platyrrhine species is considered to be infrequent with low grooming rates per hour over the course of the day (Dunbar, 1991; Ahumada, 1992; Sànchez-Villagra *et al.*, 1998), especially when compared to catarrhine species. Two problems with these assumptions are that firstly when Dunbar (1991) made his initial separation of grooming function in catarrhine and platyrrhine species, his paper suffered from having only a few platyrrhine studies with these studies focusing on few subject individuals. As is being found now in many platyrrhine species and highlighted by Sànchez-Villagra *et al.* (1998), platyrrhines not only vary considerably between individuals but also between different groups of the same species as well as between species and genera. As more information is acquired by research such as the current study, those cited above and in chapter 3, a more balanced image of alloG in platyrrhines is being formed which will allow better comparison with that of catarrhine species.

Sànchez-Villagra *et al.* (1998) cite studies on captive species as one problem for establishing a clear picture of grooming rates in platyrrhines. If this is true, then alloG rates for capuchin monkeys should be considered to be higher than those found in this study. Thus, it could be expected that wild capuchin monkeys should spend more than 5.94% of their daily activity in alloG interactions. Whilst accepting the point made above that these figures do not perhaps reflect daily grooming rates, compared to the figures for Ahumada (1992) these capuchin females groom much more regularly than wild spider monkeys (that autogroomed for less than 2.5% of their daily active time). This may result from species-specific differences. Spider monkeys and capuchins vary anatomically in that spider monkeys lack an opposable thumb and hence alloG and autoG are likely to be less effective in this species. Furthermore, the fission-fusion social structure of spider monkeys may mean that alloG is of minimal benefit to this species or that alloG serves a function only in specific contexts and situations, such as reintroductions and courtship. It may also be argued that the complex interdependency in capuchin monkeys may emphasise (or necessitate) a social role for alloG (Di Bitteti, 1997).

Lazaro-Perea *et al.* (2004) interestingly point out that they "observed allogrooming frequently and consistently in all study groups" (Lazaro-Perea *et al.*, 2004 page 627). The study of marmosets showed that 14% of observation time was spent involved in alloG, much higher than this capuchin study. This high grooming rate could likely result from observations being made on wild species but also that marmosets are cooperatively breeding animals so social cohesion is essential. There was a clear link with grooming and identity of groomers, with alpha males grooming more than all others and alpha (breeding) pairs grooming non-breeders more than vice-versa. This is the opposite of the Seyfarth model (1977) and can be explained by the suggestion that breeders are trading alloG to retain the presence of non-breeding helpers (Lazaro-Perea *et al.*, 2004). The overall amount of alloG in this platyrrhine study shows the behaviour is much more common than previously argued (Doyle, 1974; Goosen, 1987; Dunbar 1991); a result reflected by most platyrrhine studies.

Sànchez-Villagra *et al.* (1998) supported the "multiple functions" hypothesis with a study of both the social and hygienic functions of alloG. Their study recorded alloG durations, dyadic interactions, pre and post-grooming behaviour and body region preferences. This enabled them to consider many of the proposed functions of grooming. The map of body region preferences they produce (Sànchez-Villagra *et al.*, 1998, figure 1) shows a similar pattern of grooming preference to that found in the current study. The back was the preferred region for alloG and other regions preferred were mostly in the "difficult" category (for example the head). They noted no instance of alloG directed towards the ventrum (the front), which shows direct neglect of a region categorised as easy to autogroom. However, they found no link between alloG rates and body size (thought to be linked to alloG for hygiene; Sànchez-Villagra *et al.*, 1998; Dunbar, 1991) and were able to show large variation between groups and individuals, suggesting a social influence.

AutoG in howler monkeys was not observed by Sànchez-Villagra *et al.* (1998). This is important in this study as autoG rates were also very low here. Because Sànchez-Villagra *et al.* (1998) took samples of ectoparasite load on the bodies of captured subjects it is known that individuals were carrying parasites, so grooming for hygiene was required. The question therefore is why did no autoG occur if no alloG was directed towards the front of any individual? The answer may be in the observed result that ectoparasites were mainly confined to the beard region of subjects tested (Sànchez-Villagra *et al.*, 1998). This idea could also be tied to the point made in Chapter 3 that, as suggested by Sade (1966), alloG levels may be high enough to fulfil the majority, if not all, of the hygienic requirements for an individual.

The current study both reflects and contrasts with other studies, both wild and captive. AlloG rates were higher than for some other platyrrhine species but lower than in wild capuchin groups. AutoG reflected that of wild capuchins, but without empirical evidence to parasite loads in this group, it would be unwise to draw any parallels to this detail. What may be important to consider in future work is the social dynamic of the group in captivity. For example, absence of males during the day time made for an unusual social system, which, from having observed ad libitum the behaviour of the group once reunited with the males, is likely to have changed social interactions for the rest of the group, namely the adult females and especially those most dominant in the group. However, the amount and distribution of alloG observed in this group suggests both that hygiene is an important factor but similar to the other platyrrhine studies that there is something else (more socially mediated) going on.

Methods of data collection

For the purpose of testing the hygienic function of alloG, the standard practice has been to compare the pattern of alloG over the body with an assumed scale of autoG difficulty; thus directly test alloG against autoG (Hutchins and Barash, 1976; Barton, 1983a, b, 1985; Boccia, 1983; Pérez and Veà Baró, 1999). Alternatively in Tanaka and Takefushi (1993) the objects liberated from the pelage during alloG sessions were observed and recorded using video equipment. This second approach benefits from both repeatable playback and close-up observation of objects as they are removed. It also links a potential proximate cause (presence of contaminants) with a behaviour and function (alloG for hygiene). They further linked the consumption of removed parasites with insect-feeding behaviour. However, Tanaka and Takefushi (1993) point out themselves that not all debris/organisms removed from the pelage are consumed and they did not give data for the number of other grooming bouts that occurred without objects being consumed.

For further research to analyse the function(s) of alloG it may be necessary to incorporate more than one method for data collection, perhaps also importantly to link proximate cause and function together. I argue this because if, as assumed, alloG originated to serve a hygienic function, the pattern of grooming over the surface would have established itself and may be fixed, even though now it may be serving alternative functions to hygiene. This point is one of two "key issues" highlighted by Dunbar (1991) for researching the idea of links between proximate cause and function in alloG. The other key issue is that the regions of the body receiving attention during grooming may be of little relevance for the social functions, compared to whether an animal is simply involved in the interaction of alloG or not.

> "*... although social grooming involves the removal of debris from the skin and fur, this need not mean that hygiene is the sole function... it is not uncommon for behavioural or morphological features that evolved for one purpose to be 'captured'... by an entirely different functional system*"
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> "*... the sites used during grooming may not in themselves be relevant to the function of* social *grooming... the actual sites may be of marginal significance compared to the* fact *of grooming... the quantity of grooming may be of much greater significance to the animals than the mere removal of surface debris.*"
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> (Dunbar, 1991, page 122)

In the analysis of the social relationships instead of looking at proximate mechanisms or patterns over the body, research has focused on duration of grooming time. Taking the quote above from Dunbar (1991), it has been assumed that individuals that engage in more alloG are more sociable with each other compared to those animals not groomed. There is one problem with making statements based on assumptions and it is highly prevalent in alloG studies. Whenever an assumption is made there is likely to be a contradictory assumption on the same subject. Dunbar (1991) assumed that if alloG rates correlated with body size this would support the hygienic function of alloG. He assumed that bigger body size meant larger surface area and therefore more parasites or detritus. Sànchez-Villagra *et al.* (1998) followed the same assumption when testing alloG for hygiene in howler monkeys. In antelope (Hart *et al.*, 1992) the opposite idea was proposed, in that the smaller the individual (species) the more alloG would be required to minimise parasite load. This "body-size principle" (Hart *et al.*, 1992) dictated that smaller individuals could less afford parasites compared to larger individuals and supported this suggestion, noting that smaller animals would be greatly affected by the removal of large amounts of blood by engorging parasites and also the effect of parasite saliva in inhibiting developing individuals.

These two assumptions are the reverse of each other and are both supported by various authors. It is essential that such assumptions are tested before research is produced that puts these assumptions at the core of hypothetical arguments. There is a degree of this problem in the design of the current study, in that no figures for parasite load were taken and the objects removed were not recorded. By not examining objects removed (if any) the current study is again based on an assumption; the assumption that grooming pattern over the body is indicative of hygienic grooming. Before a method is chosen for collecting data in future research, the assumptions upon which the method is built must be satisfied. For example, examining autoG as well as alloG for body size could test which of the two assumptions above is correct. If autoG is proportional (or inversely proportional) to body size the interpretation could be made that body size is a predictor of hygiene. This could also be coupled with records of levels of parasite load over individual's bodies (as shown in Hart *et al.*, 1992). As well as assumptions, associations should be warily accepted. This means that just because two variables appear to occur together, it need not necessarily say that the two are directly related to each other. This is mistaking association with causation and is a major problem of working with animals where interpretations are essential to get any potential answers.

The difference in methodological approaches to data collection for exploring different functional explanations restricts comparative analysis of the functions themselves. Each function has produced different hypotheses for their effect on grooming behaviour and, as discussed in Chapter 3, these are not mutually exclusive; one hypothesis does not discount another. This has been further reinforced by the divergent methodological practices of primatologists collecting patterns of grooming for hygiene, heart rate responses for tension-reduction, pre and post- grooming behaviour for conflict resolution and reconciliation and duration times for testing social relationships. In order to strengthen research into alloG and the multiple functions it appears to serve, further research should examine the time period over which the proximate mechanisms that are related to each function can act.

There are two issues with this suggestion; one of time scale and one of associating proximate mechanisms with function. The issue of time has been raised previously by Schino *et al.* (1988) suggesting that different functions may operate over different periods of time and further that those operating over long time periods do not discount those operating in the short-term and vice-versa. The second issue considers the fact that an understanding of operating times for different functions cannot be achieved without an understanding of proximate causation. It is therefore essential that clear links between proximate triggers and functional outcomes of alloG behaviour are identified. As a further complication, just as different functions may be affected by different time periods, different proximate cues that could potentially trigger alloG for the same functional reason can also operate over different time periods. For example, in the case of hygiene, a short-term cue could be seeing another monkey attempting to autoG difficult to reach body regions, whereas, a long-term cue could be something similar to the grooming clock described for antelope species (Hart *et al.*, 1992) or simply that when animals are together after being separated (foraging, sleeping, moving) they should spend this social time alloG each other to minimise infestation and disease transmission.

If both the issues of timescale and proximate cause versus function are tackled together and advanced beyond current understanding, the establishment of a "multiple functions" hypothesis would be much closer. I am in full support of the suggestions from previous authors (Sade, 1966; Sparks, 1967; Alexander, 1974; Hutchins and Barash, 1976; Seyfarth, 1977, 1980; Barton, 1983a, b; Boccia, 1983; Dunbar and Sharman, 1984; Barton, 1985; Schino *et al.*, 1988; Dunbar, 1991; Sánchez-Villagra *et al.*, 1992; Di Bitteti, 1997; Perez and Veà, 2000; Lazaro-Perea, 2004) that alloG serves more than one function whether these are social and hygienic or not. Through studies of time-scale and proximate causes, it may become clear as to whether alloG is able to serve multiple functions at the same time (within one bout/session) or whether different alloG bouts/sessions communicate different intentions by the individuals involved.

Another feature of this highly complex idea is that some authors (for example Dunbar, 1991) discuss whether one function may operate to serve another within the same grooming bout (as opposed to both being served simultaneously by the act of grooming). For example, does reconciliation and tension-reduction occur separately, do reconciling individuals reduce the tension in the relationship or does grooming reduce tension in the relationship thus reconciling the individuals? With these ideas it is possible to contradict oneself with every next idea and perhaps requires greater consideration in future. This reinforces the suggestion of mistaking association with causation. One other study approach that may help is observations of different grooming styles and specifically observations of the context of the situations in which each style occurs.

Grooming style

While grooming style was not part of the investigation, during observations a number of different grooming styles were observed. The variety of different styles and the complexity of their use suggest more emphasis should be given to investigating the potential differences in terms of evolutionary and functional benefit of each grooming style. Boccia (1983) argued that scratching would have very little use in terms of hygiene. While she may be right, she notably failed to suggest what functional use it may serve instead. Furthermore, as scratching is not a common style, it may be that it serves to remove surface debris that can be simply brushed off. Again, the rapid and energetic alloG seen after aggressive confrontation (Sade, 1966; Sparks, 1967) would serve little use hygienically but can have high communicative value to function in reconciliation and aggression inhibition (Sade, 1966; Sparks, 1967; Schino *et al.*, 1988; Hemelrijk and Lutiejn, 1998; Aureli *et al.*, 1999, 2002; Castles et al., 1999; Manson and Perry, 2000; de Waal, 2000a).

I feel that grooming style is an area that deserves more research. It is likely that grooming style will give further insight into functional and proximate mechanisms. However, as with much of analysing alloG behaviour, there is complexity in this approach. The different grooming styles may serve one single function in different ways and alternatively one grooming style may serve more than one function. For example, picking out small bits of debris and scratching them off would be two grooming styles serving hygiene, while stroking may have thermoregulatory benefits and also hedonistic benefits that reduce tension and anxiety. By studying grooming pattern this may also help to establish the time period over which the different proximate mechanisms (and therefore functions) operate. With this in mind, it is important to reiterate points made in Chapter 2, that as different authors use different terminology for grooming styles, work needs to be done to standardise research methods (Schino, 2001).

The selfish groomer

This investigation has avoided, for the most part, suggesting whether it is the groomer or groomee that benefits from the alloG interaction. In Chapters 2 and 3 it was suggested that, to date, no idea has been proposed explicitly for a benefit to the groomer when considering alloG for hygiene. It is appropriate to say that alloG provides a hygienic benefit to the groomee because through the act of alloG the groomee is cleaned. Many authors have turned to ideas such as reciprocal altruism (Trivers, 1971) to explain how selfish individuals benefit from performing a behaviour that apparently only benefits the recipient. However, it is possible to suggest how a groomer may benefit from cleaning other individuals and, furthermore, link social interaction and proximity with the functional benefits afforded by hygienic grooming. The formulation of this idea is based on two quotations from Alexander (1974).

> "*There is no automatic or universal benefit to group living. Indeed, the opposite is true: there are automatic and universal detriments, namely, increased intensity of competition for resources, including mates, and increased likelihood of disease and parasite transmission.*"
>
> (page 328)
>
> "... *social behaviour evolves because it reduces the likelihood of disease and parasite transmission*"
>
> (page 330)
> Alexander (1974)

The first quotation is important because it highlights the fact that transmission of disease from other individuals is much quicker or easier in group-living animals because they are in closer proximity to one another. Therefore, following from the second quote, behaviours that are social in nature benefit both parties by cancelling out the negative effect of increased proximity. AlloG is a social behaviour by the definition of being an interaction between two individuals in close proximity. The idea of the *selfish groomer*, in terms of hygiene, is that it would increase an individual's fitness by cleaning a neighbouring group member, this is because it reduces the chance of parasite and disease transmission from the neighbour to the groomer. The groomer would maximise the efficiency of alloG others, i.e. limit duration of time wasted, by concentrating on those regions that cannot be groomed effectively by the neighbour whilst autoG. This part of the behaviour, therefore, benefits both groomer and groomee by minimising the duration of interactions.

This could be seen as active monitoring of the state of disease and parasite load in the group as a whole as a way of determining the potential risk for disease transmission. Alexander (1974) saw this as a 'group benefit' that benefits the individual. Any act that benefits the group as whole, by default, benefits any individual member of that group. While open to free-riders, the potential for social control (reciprocity, partner-choice) means cheating is likely to be minimised and connects sociality and hygiene together.

Furthermore, because the act of cleaning another, by this explanation, directly benefits the self, it is in the interest of the self to perform the behaviour. Spatial proximity is likely to be a mediator in partner-choice as those individuals who are most spatially close are those from whom disease and parasite transmission is most likely. Hence, the pattern of grooming distribution in alloG for hygiene, would directly match that predicted by kin selection, dominance and the Seyfarth model (Seyfarth, 1977). Because of the similarity in grooming distribution in this and other ideas, testing the principle of the selfish groomer may be too complicated to separate. Likewise the idea is put forward here as a hypothetical argument and should not be seen as an attempt to eliminate the importance of social functions in alloG.

Conclusion: Investigating allogrooming and hygiene

This study supports the hygienic function of alloG in capuchin monkeys with evidence of grooming pattern over the body surface. The results further suggest that hygiene is not the only contributing variable to alloG and autoG behaviour. Without testing this statistically, the variation over time, such as between observation periods and between individuals, suggests that alloG behaviour has other, perhaps more social, functions in addition to the hygienic function. This investigation fully supports the hygienic function of alloG and strongly suggests its inclusion in the “multiple function” hypothesis with as much emphasis as the other more social functions. This investigation has produced comparable results to that of Barton (1983a, b, 1985) Pérez and Veà Baró (1999) and Hutchins and Barash (1976). It also contradicts the results of Boccia (1983).

The divisions of impossible, difficult and easy for categories of body regions separated the body surface into a body pattern linked only to how easy it was to autogroom the region. This was dependent upon the variables of accessibility and visibility. This pattern is unlikely to be predicted by other variables and the results show that both of these variables are important. It may be important in future work to consider an analysis of individual regions for any preference over the body surface. The results of Barton (1983a, b, 1985) and Pérez and Veà Baró (1999) indicate that an analysis comparing individual body regions would have been beneficial. Furthermore, the work by these authors also suggests inclusion of other variables like posture (Barton, 1985) in future analyses to discount any potential bias.

This study has highlighted the importance of applying suitable statistical tests to data and indicates that a significant result may not always be a correct one. It is important to stress that analyses require mathematical verification to justify the use of any statistical test and not quotations from other authors. Future work on the functions of alloG is warranted but requires clear direction and stricter methodology both in data collection and analysis. By advancing current methodology, through linking proximate cause with functional outcome more, may be achieved towards understanding the complex nature of alloG interactions. To further the comment by Sparks (1967), it is important, for primatologists, now that the social functions of alloG are widely accepted, to perhaps return to this "less complex" hygienic function and explicitly assess the role of hygienic alloG for primates, in general, and begin assessing alloG as a multi-functioning behaviour. Including hygiene in a "multiple function" hypothesis or even as a tradable commodity may be a complex proposal but it is one that links sociality and hygiene firmly together.

> "*That parasite-controlling behavior should acquire a social role only illustrates the effects of group living upon the way that selection changes behavior.*"
>
> Alexander, 1974 (page 330)

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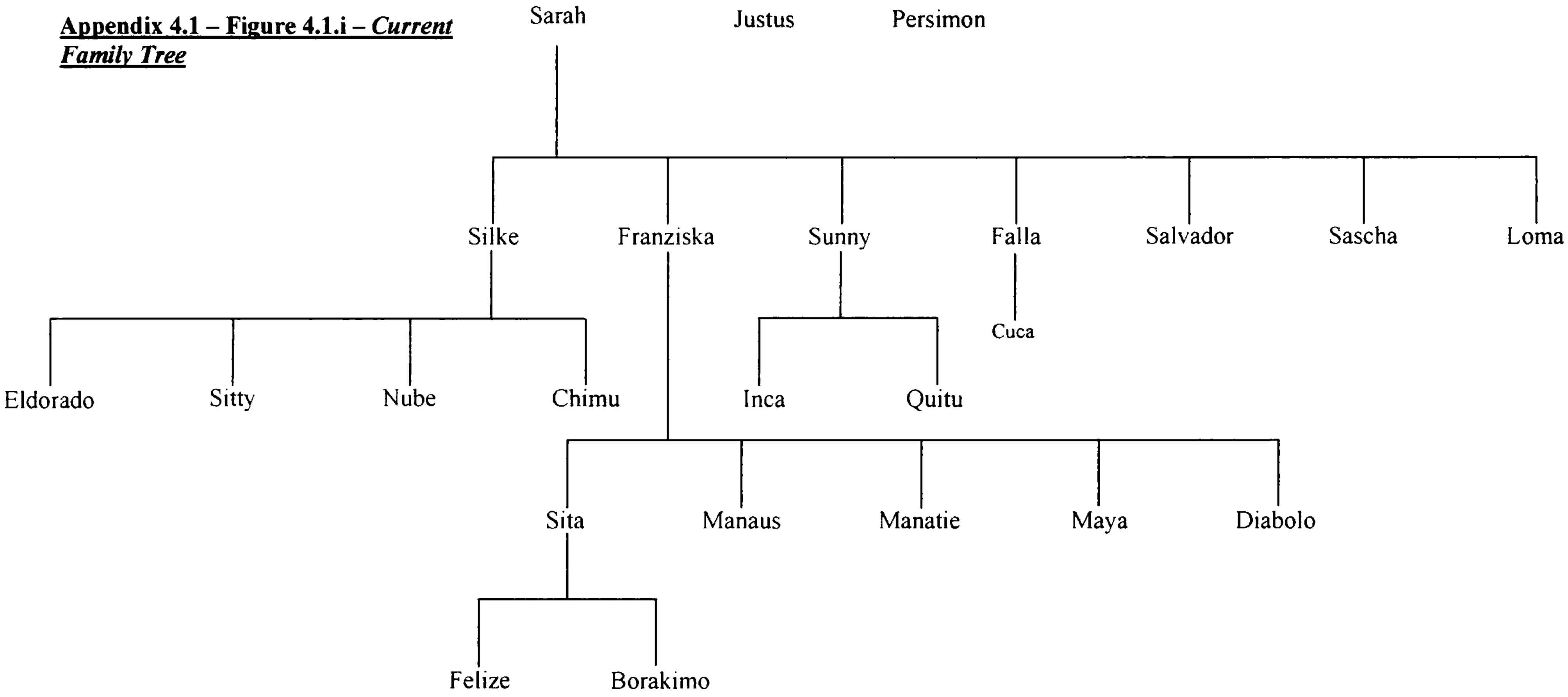
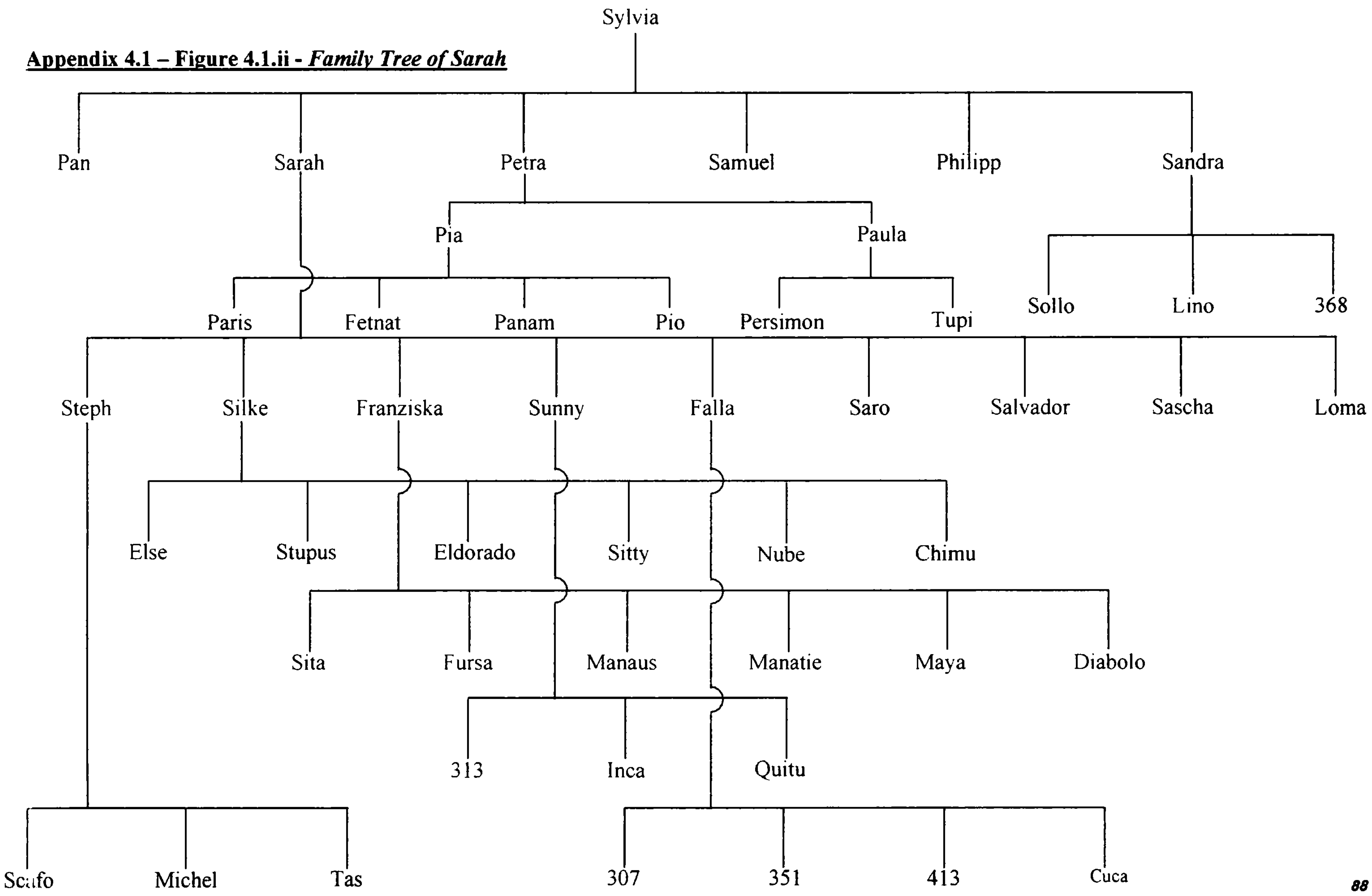
Appendix 4.1 – Figure 4.1.i – *Current Family Tree*

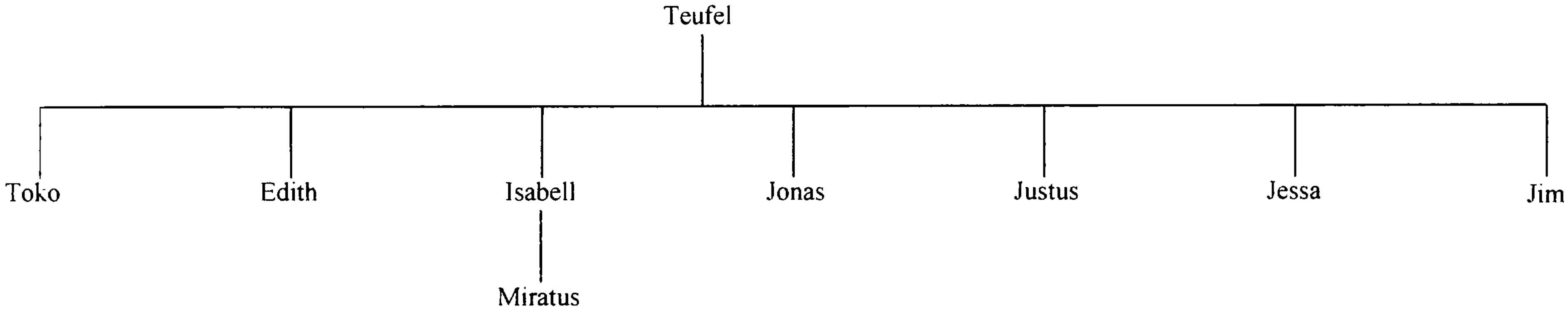


The other members of the group that were moved to LVDS have either died or been moved to other zoos around Europe. The family tree above represents those individuals in the group during the current study. *Note*: there is no scale of ages on any of these family trees. Blue represents a female and red represents a male. It is thought, Justus and Persimon are not directly related to any of the adult females so have not been linked to this tree. Paternity of the juveniles for Justus is unknown, the other breeding male (Justus' nephew), Miratus has been removed from the group. Persimon has been castrated so is not the father to any of the group's infants or juveniles. The two following family trees are for Sarah's and Justus' extended family respectively (data from Welker *et al.*, 1983).

Appendix 4.1 – Figure 4.1.ii - *Family Tree of Sarah*



Appendix 4.1 – Figure 4.1.iii –Family pedigree *of Justus*



Appendix 4.1 – *Group History*

The information described here provides a history of the founding group at Kassel University in the Institut für Zoologie und vergleichende Anatomie and is taken from two papers. The bulk of information comes from Welker *et al.* (1983) and Welker *et al.* (1987).

In 1974 the first group of animals arrived in the institute, which were imported from Paraguay. When the crates were opened it was discovered that 10 individuals died in transport and only two survived. These two were in very poor condition, covered in faeces and urine, soaking wet and had been fed extremely poor quality food. In 1975 11 animals were added to the group, 10 imported from the same area in South America with successful transportation and the other, a 17 year old male that had been given to the institute by a private owner who could no longer look after the animal. This animal, named Bubi, is thought to have been a different subspecies of *Cebus apella.* The other 12 were classified as *Cebus apella libidinosus paraguayanus* whilst Bubi was classified as *Cebus apella libidinosus libidinosus.*

> **Note:** By the classification in Rylands *et al.* (2000) the animals would have been reclassified as a different species to *apella*; first 13 would be reclassified as *Cebus libidinosus paraguayanus* (the Paraguayan tufted capuchin) and Bubi would be classified as *Cebus libidinosus libidinosus* (the bearded capuchin).

In 1977, six more individuals were added to the group that included a male called Don. The group now numbered 19 individuals, 10 females and 9 males. Bubi was directly dominant over Don (later a male called Erich would take over), however the female, Teufel (Justus' mother) was extremely attracted to Don instead of Bubi. The group was artificially divided up into three small groups (labelled A, B and C in "Tabelle 1" of Welker *et al.*, 1983). Through the research process involved in the studies at the research institute these smaller group became heavily mixed. Teufel who was originally in group B was moved into group C, which contained Sylvia (Sarah's mother). Teufel and Sylvia fought repeatedly until Teufel became dominant over Sylvia. Later Sylvia made an alliance with a third female and became dominant over Teufel. The two females remained competitive and established avoidance behaviour only coming into contact when either female was with an infant. Sylvia remained dominant in these periods of closer proximity. In the years following (and including 1975) 37 infants were born in the group up to 1984. The female, Sarah was born in the group on 25/05/1979 and the adult male Justus was born on 25/09/1981. Sarah's first infant was Stephanie who was born in Kassel on 22/06/1984 and was the 36 infant born in the group.

On 09/05/1998, 21 individuals were transferred from Kassel to LVDS. These included Sarah, Justus, Stephanie, Jim, Silke, Sandra, Pia, Miratus, Franziska, Paula, Sunny, Else, Sita, Falla, Paris, Sollo, Stupus, Scafo, Fursa, Parsimon and Saro.

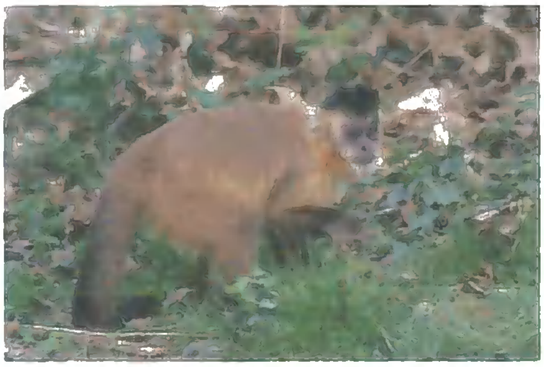
Including all recorded conceptions (live infants and stillborn foetus) the group has had 51 individuals (4 or which were stillborn foetuses).

Appendix 4.2 – *Focal Females*

▲ **Figure 4.2.i – Sarah**: (ID 133) Recognised by flattened tuft on the head pointing forward. Walks with outward-pointing hands and is missing the ends of her fingers on the left hand.

▲ **Figure 4.2.ii – Silke**: (ID 137) Short, neat tuft, straight across the front of the head. There is a scar running across her shoulder blades.

▲ **Figure 4.2.iii - *Franziska***: (ID 140) Tuft each side of the head. Very large bodied female.



▲ **Figure 4.2.iv – *Sunny***: (ID 143) Curled tufts curl inwards and are unequal in size and shape. Small narrow face with cross-eyed expression.

▲ **Figure 4.2.v – *Sita***: (ID 145) Young female with small pointy tufts either side of her head. The black cap comes down in a point to touch the black face.

Appendix 4.3 – *Island Territory*

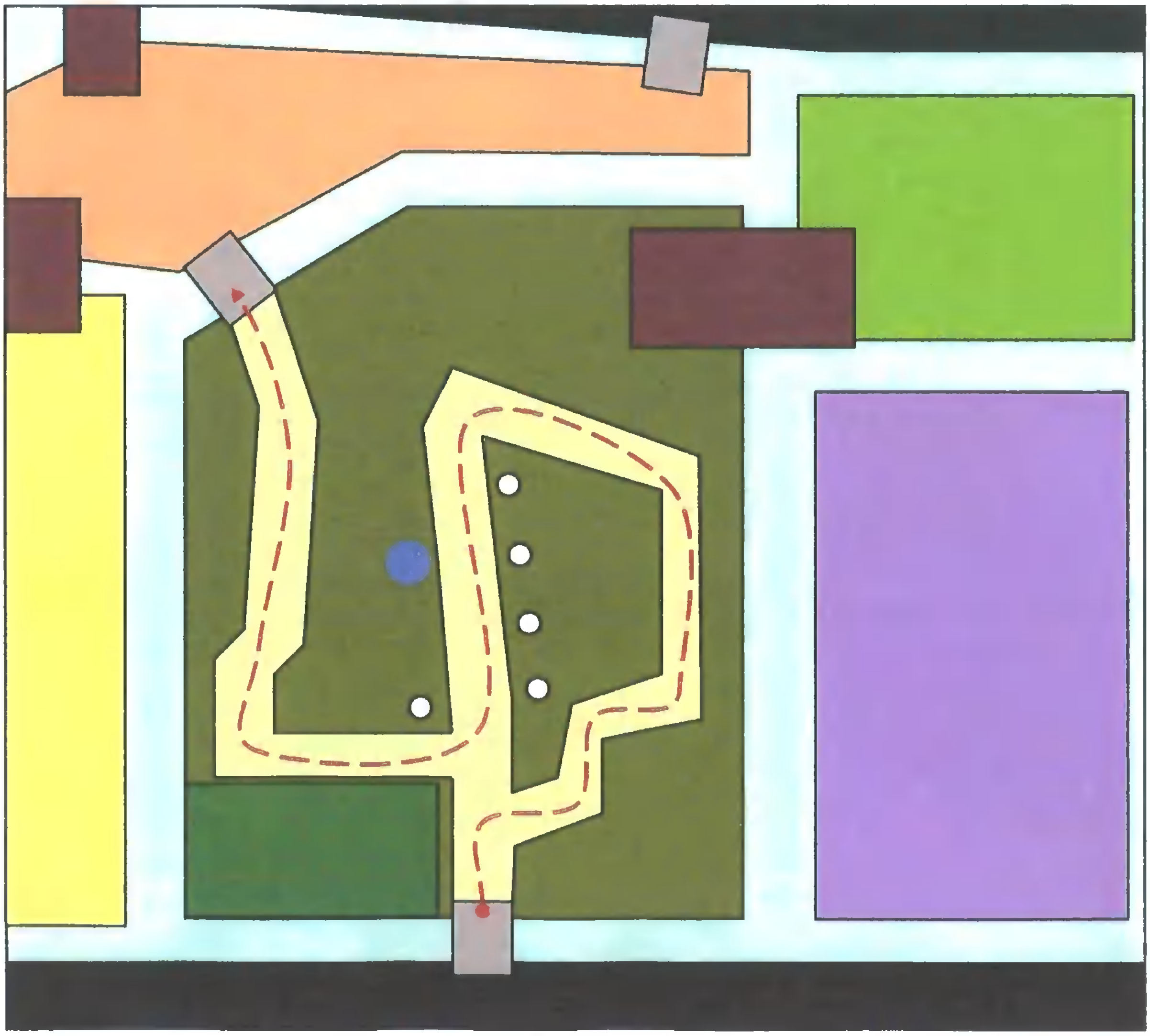
The map below shows a representative layout of the capuchin territory and surrounding lands. The overall size of FI is about 1200m^2. This diagram is not to scale.

Key:

🟩 Female Island (FI)
🟩 Male Island (MI)
🟫 Buildings (sleeping quarters)
🟩 Thick bushes (poor visibility)
🟨 Path through territory
– – – Direction of visitor route
🟪 Spider Monkey Island

🟨 Woolly Monkey Island
🟧 'Small platyrrhines' island
■ Non-animal territories
○ Feeding stations
□ Water
▩ Access bridges
🔵 Large tree containing tree-hole

▼ **Figure 4.3.i** – ***Island territory***



Appendix 4.4 – *Physical Characteristics*

The species used for surface area calculation of the "representative monkey" in the analysis were chosen based on similarity to an average adult capuchin monkey for the physical characteristics below. Data used included the white-crowned mangabey (*C. torquatus lunulatus*; Pérez and Veà Baró, 1999), the brown lemur (*E. fuluvus)*, the pygmy marmoset (*C. pygmaea)*, and the vervet monkey (*C. aethiops*; all from Barton, 1983a). The physical characteristics used were: body length, tail length and intermembral index; this data was taken from Rowe (1999).

Species	Body Length	Tail Length	Intermembral Index
Eulemur fulvus 40	450	525	72
Cebuella pygmaea 67	136	202	83.2
Cercopithecus aethiops 150	426	560	83
C. torquatus lunulatus 145	602	684	83
Cebus apella 94	419	431.5	82

▲ Table A4.4.1 – Physical characteristics chart – The data compares figures for each different species against the stats for an average capuchin adult. The number after each species name is the page number for the data taken from Rowe (1999) on that species.

Notes:

- *C. torquatus* has the common name, "white-collared mangabey" in Rowe (1999, page 145).
- *Cercopithecus aethiops* is called *Chlorocebus aethiops* in Rowe (1999, page 150).

Intermembral Index – is a ratio of forelimb length to hindlimb length and is indicative of the animal's locomotive form. Quoting from Rowe, (1999):

> "All primates are on a scale from 50 to 150… Generally an intermembral index between 50-69 indicates a species that is a vertical clinger and leaper; 69-105 indicates a species that is quadrupedal … on medium-sized forelimbs and hind limbs; and 105-150 indicates a species with long arms and shorter legs that are used for suspensory locomotion."

There was one animal rejected in this study from the study by Barton (1983a) this was the pig-tailed macaque (*Macaca nemestrina*), which was rejected because two of its physical characteristics were interpreted to differ significantly enough from that of *C. apella.* These were its intermembral index and tail length compared to body length. While the lemur, *E. fulvus,* may also have a differing intermembral index it is an arboreal quarupedal species with a similar body:tail length ratio; the ratio between tail length and body length of *M. nemestrina* is markedly different with a very short tail length and was interpreted to warrant its exclusion.

The physical characteristics from Rowe (1999) for *M. nemestrina* are given below:

Species	Body Length	Tail Length	Intermembral Index
Macaca nemestrina	515.5	191.5	92

Appendix 4.5 – *Body Surface Area (BSA)*

The data presented below was used to calculate the body surface area of the various sections of an average monkey, with similar intermembral index and body to tail length as a capuchin monkey. The data is taken from Barton (1983a) and Pérez and Veà Baró (1999). Table 4.51 shows the data for three species taken from Barton (1983a: brown lemur, *Eulemur fulvus*; Pygmy marmoset, *Cebuella pygmaea*; vervet monkey, *Cercopithecus aethiops*) and table 4.52 shows the data from Pérez and Veà Baró (1999) on the white-crowned mangabey, *Cercocebus torquatus lunulatus*. Each body part has been placed into one of the three categories used in this thesis; Barton (1983a) used only inaccessible and accessible to categorise the body regions and while Pérez and Veà Baró (1999) used three categories classification was not exactly the same as that used here. To show how the data was corrected after totalling the percentage data full decimal places (used when calculating the data in Mircosoft Excel®).

▼ **Table 4.5.1** – ***Body Surface Area*** (from Barton 1983a) – The values in the middle three columns are percentages of the total BSA taken up by each individual region of the body (see left hand column). The average for the three species is shown in the right hand column this was added to the data for *C. t. lunulatus* to produce an average monkey.

Body Region	Brown Lemur (%)	Pygmy Marmoset	Vervet	Average
Upper Back	3.8	3	4.4	3.733333
Middle Back	7.5	8.3	6.9	7.566667
Lower Back	5.1	4.7	3.9	4.566667
Impossible	**16.4**	**16**	**15.2**	**15.86667**
Head	2.7	5	3.2	3.633333
Face	2	2.4	2.3	2.233333
Neck	3.2	3	3	3.066667
Dorsal Brachium	1.8	4.45	1.4	2.55
Side	10.8	9.4	11.8	10.66667
IC/ SS	0.1	0.5	0.8	0.466667
Difficult	**20.6**	**24.75**	**22.5**	**22.61667**
Anterior Body	11.9	10.4	15.2	12.5
Antebrachium	3.6	3.9	2.8	3.433333
Ventral Brachium	1.8	4.45	1.4	2.55
Groin	0.5	0.8	3.2	1.5
Leg	9.9	9.9	8.7	9.5
Foot	3	3.7	6.2	4.3
Hand	1.9	2.1	1.1	1.7
Tail	20.8	14.6	12.1	15.83333
Thigh	9.2	9.3	11	9.833333
Easy	**62.6**	**59.15**	**61.7**	**61.15**

▼**Table 4.5.2** – ***Body Surface Area*** (from Pérez and Veà Baró, 1999) – The percentage of the total BSA taken up by each individual region of the body. The data was added to the average of the Data from Barton (1983a) to produce an average monkey, used in this thesis.

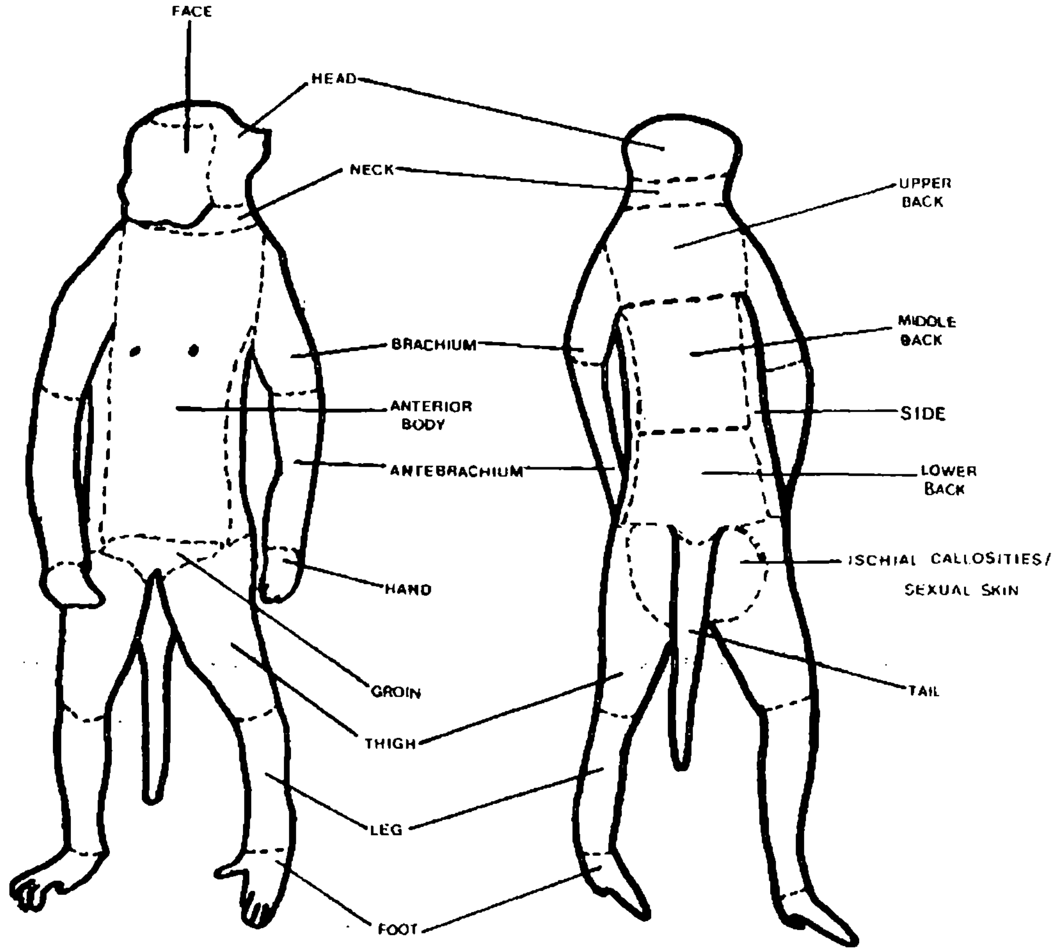
Body Region	Mangabey (%)
Upper Back	3.363
Lower Back	2.752
Impossible	**6.115**
Face	1.691
Head	3.703
Neck	1.471
Anogenital	1.251
Dorsal Arm	5.4995
Flank	5.835
Difficult	**19.451**
Ventral Arm	5.4995
Tail base	4.504
Chest	5.034
Distal tail	3.162
Belly	5.314
Forearm	9.538
Hand	4.624
Thigh	14.993
Leg	13.952
Foot	7.807
Easy	**74.4275**

▼ **Table 4.5.3** – *Average BSA* – The data from Barton (1983a) and Pérez and Veà Baró (1999) was used to calculate the average percentage BSA for the three categories used to classify the ease of grooming each region. The average did not total up to 100 (as using percentage data) the error was calculated by subtracting the total average from 100, the remaining difference (error) was divided by three and the result was then added to each category to total up to 100% of the BSA (right column).

	Mangabey	Barton's 4	Average	Corrected averages
Impossible	6.115	15.86666667	10.99083	**11.05303**
Difficult	19.451	22.61666667	21.03383	**21.09603**
Easy	74.4275	61.15	67.78875	**67.85094**
		Total	**99.81342**	**100**
		Error	0.186583	
		Error over 3	0.062194	

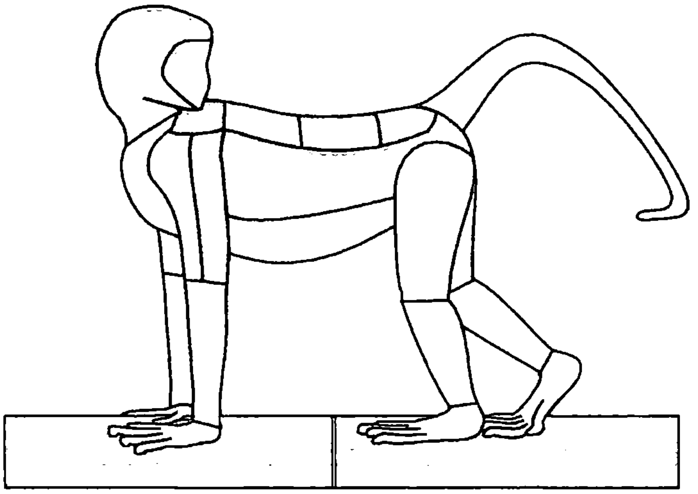
Appendix 4.6 – *Body Design - Barton*

▼ **Figure A4.6.i** – ***Body Design – from Barton (1983a)*** - Figure A4.61 is from Barton (1983a) and shows a representation of the divisions of the body surface area used calculating the "correction factor" of the differing sizes of body surface area contained within the two categories of "accessible" and "inaccessible". The image is reproduced here with permission from the author.



Appendix 4.6 – *Body design - Pérez and Veà Baró*

Figure A4.6.ii shows a reproduction of the figure used in Pérez and Veà Baró (1999) and the divisions over the body surface. The colour coding has been used to show the three category types for the current study. Note that there is an extra division in the back region for this image as the original (figure 1, Pérez and Veà Baró, 1999, page 228) was only divided into two regions.



Δ **Figure A4.6.ii** – ***Body Design quadruped*** – Shows the divisions used in this study for the body design drawn originally in Pérez and Veà Baró (1999). This image has been drawn for this thesis and is not a copy of that in the original paper.

Appendix 5.1 – *Total dataset as percentages*

The duration data used in the chi-squared tests was converted to percentages. Table A5.1 shows the entire dataset converted to percentages. This dataset was used in initial analyses before the data was refined to include only completed bouts (see table 5.3, Chapter 5). These data correspond to the results of the chi-squared tests shown in table 5.4, Chapter 5.

S'02	AlloG Given				AlloG Received				AutoG			
	E	D	I	Total	E	D	I	Total	E	D	I	Total
Sarah	26.56	39.02	34.42	100.00	31.54	34.92	33.54	100.00	100.00	0.00	0.00	100.00
Silke	0.00	58.95	41.05	100.00	8.37	46.48	45.15	100.00	-	-	-	-
Franziska	25.41	41.33	33.26	100.00	16.44	31.72	51.84	100.00	100.00	0.00	0.00	100.00
Sunny	8.05	72.48	19.46	100.00	8.85	41.75	49.40	100.00	100.00	0.00	0.00	100.00
Sita	18.41	54.36	27.23	100.00	8.19	44.44	47.37	100.00	100.00	0.00	0.00	100.00
	23.90	43.13	32.97	100.00	20.16	38.08	41.76	100.00	100.00	0.00	0.00	100.00

A'03	AlloG Given				AlloG Received				AutoG			
	E	D	I	Total	E	D	I	Total	E	D	I	Total
Sarah	15.07	43.08	41.85	100.00	8.37	35.68	55.95	100.00	48.83	46.83	4.33	100.00
Silke	20.05	49.74	30.21	100.00	0.00	71.52	28.48	100.00	74.55	25.45	0.00	100.00
Franziska	21.42	47.45	31.13	100.00	7.05	29.24	63.71	100.00	79.55	20.45	0.00	100.00
Sunny	0.00	100.00	0.00	100.00	3.81	27.82	68.38	100.00	19.32	80.68	0.00	100.00
Sita	3.47	47.89	48.64	100.00	14.97	62.43	22.60	100.00	100.00	0.00	0.00	100.00
	15.74	46.66	37.60	100.00	7.53	36.57	55.90	100.00	58.30	39.25	2.45	100.00

▲ **Table A5.1** – ***Percentage data – entire dataset*** – The duration data for each female for each body region is shown as percentages of total grooming. Data are presented as given and received AlloG and AutoG and are separated by season (S'02 and A'03). Note: that Silke did not autogroom herself in September so is not given a percentage of grooming in this case.

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