The Effects of Complexity, Choice and Control on the Behaviour and the Welfare of Captive Common Marmosets (*Callithrix jacchus*)

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Conferences Presentations

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Abstract

There are numerous guidelines recommending that captive primates live in complex environments in which they have the opportunity to make choices and the ability to control aspects of the environment, despite the lack of quantitative evidence to suggest these qualities improve welfare. Complexity, choice and control (the ‘Three Cs’) are inter-related and therefore it is complicated to separate their effects. The main aim of this thesis was to examine how the ‘Three Cs’ affect welfare, using the common marmoset (*Callithrix jacchus*) as a model. Behavioural measures and preference tests were used to determine the impact and significance of the ‘Three Cs’ on welfare. Experimental manipulations were natural (i.e. access to outside runs), or unnatural (e.g. pressing a button to control additional illumination). In a series of different studies, marmosets were moved to larger and more complex enclosures, were allowed to choose between indoor cages and outdoor complex enclosures and were able to control additional white light or coloured lights in their home enclosures. The results of these studies show that appropriate levels of each of the ‘Three Cs’ had a positive influence on the welfare of the marmosets, especially on youngsters. Although having control over light, and increased illumination itself improved welfare, providing a choice of access to outside runs (which were more complex and allowed the marmosets greater control over their activities) resulted in the greatest welfare improvement for marmosets of all ages. Loss of access, or control, did not appear to have a negative impact.

The marmosets were housed in pairs or in family groups, in the different studies. A cross-study comparison shows that the composition of the groups affected the behavioural response of adult marmosets to environmental enrichment. Unexpectedly, it was also found that, when housed in standard laboratory conditions, adult marmosets were more relaxed when housed in pairs than when housed with their offspring.

A secondary aim of the thesis was to quantify welfare indicators and activity budgets of common marmosets in a range of different social and physical contexts, and to compare this with the behaviour of wild marmosets, to increase our understanding of what is “normal” in captive situations. It is concluded that it is critical to sub-divide locomotion and inactivity into different levels to interpret these measures accurately. Levels of calm locomotion increased in enriched environments, while levels of relaxed inactivity and scent marking decreased. A number of recommendations for the care and housing of marmosets are made.

List of Colour Plates

Chapter 1

The Welfare of Captive Animals

"Experiments using animals have played a crucial role in the development of modern medical treatment, and they will continue to be necessary" (Botting & Morrison, 1997, p. 83). As a result, a huge number of nonhuman animals including nonhuman primates are being used every day in medical, psychological and biological research. Our basic duty as human beings is to ensure the welfare of those individuals who serve to fulfil our egocentric desires (Remfry, 1987; Reinhardt, 1997a). The overall objective of the present thesis is to seek more ways to improve the welfare of captive animals in general, and that of common marmosets (*Callithrix jacchus*) held in research facilities in particular.

1.1 THE SIGNIFICANCE OF THE WELFARE OF ANIMALS IN RESEARCH

The belief that animals (at least vertebrates) are sentient has raised the matter of animal welfare (Dawkins, 2006; Webster, 2006). The term 'animal welfare' "arose in society to express ethical concerns regarding the treatment of animals" and has been "adopted as a subject of scientific research and discussion" (Duncan & Fraser, 1997, p. 20). Accordingly, the fundamental motivation for the study and promotion of animal welfare is ethical (Tannenbaum, 1991). However, with the development of the study of animal welfare it has been shown that the welfare of the research animals is significant not only for ethical reasons, but also for the quality of the research (e.g. Coe et al., 1987; Baumans, 1997; Chance et al., 1997; Kempermann et al., 1997;

Morton, 2000; Weed & Raber, 2005; Kozozrvitskiy et al., 2005), and for economic reasons (e.g. reduced mortality rates, Manteca, 1998).

Good animal research is based on normal, healthy animals (unless the study is of a diseased animal). Scientific methods assume the absence of confounding factors and uncontrolled variables. However, it is clear that poor psychological well-being of the study animals or the presence of non-uniform or non-identified stressors might introduce unwanted variables into an experiment, resulting in increased variance and non-repeatable data (Poole, 1997; Weed & Raber, 2005). Furthermore, a decrease in the variation of the study animals would reduce the number of individuals used (Baumans, 1997).

1.2 THE DEFINITION OF ANIMAL WELFARE

The welfare of an animal refers to the state of the animal in relation to its environment (Broom, 1991a, 1996), and to the animal's quality of life (Duncan & Fraser, 1997). These factors involve various elements such as behavioural repertoire, physical health and condition, and mental health, and can be measured in the short and long term (Broom & Johnson, 1993). Broom (1988, 1991a, 1991b) also stressed that the welfare of an animal is a characteristic of the individual, and not something given to it, and hence, can be measured. However, Dawkins (1998) noted that it is clear that no single measure of welfare is sufficient on its own, but there is still disagreement regarding the significance of each measure and the link between them. Further, she argued that "there is a persistent tendency to believe that a good measure of welfare…is attainable if we only knew how to construct it" (p.307).

Several scientists stated that it is impossible to define the term ‘animal welfare’ as we might define a technical term, and instead we have to “set out the underlying values” (Duncan & Fraser, 1997, p. 20; Tannenbaum, 1991; Sandøe & Simonsen, 1992; Mason & Mendl, 1993). On the other hand, Broom (1988) defined the welfare of an individual as “its state as regards its attempts to cope with its environment” (p. 5). Webster (1994) argued that single sentence definitions such as Broom’s do not really advance our understanding, and then gave his own single sentence definition: “the welfare of an animal must be defined therefore not only by how it feels within a spectrum that ranges from suffering to pleasure but also by its ability to sustain physical and mental fitness and so preserve not only its future quality of life but also the survival of its genes” (Webster, 1994, p. 11). Whilst defining animal welfare is important, in order to improve research on animal welfare, definitions alone are not sufficient and we have to be more practical. Duncan and Fraser (1997; Fraser et al., 2000) presented three main approaches of conceptualising animal welfare: the subjective experience approach, the biological functioning approach, and the natural living approach. These three main schools of thought are discussed in further detail.

1.2.1 The subjective experience approach

Most people believe now that animals can experience subjective feelings such as pleasure and suffering, hence it is natural to use subjective experience when evaluating the treatment of animals (Duncan & Fraser, 1997). The animals’ capacity to experience suffering and happiness is central to the concern about animal welfare (e.g. Singer, 1990). Similarly, the subjective feelings of animals have been emphasized as a key component in the research of animal welfare (Dawkins, 1980, 1990, 1998; Duncan & Petherick, 1991; Duncan & Fraser, 1997), or even as the only thing that matters (Duncan, 2006). However, Barnard and Hurst (1996) argued that animal welfare will always be difficult to measure because it relies on the understanding of other species' perception and decision rules. In the absence of such fundamental understanding, it may be impossible to interpret behavioural, physiological, and clinical measures.

Methods to assess welfare according to the subjective experience approach

According to the 'subjective experience' approach, negative subjective states such as pain, fear, frustration, hunger, and thirst will reduce animal welfare, while positive experience such as comfort, contentment, and pleasure will improve animal welfare. However, there is still much research to be done in order to reach a sufficient understanding of these subjective feelings of animals (Duncan & Fraser, 1997). Several methods have been suggested in order to understand the feelings of animals. One of these methods is the study of animal preferences for different environmental conditions, and the strength of the animals' motivation to obtain or avoid certain features of the environment. The fundamental assumption of the research of preference tests is that animals will prefer environments in which they experience more comfort and pleasure and less negative emotional states (e.g. Broom, 1988; Cooper & Mason, 2000; Mendl, 2001; and see below). Another method which can provide information about animals' feelings towards environmental features or events is the anticipatory behaviour that animals perform in the gap between a given signal and the occurrence of a forthcoming event (Spruijt et al., 2001; van der Harst et al., 2003).

A different approach is to link the performance of abnormal behaviour as a symptom of some form of negative affective state. For instance, the performance of stereotyped behaviour by captive animals or the appearance of behavioural patterns out of context have been interpreted as an indicator of different types of negative affective state such as boredom and frustration (Wemelsfelder, 1990, 1993; Mench & Mason, 1997; Mason & Latham, 2004). However, it is important to point out that the presence of stereotyped behaviour is not necessarily an indicator of poor welfare, and may, for example, remain as ‘scars’ of previous negative experience (Mench & Mason, 1997; Mason & Latham, 2004). Further, careful observations of normal behaviour can provide us with a great deal of information about the animal’s preferences, requirements, dislikes, and the animal’s internal state, as behaviour is the first reaction of an animal to the environment (Mench, 1998b). Similarly, vocal signals can also provide information about the animal’s subjective experience (Mulligan et al., 1994; Weary & Fraser, 1995). Dantzer and Morméde (1983) suggested that the reactions of animals to environmental situations are expressed in hormonal and behavioural changes, and as these two classes of responses are closely related, both of them can be used in order to measure the animals’ subjective state.

Wemelsfelder (1997b, 2003) suggested that the assessment of ‘whole animal’ expressions allows us to describe emotional experience as a dynamic, fluid, multi-faceted process. Wemelsfelder and co-workers (2000) evaluated the welfare of captive pigs using categories of attentional style (e.g. enthusiastic, timid, curious, or bored) which provided (according to the authors) empirical access to the quality of the animal’s experience. One criticism of the above may be that qualitative assessment of the animal’s experience may be affected by the objective interpretation of the observer. However, studies have shown consistently high intra- and inter-observer reliability (Wemelsfelder, 1997b).

Objections to the subjective experience approach

The fundamental objection to the subjective experience approach (and even to the overall idea of animal welfare) is the view that nonhuman animals are not sentient. Dawkins (2006) described some scientific evidence to negate this view; however, she also stressed that the study of sentience (in both humans and other species) is one of the hardest problems in biology, and more research is needed. A more moderate objection to the subjective experience approach is that scientists are unable to evaluate the mental state of an animal as humans cannot really understand other species' perceptions (Curtis, 1985). However, Duncan (2006) argued that in order to assess the welfare of a captive animal, an indication of how positive or negative that animal is feeling would be necessary. Further, these indications would have to be indirect as "the feelings and emotions of animals, like the movement of subatomic particles, cannot be observed directly" (Duncan & Fraser, 1997, p. 23). In addition, new research methodologies may provide us with additional knowledge regarding different aspects of the subjective experience of nonhuman animals. For example, the study of animal cognition should help us to understand the animals' points of view, and therefore improve our understanding of animal welfare (Bekoff, 1994, 2000; Kirkwood & Hubrecht, 2001). Further, neurophysiological research has provided an insight into the similarities between the brain of human and nonhuman animals, and may therefore help to clarify what kind of feelings animals are likely to experience (Manteca, 1998).

1.2.2 The biological functioning approach

A second view is that the welfare of an animal is correlated to the biological functioning of the individual. According to this view, disease, injury, and malnutrition will be signs of reduced welfare of an animal, while high levels of growth and reproduction, ultimately high rates of longevity and biological fitness, and normal functioning of physiological and behavioural process will indicate good welfare (Duncan & Fraser, 1997). Different scientists have adopted the biological functioning approach for various reasons. For instance, Curtis (1985) argued that the assessment of welfare cannot include an evaluation of mental suffering, simply because scientists are unable to measure it. According to Curtis (1985) the evaluation of welfare should take into account available evidence such as physiological, immunological, behavioural, and anatomical indicators of stress and distress (although how to interpret these indicators must still be developed and refined). Two further reasons are given by Duncan and Fraser (1997) for the adoption of the biological functioning approach. First, scientists attach little or no importance to how an animal feels. Second, the organization of different indicators of welfare in a hierarchically ordered manner put the physiological needs in the highest position (Curtis, 1985).

Methods to assess welfare according to the biological functioning approach

It is relatively easy to evaluate animal welfare using the biological functioning approach. It is easier for example to indicate that an animal is in a poor physical state than that it is unhappy (Duncan & Fraser, 1997). Further, it is possible to measure biological functioning in the short and long term. Short term measurements will include, for example, behavioural indicators of pain, heart rate, body temperature, and levels of stress related hormones. Long term measurements will include, for instance, reproductive success, longevity, weight changes, measures of the functioning of the immune system, condition and quality of skin and coat, gait pattern, rate of growth and aging. (Novak & Drewsen, 1989; Broom & Johnson, 1993).

Many scientists who use the biological functioning approach to animal welfare have been greatly influenced by the concept of stress (Duncan & Fraser, 1997). For example, it has been suggested that “if an animal is suffering from stress, its well-being is jeopardized” (Moberg, 1985, p. 46). Moberg (1985) also argued that the pre-pathological state can be used as an indicator of stress and a risk for the animal’s well-being. However, it has been suggested that the term ‘stress’ is not suitable in relation to animal welfare for several reasons. First, the term ‘stress’ itself is not easy to define or to measure. Second, activity that is associated with stress may be pleasant or unpleasant. Alternatively, the term ‘distress’ was suggested as more suitable, as distress is always disagreeable, and it may be more appropriate and more specific to characterize welfare as the absence of distress (Selye, 1974; Novak & Drewsen, 1989). However, even the use of the term distress in association to welfare is problematic as it is possible to find a situation in which an animal might neither experience distress nor good welfare, for example a moderately bored monkey (Novak & Drewsen, 1989). Another way to link the biological functioning of an animal to welfare is by the fulfilment of the animal’s needs (for survival, health and comfort). It has been suggested that these needs differ in importance for the animal, and humans cannot easily assess the relative importance of the different needs (Duncan & Fraser, 1997). However, the more adequately the animal’s needs are met, the longer that animal may be expected to live (Duncan & Fraser, 1997).

Objections to the biological functioning approach

There are few objections to the biological functioning approach. However, in some cases the interpretation of biological functioning and its link to animal welfare are not clear. When the animal's immediate functioning is compromised there is likely to be little disagreement that the quality of the life of the animal is affected. However, the opposite is not always true; an animal can be healthy and still experience poor welfare. Therefore, the biological approach can provide only information concerning poor welfare, with fewer indicators of good welfare. In addition, the link between other aspects of functioning, such as growth rate, or levels of stress hormones is less obvious, and there is little consensus on the baseline that should be used in assessing such measures (Duncan & Fraser, 1997; Mench, 1993). Finally, different measures do not always co-vary, the significance of some measures is difficult to interpret, and sometimes a repeated study might yield different results, as a small change in the environmental conditions which might be imperceptible to humans, may play a significant role for animals (Mason & Mendl, 1993; Rushen, 1991, 2003).

1.2.3 The natural living approach

An alternative approach is that of 'nature knows best', which means that animals experience enhanced psychological functioning when they display the full behavioural repertoire shown by the same species under natural conditions, and that to promote the welfare of animals we should raise them in natural environments (Novak & Drewsen, 1989; Lindberg & Coe, 1995; Duncan & Fraser, 1997). The fundamental rationale behind this approach is that the species typical behaviour is what the animals have been programmed to do or to be (Morton, 2003). Shepherdson (1990) suggested that natural behaviour is desirable for two reasons. First, its performance indicates that the captive environment is providing similar characteristics to those found in the wild (e.g. complexity and control), and most animals have evolved the physiology and behaviours necessary to cope with their natural habitats. Second, natural behaviour is desirable because animals have 'behavioural needs' and an environment that does not cater for these needs may cause frustration and suffering (Hughes & Duncan, 1988).

Methods to assess welfare according to the natural living approach

The most common welfare assessment according to the natural living approach is the comparison of the behavioural repertoire of captive animals to that of wild counterparts; this comparison includes the actual display of a certain behavioural pattern, and the frequency and duration of its performance. Dawkins (1998) argued that there are no general rules to predict whether a given behavioural pattern *per se* is important for enhancing the welfare of captive animals. However, if one takes the moderate view to the natural living approach, then the measure of the preferences of an animal and its motivation to perform certain species typical behaviour in certain circumstances or to reach a specific feature of the animal's natural habitat would lead us to possibilities of better housing and management conditions in captivity. In this respect methodologies are similar to that of the subjective experience approach. Another method is to examine the probability that captive animals would survive in their natural habitat, shown by reintroduction to it (Novak & Suomi, 1988); however, the logistics and ethical considerations of this approach preclude its use in most cases.

Objections to the natural living approach

There are many objections to the view that captive animals should exhibit a full range of species typical behavioural repertoire. First, the phrase 'range of species typical behaviour' is vague and unspecified. It is unclear whether the exact frequency and duration of a specific behaviour should be considered (Novak & Drewsen, 1989). Second, if a full range of species typical behavioural repertoire is required in order to conclude good welfare, then in most populations of captive animals the welfare will be considered poor. Further, the composition of captive populations is often different from that of wild population because of space and/or other restrictions. For instance, when animals are housed in single sex groups, the performance of hetero-sexual behaviour patterns is prevented. Would the welfare of such animals always be considered poor as a consequence? Third, a strong objection to the natural view is that not all species typical behaviours are necessary for captive animals, and the absence of a particular behavioural pattern would not necessarily compromise animal welfare (Rosenblum, 1991; Veasey et al., 1996a, 1996b; Dawkins, 1998). Moreover, some natural behavioural patterns (e.g. infanticide, injurious aggression) may harm the welfare of animals in captivity (Novak & Drewsen, 1989) and would be considered as undesirable in captive environments. Poole (1996) suggested that animals experience severe and even fatal problems in nature, and their natural behaviour "most often represents a life and death struggle for survival" (p. 218). Therefore, the assumption that natural behaviour is an indicator for good welfare is unrealistic.

Furthermore, natural environments themselves are varied, and do not always offer the best quality of life for wild animals. Hence, the notion that if an element is present in the natural habitat it is desirable in captivity is not necessarily accurate. Besides, the natural environment of an animal from the human's point of view is often different from the animal's conception of this natural habitat (Rosenblum, 1991), and when designing an exhibit in the interest of aesthetic naturalism from an anthropomorphic perspective it may offer few behavioural opportunities to the animals (Shepherdson, 1998). In addition, many animals now live nearer to human settlements in the wild in habitats different to those in which they originally evolved. In many of these wild populations previously unseen behaviours, such as feeding from rubbish tips, may be observed. The performance of such behaviours, like the performance of new behaviours (or the same behaviours in different contexts) by captive populations, is not necessarily a sign of reduced welfare; instead it may indicate adaptation to the different environment, as animals will modify their behaviour to best fit their environment (Veasey et al., 1996b). Finally, captive animals may be eager to perform activities, such as learning a non-natural foraging task, which may be highly artificial but would offer a challenge to the animals' intelligence and ingenuity (Poole, 1991a, 1996; Wemelsfelder, 1997a).

In addition to the above theoretical disadvantages of the natural living approach, there are some logistical problems in comparing the behaviour of wild and captive animals. The main problems are that: 1) there may be a bias in data recorded in wild populations as the animals will naturally avoid humans and they are often more visible when carrying out particular behaviours, providing an inaccurate wild activity budget; 2) the behaviour of wild animals may be affected by temporal and geographic variations and therefore it is difficult to generalize across a whole species from wild studies; 3) different observation methods used in wild and captive studies may preclude valid comparisons and 4) variation in subspecies together with genetic and individual differences between wild and captive populations may also affect results (see Veasey et al., 1996a, 1996b).

To sum up, the performance of a natural behavioural pattern has aesthetic and educational advantages (especially in zoos), although its significance from the welfare point of view is not always clear. Even though a captive animal performing the full natural behavioural repertoire is more likely to have better welfare than one that is not, the opposite may not be true; an animal not performing the full natural behavioural repertoire is not necessarily suffering (Veasey et al., 1996b). In addition, more research is needed concerning the importance of specific characteristics of the natural habitat and the significance of the performance of particular behavioural patterns in certain circumstances, in order to allow accurate judgements of animal welfare (Duncan & Fraser, 1997). Nevertheless, the study of wild populations in natural habitats can give us an important benchmark for the assessment of the welfare of captive animals, and ideas for the improvement of captive environments (Mellen et al., 1998; Roush et al., 1992).

1.2.4 Integrated approaches for animal welfare

The three approaches to the study of animal welfare, although based on different basic principles, will often lead to similar conclusions since both natural behaviour and subjective feelings are adaptive and should generally promote biological functioning (Duncan & Fraser, 1997). However, the different criteria for animal welfare do not always produce similar conclusions. In some captive environments the performance of natural behaviour may no longer be the best way to achieve functional outcomes (Duncan & Fraser, 1997). With regard to domestic animals, genetic changes may also lead to conflict between the different approaches for animal welfare. A common recommendation to address the contradiction between the different criteria for animal welfare is the usage of multiple measures (Novak & Suomi, 1988; Crockett, 1998; Dawkins, 1998).

Dawkins (2003, 2004) suggested that for an integrated approach to assess the welfare of an individual we really have to answer only two questions:

1) Is the animal healthy?
2) Does the animal have what it wants?

According to Dawkins, these two questions are between them a succinct way of capturing both the physical and mental aspects of animal welfare and the key to answering them is the behaviour of the animal. Similarly, Webster (1994) suggested an integrative approach for the welfare of captive animals, well known as the ‘Five freedoms’:

1) Freedom from thirst, hunger, and malnutrition (from the subjective experience approach).
2) Freedom from discomfort (subjective experience).
3) Freedom from pain, injury, and disease (biological functioning).
4) Freedom from fear and distress (biological functioning and subjective experience).
5) Freedom to express normal behaviour (natural living).

Again here, the different approaches have been integrated to provide a fuller picture of animal welfare.

1.2.5 The behaviourally integrated animal welfare approach taken in the present thesis

In the present thesis a behaviourally integrated approach is adopted in the contexts of both the nature of the attempts to improve the welfare of captive common marmosets (*Callithrix jacchus*) and in the methods used to evaluate their welfare. This thesis does not aim to integrate across physiological and behavioural domains; rather it attempts to synthesise different behavioural perspectives to evaluate welfare as expressed in behavioural outcomes. Many aspects of the natural habitat cannot be reproduced in the captive environment (for practical, financial, or management reasons), and therefore, at the end of the day, captive animals live in artificial environments (Shepherdson, 1988). Further, it is not clear whether the performance of a specific natural behaviour *per se* is beneficial for captive animals, or the consequences of this performance (Veasey et al., 1996b). Thus, it may be more beneficial for captive animals to restore natural contingencies even by the performance of unnatural behaviours.

In the present thesis different aspects of characteristics of the natural environment are provided to the marmosets. However, these natural characteristics do not simply refer to the physical elements of the natural habitat, but also the natural contingencies that wild animals' experience. However, in some cases (see Chapters 7, 8, and 9) an unnatural behaviour is needed to gain the natural contingency (i.e. a behavioural engineering approach is used, see below). In particular, the effects of three natural features on the behaviour and the preferences of the marmosets are investigated:

1) The effects of physical (Chapters 4, 5, and 6) and social (Chapter 4) complexity.

2) The effects of choice between different parts of the cage (Chapter 4), or between different environments (Chapter 6).
3) The effects of controllability over different aspects of the captive environment (Chapters 7, 8, and 9).

In all studies, behavioural measures are used to evaluate the welfare of the monkeys, and a comparison to the natural behaviour of wild common marmosets is carried out in the General Discussion (Chapter 10). Behaviour is a very easily observed, non-invasive, and non-intrusive measure of welfare and can provide good cues about the internal, subjective, state of animals, together with their preferences and needs (Mench & Mason, 1997; Dawkins, 2004). Further, comparison to the natural behavioural pattern may give us an indication for both positive and negative welfare states. On the other hand, the performance of abnormal behaviours, or natural behaviours out of context or in unnatural frequency or duration, may indicate disturbance (Mench & Mason, 1997). Finally, Dawkins (2004) argued that behaviour is "the result of all of the animal's own decision-making processes…the ultimate phenotype" (p. S4). In addition to the behavioural measures, in Chapters 4 and 6 the preferences of the marmosets are measured, and these preferences may be influenced by the subjective experience of each individual.

1.3 ATTEMPTS TO IMPROVE THE WELFARE OF CAPTIVE PRIMATES

Appleby (1999) and Fraser (1995) argued that scientists put too much effort and attention into the definition of animal welfare while we should concentrate more in the attempt to solve animal welfare problems. The most popular way to describe the attempts to enhance welfare is by using the term ‘environmental enrichment’. “Environmental enrichment is the improvement of animal welfare through manipulation of the captive environment” (Shepherdson, 1990, p. 42). There are two main approaches for the study of environmental enrichment. The first one is the natural approach, which relies upon the attempt to mimic the wild habitat in captivity to provide natural stimulations for captive animals (e.g. Mallinson, 1975, 1982; Markowitz, 1982; Chamove 1989; Chamove & Rohrhuber, 1989; Moore, 1997; Rothe, 1999; and see Young, 1998, 2003). The second approach is that of behavioural engineering, which relies upon providing artificial devices that the animals can operate to receive a reward (Forthman-Quick, 1984; O’Neill et al., 1991; Ogden et al., 1993; and see Young, 1998, 2003). It is very common for scientists to favour just one of these approaches and criticise the other (Forthman-Quick, 1984). Criticism concerning the natural approach comprises the argument that “the provision of natural stimuli does nothing to establish the all important connection between behaviour and its natural end point” (Young, 2003, p.8). On the other hand, criticism against the behavioural engineering approach claims that “behavioural engineers only succeed in promoting the performance of abnormal behaviours” (Young, 2003, p.8). Nevertheless, Forthman-Quick (1984) suggested that there is nothing mutually exclusive in the two approaches, and the two methods might be combined to solve problems encountered in the life of captive animals.

An example for the combination of the two approaches is given in the present thesis (Chapters 7, 8, and 9). The concept behind the idea of providing captive animals with control over aspects of their captive environment is rooted in the natural approach of adopting elements of the natural habitat into the captive environment.

However, in this thesis, the way this approach is performed is by giving the animals control over light by touching a touch sensitive button, which is artificial in both the behaviour required to control it and its result. However, Barber and Kuhar (2006) suggested that animals use their natural behavioural repertoire even when using artificial enrichment items “because after all, the process of using behaviour to exert control over their environment is entirely natural” (p. 17).

Most of the attempts to enhance the welfare of captive callitrichids have involved feeding enrichment (e.g. McGrew et al., 1986; Scott, 1991; Kelly, 1993; Box et al., 1995; Forster, 1996; Glick-Bauer, 1997; Rapaport, 1998; Roberts, et al., 1999; Herron et al., 2001; Queyras et al., 2001; Vignes et al., 2001; de Rosa et al., 2003; Chamove & Scott, 2005; Rensing & Oerke, 2005). Further attempts have involved the provision of various novel objects or cage furniture (e.g. Menzel & Menzel, 1979; Box, 1984a, 1988; Kitchen & Martin, 1996; Vitale et al., 1997; Ventura & Buchanan-Smith, 2003; Hardy et al., 2004), or the adoption of elements of the natural habitat into the captive environment (e.g. Mallinson, 1975, 1982; Stein et al., 1979; Chamove, 1989, 2005; Chamove & Rohrhuber, 1989; Chamove & Moodie, 1990; Price & McGrew, 1990; Moore, 1997). In Chapter 2, only research on the effects of the physical and social complexity of the environment, together with the effects of the provision of choice or controllability are discussed, as these are the main topics of the present thesis.

When studying animal welfare, it is necessary to establish a set of goals prior to the implementation of the environmental enrichment. For the present thesis these goals are:

1) Preventing or reducing abnormal behaviour, or the performance of natural behaviour out of context, or at abnormal frequencies/durations.
2) Increasing the range (number) of desirable species typical behaviour patterns.
3) Increasing the normal distribution (i.e. species typical duration of performance) of behaviour patterns.

(Modified after Chamove & Moodie, 1990).

The General Discussion of the thesis (Chapter 10) examines the effects of complexity, choice and control on the behaviour of the marmosets in the light of these goals.

Chapter 2

The ‘Three Cs’: Complexity, Choice, and Control

“When I use a word,” Humpty Dumpty said, in rather a scornful tone,
“it means just what I choose it to mean, neither more nor less.”
“The question is,” said Alice, “whether you can make words mean so many different things.”
“The question is,” said Humpty Dumpty, “which is to be master-that's all.”

(Lewis Carroll, Through the Looking-Glass, 1871, reprinted in 1971, p.190)

The terms complexity, choice and control, in the context of animal welfare, are being used repeatedly in theoretical and experimental publications as well as in legislation. Nevertheless, the exact meaning of these terms, together with the differences and links between them are not clear. There is no one approach to link these terms, and no obvious way to distinguish between them. One could state that the three terms are equivalent in relation to behaviour, saying that when an organism lives in a complex environment, it has a choice between the various components of its environment, and by having some choice, the organism can experience some control. However, this is only one of many ways to link these three terms and these various ways will be discussed in this chapter. The term predictability is also frequently used in the context of animal welfare, and is associated with complexity and control; however, as the effects of predictability are not discussed in the present thesis, the meaning of this term and its links to complexity and control will be discussed only briefly.

2.1 THE IMPORTANCE OF COMPLEXITY, CHOICE AND CONTROL IN LEGISLATION

The significance of complexity, choice and control (or at least aspects of them) is mentioned in British and European legislation and in International guidelines for the welfare of primates in captivity. British legislation points out that "…a complex and unpredictable cage environment is therefore necessary…" (Home Office, 2005). European legislation also refers to the importance of complexity for captive primates, "…they require complex, enriched environments to allow them to carry out a normal behavioural repertoire". In addition, it stresses that "…opportunities for achieving objectives (some control over the environment) should be provided" (revision of Appendix A, Council of Europe, 2004). The International Guidelines for the Acquisition, Care, and Breeding of Nonhuman Primates (IPS, 1993), similarly to the European legislation, mention the importance of control, "…the animal should also be able to exert some control over its environment". Furthermore, in their reference to the importance of a complex environment, these guidelines distinguish between the social and the physical environment, "Ideally, monkeys should be kept in large cages or compounds where a complex social and physical environment can be provided" (International Primatological Society, IPS, 1993).

In contrast to British, European, and International legislation and guidelines, US legislation does not mention the importance of complexity, or that of control. None of the above legislation and guidelines mentions the significance of choice for captive primates. Moreover, none of them specifies or explains their statements regarding the significance of complexity of the captive environment or of control over the environment in regards to the welfare of primates in captivity.

2.2 USE AND OVERUSE OF THE TERM ‘CONTROL’

Similarly to legislation that uses the word ‘control’ without any explanation of the meaning of it, many animal welfare scientists use the words ‘control’ and ‘controllability’ in a wide rage of contexts. In many of these cases, one could argue that the word choice or even complexity might be more appropriate. The use of the word ‘control’ appears to be increasing among scientists in the study of environmental enrichment. For instance, in the 7th International Conference on Environmental Enrichment (New York, 2005) several researchers used the term ‘control’ to describe a wide range of studies. Reiss (2006) “provided a social group of bottlenose dolphins (*Tursiops truncates*)…with an underwater keyboard system that was designed to give them rudimentary choice and control over some environmental contingencies” to investigate the developmental and functional aspects of dolphin vocal learning (p. 27). Coppola and co-workers (2006) provided shelter housed dogs with the opportunity to experience social contact and argued that “social contact is one aspect that allows for some individual control” (p. 232), while others use the term social complexity or even social enrichment for identical conditions (e.g. O’Neill, 1988; Schapiro et al., 1996; Rennie & Buchanan-Smith, 2006b).

Similarly, Bosso and colleagues (2006) presented some enrichment items (e.g. leaves, ropes, balls, etc.) to a single male jaguarundi (*Herpailurus yagouaroundi*), and also argued that “an enriched environment offers a captive animal a degree of control over its environment because it allows the animal to make choices” (p. 290). In contrast to the above, other researchers have used the terms environmental complexity or simply environmental enrichment to describe similar techniques to enhance the environment of captive animals (e.g. Westergaard & Fragaszy, 1985; see Young, 2003 for review).

In the same conference, Gilbert-Norton and Gee (2005) presented a study in which they used the contrafreeloading (CFL) method to allow Abyssinian ground hornbills (*Bucorvus abyssinicus*) and barefaced currasows (*Crax fascioloata*) “a simultaneous choice of visible (free) and hidden (earned) mealworms in a compartmented foraging box”. They also stressed “CFL updates information about unpredictable resources, giving control over stochastic environments…” (p. 40), while others have argued that the animals were simply allowed to choose between different feeding opportunities (e.g. Osborne, 1977; Reinhardt, 1994).

Other researchers have also confused the meaning of the word ‘control’ with those of the words ‘choice’ and ‘complexity’. Owen and co-workers (2005) provided giant pandas (*Ailuropoda melanoleuca*) with the choice between an outdoor exhibit and an off-exhibit area, saying that “in the choice condition the pandas had access to greater stimulus diversity…and they also had control over where to spend their time” (p.479). Another example is the study of Videan and colleagues (2005) in which captive chimpanzees (*Pan troglodytes*) were provided with different types of enrichment (fixed, moveable, malleable, and destructible). The chimpanzees showed higher levels of usage of the destructible items, and the authors concluded that the chimpanzees preferred the most controllable items. Previous studies have shown very similar results concerning the preference for destructible items, but did not mention the aspect of controllability of those objects (Brent & Stone 1992, 1998; Shefferly et al., 1993). The difference between Videan and co-workers’ study (2005) to the similar previous ones was that Videan and her colleagues used the ‘Grades of controllability in novel objects’, a scheme offered by Sambrook and Buchanan-Smith (1997, p. 212). However, they used only the lowest grades (i.e. Fixed, Movable, and Malleable), and ignored the two highest grades (i.e. Analogue and Digital) of controllability that Sambrook and Buchanan-Smith (1997) suggested. In another study, Sambrook and Buchanan-Smith (1996) studied the qualities of complexity of, and control over, novel objects (children’s toys) on the interest shown by four species of guenons (*Cercopithecus diana*, *C. hamlyni*, *C. neglectus*, and *Allenopithecus nigroviridus*). As the authors note, one can only have control over responsive entities. Therefore, whilst investigating whether control was enriching, they manipulated the responsiveness of the objects. They manipulated the levels of responsiveness and complexity of novel objects and suggested that controllability (as measured by responsiveness) is more effective than complexity in eliciting the monkeys’ interest.

My last example for the usage of the word control in research on the welfare of captive primates is the study of Vick and colleagues (2000). In this study the authors offered one group of each of two macaque species (*Macaca arctoides* and *M. sylvanus*) a fruit shaker in three different conditions: empty, filled with peanuts (made a rattling noise, but peanuts could not fall out), and ‘foraging’ (peanuts could fall out through a tube). The authors found that the macaques used the fruit shaker the most when it could be used as a foraging device, and suggested that their results “support the importance of control and complexity as features of novel object enrichment” (p. 190). In contrast, there is a large collection of studies on the effects of feeding enrichment, which have not considered the effects of controllability on the welfare of captive primates (see Young, 2003 for review). In human research, there is also confusion between the words ‘control’ and ‘choice’. For instance, in two different studies, students were allowed to choose the sequential order of a pack of tests that they had to take. In both studies, the researchers mentioned that the participants were given personal control over their tasks (Mandler & Watson, 1966; Burger, 1987).

To sum up, since the importance of controllability for the welfare of captive animals was raised in the 1980’s (e.g. Markowitz, 1982; Chamove & Anderson, 1989; Snowdon & Savage, 1989; Novak & Drewsen, 1989) it has become quite popular to use this term in various contexts where it was not used before. Moreover, many scientists use this term almost without consideration of the exact meaning of it. The aim of the present chapter is to illustrate the confusion between the terms complexity, choice and control (especially between choice and control), and to raise questions concerning the meanings of these three words together with the differences and the links between them.

2.3 COMPLEXITY

2.3.1 Complexity in the natural environment

“The ‘environment’ for a social animal includes not only other species of animal and plant (setting problems if they are predators, competitors, parasites, or food) and the physical world (setting problems of temperature control, light and dark, and so on), but also its own companions” (Byrne, 1995, p. 195). Consequently, it has been suggested that the term ‘environmental complexity’ may be divided into two separate terms: ‘physical complexity’ and ‘social complexity’ (Byrne, 1995; Sambrook & Whiten, 1997). The physical environment of wild animals is complex, and they must deal with seasonal and daily changes. For example, the weather changes with the seasons, and animals may have to cope with rain, wind and fog as well as sunshine. These weather conditions are also unpredictable. Furthermore, the times of sunrise and sunset may vary, leaving the animals differing amounts of time to engage in various activities. One crucial activity is foraging for food that is not always available in the same places or in the same quantity or quality. Even the immediate physical environment of wild animals is complex and may be unpredictable; for example, broken or growing branches on familiar paths may mean the animal needs to find new routes.

The social environment of wild animals is also complex, arguably more so than the physical environment, as the animal has to deal with other individuals, who may respond to the animal's behaviour in many different ways, while physical objects are more limited in response. In other words, the individual's conspecifics may be serious potential competitors for both food resources and mates. Furthermore, the behaviour of social companions may change rapidly and in response to the individual's actions, and also may present challenging problems as conspecifics are likely to have similar intelligence to the animal itself (Byrne, 1995). In addition, the presence of other nonhuman animal species, and even of humans, can also be seen as part of the animal's social environment (e.g. Young, 2003).

2.3.2 Complexity in the captive environment and its implications for animal welfare

The complexity of the captive environment, similarly to that of the natural habitat, also includes several dimensions: the presence of other individuals, the presence of manipulable objects, and the physical structure of the enclosure (Sambrook &

Buchanan-Smith, 1997). The importance of the physical complexity of the captive environment for the welfare of its occupants has been emphasized by several scientists (e.g. Snowdon & Savage, 1989; Novak & Drewsen, 1989). The complexity of the rearing environment may have significant effects on the developing animal, and may find expression in behaviour, reproduction, physiology, and brain morphology (Faucheux et al., 1978; Turnquist, 1983, 1985; Carlstead & Shepherdson, 1994; Benefiel & Greenough, 1998). One of the main differences between the natural habitat and the captive environment is the degree of complexity of these environments. Although quantification of complexity is problematic (Sambrook & Buchanan-Smith, 1997; Sambrook & Whiten, 1997), it is obvious that captive environments are less complex than natural environments. However, it is important to emphasize that not all aspects of complexity in the wild habitats are good (e.g. extreme weather conditions, predators), and in captive environments we try to replicate only the positive aspects of complexity (e.g. physical complexity, social group composition).

The social environment of captive animals is also frequently less complex than that of wild animals, as the size of captive groups is often smaller in comparison to wild populations. However, this depends very much on the social structure of the species, and some species are much easier to cater for than others in respect to social needs. Two examples of species with large groups and/or complex social organization, which are difficult to replicate in captive environments, are described. First, a troop of rhesus macaques (*Macaca mulatta*) may include up to 110 individuals (with an average group size of 59 individuals) in the wild (Southwick et al., 1996), but it is very rare to see such big groups in captivity. Second, hamadryas baboons (*Papio hamadryas hamadryas*) have a very complex four-level social structure. The basic unit is one male with multiple females, and two to four basic units with bachelor followers make up a clan. Several clans form a band (about 60 individuals), and several bands form the final social level, a troop (Kummer, 1971; Sigg & Stolba, 1981). Here again, most captive environments are not big enough, nor do captive groups contain enough individuals to form such a complex social structure. As a solution, Novak and colleagues (1994) and Young (2003) suggested that if it is impossible to mimic the size and complexity of wild troops in captivity, natural subgroups are a preferred option.

The importance of social companionship to the welfare of captive social animals in general and captive primates in particular is widely documented in scientific publications (e.g. Wolfensohn & Honess, 2005; Rennie & Buchanan-Smith, 2006b), and in international guidelines (IPS, 1983; United States Department of Agriculture, 1991; Council of Europe, 2004; Home Office, 2005). Social interaction is critical in many primate species (Novak & Drewsen, 1989), however, there is more to consider about the social environment of captive primates than just housing animals in groups, as the composition of the social group may also affect the psychological well-being of the animals. A common attitude is that the closer the social environment in captivity is to the natural social environment, the better for the welfare of the captive animals (e.g. IPS, 1983; Bennett & Davis, 1989; Poole, 1990; Visalberghi & Anderson, 1993; Buchanan-Smith, 1994, 1997a; Novak et al., 1994; Wolfensohn & Honess, 2005; Honess & Martin, 2006; Rennie & Buchanan-Smith, 2006b). However, this is a debatable view (Dawkins, 1990; Mendl & Newberry, 1997) as social housing entails potential advantages together with disadvantages for the individual (Coe, 1991; Mendl & Newberry, 1997), and surprisingly little research has been done on the effects of group composition on the welfare of captive primates (but see below). The differences in the physical and the social complexity between the natural and captive environments also lead to a decrease in the complexity of the behavioural repertoire exhibited by captive animals (Poole, 1998; Buchanan-Smith, 1997b).

2.3.3 The relationship between complexity and predictability

As mentioned above, the complexity of the captive environment is reduced compared to natural environment. This reduction in complexity leads to an increase in predictability of stimulation, which is considered to lead to boredom. Therefore, environmental complexity and predictability are inversely related; when one declines, the other usually increases. Consequently, an abrupt increase in environmental complexity is not desirable either, as high levels of unpredictability may lead to tension and stress (Chamove & Anderson, 1989; Buchanan-Smith, 1997b).

2.3.4 Effects of the complexity of manipulable objects

Almost all research on the effects of environmental enrichment could be considered to be research on the effects of environmental complexity. However, only studies on the effects of objects of different levels of complexity will be reviewed here. Further, there are two different types of studies that examine the effects of object complexity on the behaviour or preference of captive animals. The first is the study of the effects of visual complexity on the preferences of animals. In this type of study animals have to indicate their preferred object; they may indicate in different ways. The other type is the study of the effects of tactile complexity, and frequently in these studies the animals are observed and the effects of the complexity of the objects on their behaviour are examined. Although it might be expected that complex objects might evoke more interest from captive primates than simple objects, the results of previous studies are contradictory. In a study of the effects of the visual complexity of an object, Butler (1954) showed that monkeys (the species was not mentioned) preferred stimuli (judged by opening a door to view the stimulus) that were more complex (another monkey, or an electric toy train) over more simple stimuli (food or an empty incentive chamber). Similarly, Humphrey (1972) showed that rhesus macaques preferred complex over simple visual patterns when they were given the choice by pressing a button that allowed the chosen stimuli to remain on a screen. Sackett (1966) not only showed that infant rhesus monkeys preferred complex visual patterns (judged by visual attention) over simple patterns, but he also showed that this preference increased with the age of the monkeys.

Jaenicke and Ehrlich (1972) studied the effects of the tactile complexity of manipulable objects and showed that animate stimuli (cat, snake) elicited much more interest in great galagos (*Galago crossicaudatus*) and slow lorises (*Nycticebus coucang*), than inanimate stimuli (an empty box). Weld and co-workers (1991) found that the shape and the substance of manipulable objects played a significant role on their effectiveness as enrichment devices for long-tail macaques (*Macaca fascicularis*), as the monkeys preferred more flexible objects and the ring shaped ones (which were probably the easiest to manipulate). In contrast to the above, Sambrook and Buchanan-Smith (1996) found no effects of the visual complexity of novel objects on the interest of captive guenon monkeys.

Environmental change may also have beneficial effects on captive animals. For example, Line and co-workers (1991b), Paquette and Prescott (1988), and Morgan and colleagues (1998) suggested that rotation of enrichment objects may result in higher levels of use, and continuation of the positive effects of the enrichment. Rotation of objects increases the environmental physical variability and complexity, which in turn, reduces predictability, and thus reduces boredom. However, Bayne (1989b) enriched the cages of several macaque species (*Macaca mulatta*, *M. arctoides*, and *M. fascicularis*) with nylon balls. She mentioned that laboratory technicians reported great difficulties in removing the balls from the monkeys' cages, and suggested that the rotation of enrichment objects may inject an element of stress into a program designed to improve the psychological well-being of the animals by periodically removing part of the animals' territory and replacing it with a novel object. Weld and Erwin (1990) studied the effects of providing pet toys in rotation to long-tail macaques. In contrast to Bayne (1989b), they did not report any effects of the rotation procedure. However, although they found a reduction in abnormal behaviour in the presence of the enrichment objects, this influence reduced after the enrichment was removed. Furthermore, the same reduction in abnormal behaviour was found when the monkeys were exposed to two objects for a long period (18 weeks) without rotation. The manipulation rate (but not the level of abnormal behaviour) decreased, when one object was removed (and the monkeys no longer had any choice). Hence, the rotation procedure did not have a significant influence on the behaviour of the monkeys.

2.3.5 Effects of physical complexity

One of the problems of the research of effects of complexity on the behaviour of nonhuman primates is that stimuli that may appear complex from the experimenter's point of view may not be received as such by the experimental animals (Fetterman, 1996). Another problem is the difficulty of an explicit quantification of environmental complexity (Sambrook & Buchanan-Smith, 1997). Nevertheless, in all the studies that are reviewed in this section, the authors defined the environment as complex. Several researchers studied the effects of floor bedding on the behaviour of captive primates, and the common outcome of these studies was positive effects of more complex floor bedding on behaviour as compared to bare concrete or grid floors (*Callithrix jacchus* and *Saguinus oedipus*: McKenzie et al., 1986; Dettling, 1997; *Macaca arctoides*: Anderson & Chamove, 1984; *Cebus apella*: Westergraad & Fragaszy, 1985). In contrast to the above, Hardy and co-workers (2004) found that common marmosets spent more time on the cage floor, and visited it more frequently, when the floor was comprised of a wire grid than when it was a sawdust filled tray (which is more complex, at least from a human point of view). This demonstrates species differences in response to complexity, which in this case may be related to the callitrichids' being better able to grip on a wire grid.

When considering the complexity of the whole captive environment there is a strong agreement on the positive effects of more complex environments on welfare (*Callthrix jacchus*: Kitchen & Martin, 1996; Kerl & Rothe, 1996; *Pongo pygmaeus*: Tripp, 1985; Perkins, 1992; *Gorilla gorilla gorilla*: Ogden et al., 1993; *Pan troglodytes*: Jensvold et al., 2001; *Macaca mulatta*: Schapiro et al., 1997). In addition to the behavioural effects of physical complexity, Kozorovitskiy and co-workers (2005) showed that a one-month stay in a complex environment (larger cage which was equipped with straw nests, vegetation, and unique objects) enhanced the biochemical structure of the brain of marmosets (the exact species was not mentioned). However, when the size of the enriched cage was doubled, it did not elicit more physical changes. Further, it has been argued (e.g. Novak, 1989; Poole, 1990; Buchanan-Smith, 1997a), and shown empirically (Kerl & Rothe, 1996; Gaspari et al., 2000), that the complexity of the cage has a greater influence on welfare than the size of it.

Another element of complexity in the natural habitat is environmental changes which may affect the animals in either positive or negative ways. In captive environments there are also daily events, both pleasurable and aversive to the animals (e.g. feeding; lights coming on and off; health checking and cage cleaning). Line and co-workers (1991a) found rhesus monkeys to be affected by all these events (heart rate and activity levels increased rapidly in response). However, the responses to less frequent procedures (e.g. tuberculin testing and cage changing) were larger in magnitude and longer lasting than for frequent procedures. The difference in response may be because these latter events were more substantial, perceived more aversively, or less frequent. Alternatively, it may be the predictability of the daily events that minimizes their effects on monkeys' well-being.

2.3.6 Effects of social complexity

The importance of social interactions in general and of natural social housing in particular was discussed above. The social environment of primates in captivity may be comprised of relationships with conspecifics, with animals of different species, or with humans. However, only the first and the last types of relationships will be discussed as they are relevant to the laboratory environment.

Individual housing

The negative impact of social isolation has been shown in many studies (e.g. Harlow, 1958, Harlow & Harlow, 1966; Anderson & Chamove, 1980; Caine & Reite, 1981; Ridley & Baker, 1983; Reite & Capitanio, 1985; Chalmers & Locke-Haydon, 1986; O'Neill, 1988; Bellanca & Crockett, 2002). Poole (1990) even argued that marmosets are usually housed in social groups because they may die if kept singly for too long. Several studies have also demonstrated the interaction between social conditions and the effects of environmental enrichment. Chamove and Scott (2005) found that individually housed common marmosets used a foraging device for larger proportions of time than socially housed individuals, which may suggest that individually housed individuals were more bored. Queyras co-workers (2001) found that an unfamiliar enrichment device (box filled with coloured drinking straws) was not effective for common marmosets which were separated from their social group, as the activity of the monkeys tended to decrease and the frequency of phee (contact) calls increased. The same device did not elicit the same negative reaction when introduced to the marmosets in their social group, suggesting that social companions reduced anxiety of the marmosets.

Pair housing

The housing of primates in pairs (except in monogamous species) is also viewed as inappropriate (Wolfenshon & Honess, 2005). Although the housing of young with their mothers is important, in species in which young are usually brought up in complex social groups, the housing of infants in pairs with their mothers was also found to cause abnormalities in the behaviour of the young individual later in life (Mason, 1991) or in the relationship between the infant and the mother (Castell &

Wilson, 1971). Further, for marmoset monkeys, Rensing and Oerke (2005) suggested that different sex pairs can be housed together, however, the housing of female-female pairs was considered to be undesirable as the positive benefits of this group composition appeared to be limited. The authors considered the levels of aggression (within female-female pairs) reported in Majolo and colleagues (2003) to be too high, and the levels of allogrooming too low to demonstrate good affiliative relationships. Similarly, Mallapur and co-workers (2005) showed that lion-tailed macaques (*Macaca silenus*) performed higher level of allogrooming when housed in groups than when housed in pairs (of different or same sex). However, several studies have shown that pair housing may be beneficial even for species that live in large groups under natural conditions (Reinhardt, 1989, 1990, 1991).

Group housing

The argument that natural social composition will be most beneficial for captive primates does not always rely upon scientific evidence, and previous research on the effects of group composition is contradictory. Erwin (1979) found that the absence of males in captive groups of macaques can elicit aggression between the females, as male macaques normally regulate female aggression. Petit and Thierry (1994) showed the same effects upon the absence of an adult in a group of juvenile Tonkean macaques (*Macaca tonkeana*). In addition, de Vleeschouwer and colleagues (2003) found that social groups of golden-headed lion tamarins (*Leontopithecus chrysomelas*) are less stable when there is a high proportion of males or a large number of sons. The level of aggression is even higher when all offspring are older than one year, or when the dominant female is treated with contraception.

However, Young (2003) noted that although it is believed that parenthood is in itself an enriching experience, there is no scientific evidence to support this suggestion. Further, Baker and co-workers (2000) showed that the housing of chimpanzees in large and more natural social groups caused a significant increase in levels of minor wounding as compared to small and medium groups, while the composition of the group had no effects on levels of serious wounding. This suggests that the optimum group size may depend upon enclosure size and a compromise may have to be reached. In addition, it was found that female golden-lion tamarins (*Leontopithecus rosalia*, French & Inglett, 1989) and Wied's black tufted-ear marmosets (*Callithrix kuhlii*, Schaffner & French, 1997) exhibit higher levels of aggression towards intruders when housed in large groups than when housed in pairs or in small groups. One suggestion to improve the welfare of group-housed primates is to divide the enclosure into several smaller areas to facilitate visual and social separation for individuals (Rumbaugh et al., 1989; Westergaard et al., 1999). This method not only allows the existence of the natural social composition in captivity, but also provides the individuals with natural strategies to cope with social problems.

Social interaction with humans

The significance of the interaction between captive animals and the humans around them has been emphasized by many authors. The nature of human-animal interactions may affect the well-being of both animals and humans, and may improve science (e.g. Roberts, 1989; Hemsworth & Gonyou, 1997; Bayne, 2002; Waitt et al., 2002; Rennie & Buchanan-Smith, 2006a). Cosgrove (2004) even argued that interaction with humans is the most important form of environmental enrichment that can be provided for animals in captivity. Another important aspect of the human-animal interaction is that animals appear to adapt more readily to training, which also may serve to reduce stress for both animals and humans (Bassett et al., 2003), when they have been habituated to human contact (Scott, 1991).

2.3.7 The study of environmental complexity in the present thesis

In the present thesis, I demonstrate the effects of increasing both physical and social environmental complexity on the behaviour of captive common marmosets. In Chapter 4, a study on the effects of the size and the height of the cage on the behaviour of pair-housed individuals is presented (i.e. physical complexity is manipulated). Another study describes the effects of the composition of the captive group (pairs, small family groups, and large family groups) on the behaviour and the welfare of adult animals (social complexity). In Chapter 5, the effects of the transfer of a family group of marmosets from their standard laboratory cage to a larger and more complex enclosure (and back to a standard cage) on the behaviour of the animals is described (physical complexity).

2.4 CHOICE

It is obvious that wild animals in their natural habitat experience a great amount of choice in their everyday life (food, mates, sleeping site, etc.). However, even in the natural habitat the choice is sometimes restricted (limited food resources, competition with counterparts, risk of predators, limited territories, etc.). Nevertheless, an important point is that choice availability in the captive environment is much more restricted, primarily because of limited space, food, and social opportunities.

2.4.1 The joy of choosing

Previous research has shown that humans and animals enjoy the act of choosing. Bown and co-workers (2003) showed that people prefer options that allow them to make further choices over options that do not. When humans had the choice between a solitary item and a pair of items between which they would then make a further choice, they preferred to have the option to make more choice. Similarly, when pigeons had to choose between pecking one ‘free-choice’ key, which led them to two other keys (which could be pecked to obtain food), and another ‘fixed-choice’ key, which led them to a single key (which also provided food when pecked), they showed preference for the ‘free-choice’ key, even though the ultimate result was identical (Cerutti & Catania, 1997).

Another study showed that the choice between outdoor exhibit and an indoor off-exhibit was beneficial for giant pandas. Owen and co-workers (2005) pointed out that both enclosures provided benefits for the pandas, and suggested that “the fact that pandas were exposed daily to all stimuli and behavioural opportunities present in both enclosure areas renders the ethological needs and stimulus diversity hypotheses less plausible, leaving the choice/control as perhaps the most parsimonious alternative” (p. 480). However, this suggestion is arguable for two reasons. First, before the study commenced the pandas usually had the choice between the two enclosures, and only for the baseline phase of the study was the access to the off-exhibit enclosure blocked. Hence, in the baseline phase of the study, the pandas experienced loss of choice that might have affected their behaviour. Second, the assumption that pandas were exposed daily to all stimuli and behavioural opportunities was not accurate since exposure to the indoor off-exhibit area during the day provided the pandas with benefits that the outdoor part of the enclosure could not offer, such as refuge from zoo visitors, or from non-preferred weather conditions. Therefore, perhaps it was not simply the ability to choose between two parts of the enclosure which affected the behaviour of the pandas, but the benefits that the indoor enclosure provided them. Thus, although it is likely that choice is beneficial, further research is required to determine how important it is, and how best to incorporate choice into captive environment to improve welfare.

2.4.2 Choice for primates and its implications for welfare

"Choice is not something that can be directly observed. The individual does this or that and in consequence, is said to choose. The term has unfortunate overtones of conscious deliberation and weighing of alternatives for which the behaviour itself-response A or response B- provides no direct evidence" (Staddon & Cerutti, 2003, p. 133). Most studies on the choice of nonhuman primates in particular, and animals in general, do not study the effects of choice *per se* on welfare, nor the motivations for the animal's choice, but simply identify the individuals' preferred choice (with the exception of Owen et al., 2005, and Reiss, 2006).

One study that showed that rhesus monkeys weigh the consequences (or at least the immediate ones) of their choice is that of Widholm and co-workers (2001). In this study, two adult rhesus monkeys had to deposit tokens into slots in order to get food. The monkeys were given a choice between two different slots, in one the tokens were kept (but food was obtained), while in the other one the tokens were returned to the monkey (together with food reward). In most cases, the monkeys chose the 'token returned' slot. Only when the amount of obtained food was six times larger in the ‘token kept’ slot compared to the ‘token returned’ slot, the monkeys chose the former slot. Therefore, the monkeys chose to increase the number of reinforcers earned, even when this preference reduced the rate of food reinforcement. Hence, the tokens appeared to act as reinforcement in themselves, or the monkeys may have associated having more tokens with the potential of obtaining more food. In addition, Washburn and colleagues (1991) showed that rhesus monkeys reliably performed better on video tasks if they were allowed to choose their task, rather than if the task was assigned to them.

Further examples of choice studies on callitrichids are the studies of Pines and his colleagues (2002, 2003), in which common marmosets could choose between indoor and outdoor, and between small and large indoor cages. However, in these studies, again, no effects of the choice *per se* were studied, but rather the monkeys’ preferences, together with the effects of these preferences on their behaviour (these studies will be discussed in more detail in Chapter 6). Petto and Devin (1988) studied food choice in a group of marmosets, and showed (apart from the outcomes of the preferred food items) that the choice of each individual in the group was affected by the choice of his/her group mates. This conclusion of Petto and Devin’s study is even more valuable than the finding of the preferred food items, since it raises an important difficulty of choice research. Most choice studies are defined as preference tests, and although many scientists use this method to evaluate captive environments and environmental features (e.g. Bayne et al., 1992b; Bateson & Kacelnik, 1995; Van de Weerd et al., 1998; Widowski & Duncan, 2000; Warburton & Mason, 2003; Taylor et al., 2006), the value of these studies is debatable. Both sides of this debate are presented below.

2.4.3 The pros and cons of preference tests

"An animal is generally deemed as preferring an option if it spends more time with it, chooses it more often, or has a shorter latency to approach it. The usual assumption in the welfare literature is that the rank and magnitude of these behavioural preference measures are likely to reflect the animal's underlying motivational priorities…" (Bateson, 2004, p. S115). Alternatively, Van Rooijen (1984) argued that preference tests can be used to put environmental factors on a scale ranging from those the animal experiences as very positive to those the same individual experiences as very negative, but they do not measure motivation. According to either of the above points of view, when we provide an animal with a choice of various options, we presume that the animal will go to the one where he/she would experience greater well-being. Nevertheless, many factors such as previous experience, cost of options, availability of cues, the number and type of options, the animals' condition and situation, and the nature of the choice test itself, may affect the animal's choice (Lockard & Haerer, 1968; Novak & Drewsen, 1989; Fraser & Matthew, 1997; Warburton & Mason, 2003; Bateson, 2004; Kirkden & Pajor, 2006).

In addition to the above disadvantages of preference tests, the animal's preferences may not always indicate the best conditions for its well-being. For instance, choices that would be adaptive for wild animals may not be beneficial for the same animals when in captivity (Bateson, 2004). Further, lower animals cannot be expected to weigh up the long-term consequences of their decisions as human beings would (Duncan, 1978), and the link between the animals' choice and their welfare may break down if they are required to choose between short-term and long-term benefits (Fraser & Matthews, 1997). However, Bateson (2004) argued that as long as the physical health of the animal is not severely influenced, the welfare of the animal may still be improved by experiencing its own choice, even if the long term consequences of the choice are not adaptive. Furthermore, it is important to distinguish benefits that derive from the act of choosing and the meaning of the choice itself (Novak & Drewsen, 1989).

To sum up, when carrying out preference tests, it is important to consider their down sides, and to take a number of independent measures in order to assess the animal's preference. However, although the interpretation of preference tests is debatable and scientists should consider the outcomes of preference tests very carefully, according to Duncan (1978), the argument that 'the animal itself preferred' a particular option, is extremely powerful and provides the best reason to continue the practice of preference tests in the research of animal welfare.

2.4.4 Benefits of the provision of choice for captive animals

"Modern western culture seems devoted to the maxim that the more choice the better. Thus it is not surprising that certain explanatory models in both biology and economics are generated by the assumption that animals and humans prefer choice." (Hutchinson, 2005, p. 74). The significance of the ability to choose has not been determined in nonhuman animals but there are a number of arguments to suggest that choice is important for welfare. The provision of choice for animals in captivity may be beneficial for several reasons (Hutchinson, 2005), and many of these have links with complexity. First, individuals can have an alternative place to sit (stand, rest, eat or any other activity) when other places are occupied by cage mates. Second, the provision of variety saves keepers and researchers from having to identify individuals' preferences. Third, different individuals may have different preferences, and favoured options may vary between individuals in the same enclosure. Fourth, preferred options may change. Fifth, it has been suggested that for humans one important attraction of choice is that people feel in control, which may be true for animals also (but again, it is important to define choice and control and the links between them).

Hutchinson (2005) pointed out that the ability to choose is frequently a part of environmental enrichment, but it is still unclear whether the ability to choose *per se* is what is important. However, the same author also argued that opportunity to choose between various options might be attractive in exercising the mind of a bored animal. Further, Markowitz (1982, p. 197) emphasized that “we should leave as many decisions as possible to the animals” in order to provide them with increased behavioural opportunities. However, it is important to reiterate that in most situations, choice is identical to complexity. Hence, by providing captive animals with a more complex environment we actually provide them with more choice, and vice versa.

2.4.5 The study of the effects of choice in the present thesis

In the present thesis, I present the results of two studies (Chapter 6) in which family-housed marmosets were allowed to choose between their standard indoor home cages and larger and more complex outdoor cages. In these studies, similar to previous studies, the effects of the choice *per se* were not studied. However, the comparison between the results of these studies and the results of the study on the effects of cage size and complexity on a family group of marmosets provides a nice illustration of the beneficial effects of choice *per se*.

2.5 CONTROL

Control is the most complicated term of the ‘Three Cs’. As mentioned above, many scientists use it in the context of animal welfare, as well as in research on human psychology, in various ways and on many levels.

2.5.1 The definition of control

There are several different definitions of control, and they may refer to different levels of control. Seligman and colleagues (1971) argued that “Any time there is something S [subject] can do or refrain from doing that changes what it gets, it has control…when a response will not change what S gets, the response and reinforcer are independent…subject cannot control the reinforcer and the outcome is defined as uncontrollable.” (p. 350). Seligman talked about ‘what the subject gets’, which could refer to anything from getting some food, to changing the whole environment. Weinberg and Levine (1980) were rather more specific (although they related control only to aversive stimuli, particularly electric shocks), and wrote, “Control can be defined as the ability to make active responses during aversive stimulus. These responses are frequently effective in allowing the animal to avoid or escape from the stimulus; but might also provide the animal only with opportunity to change from one set of stimulus conditions to another (i.e. to modulate the environment) rather than to escape from the shock entirely.” (p. 45).

Sambrook and Buchanan-Smith (1997) emphasized that “Controllability is clearly an interactive property.” (p. 208), and offered an operational definition to enable the measurement of control, “…the difference in likelihood of an event occurring depending on an animal’s behaviour. If the animal’s behaviour does not influence the likelihood of the event then the event deemed uncontrollable.” (p. 208). Other scientists have provided other definitions for control (see Skinner, 1996, p. 567), however, all these definitions are more or less the same. Rosenblum (1991) added the point that “given the inter-specific variation in cognitive, perceptual, and motor capacities, control over the environment means something quite different for one species than for another…” (p. 49). This point is very significant when studying the welfare of animals in captivity.

From the above definitions, it appears that there are different ways in which an individual might control its environment. The first way is controlling an object inside the environment. The second is controlling different aspects of the environment and the third way, according to Weinberg and Levine (1980), is when the animal can control its surroundings by moving to another environment. Moreover, even within each category there are different levels of control, as has been suggested by Sambrook and Buchanan-Smith (1997). These different ways and levels of control will be discussed more thoroughly in the General Discussion (Chapter 10).

2.5.2 Implications of controllability for animal welfare

The main difference between captive and wild environments lies in the differential availability of control (Chamove & Anderson, 1989; Carlstead, 1996), while the main adaptive aspect of behaviour is the ability to control (Sambrook & Buchanan-Smith, 1997). Consequently, several scientists suggested that we should provide captive animals with as many opportunities to control their environment as possible (Bayne, 1989a; Line et al., 1990a; Scott, 1991; Warburton, 1991; Rosenblum & Andrews, 1995; Buchanan-Smith, 1997a; Barber & Kuhar, 2006). Snowdon and Savage (1989) even argued that controllability “is a key aspect of most good environmental enrichment” (p. 81), as “animals cannot passively receive environmental events; they must be able to act on the environment and consequences must result from their actions”.

The development of a sense of control over the environment is a critical component of psychological well-being (Snowdon & Savage, 1989), and it is a “deep seated motivational variable of phylogenetic as well as ontogenetic origin” (Overmier et al., 1980, p. 1). Burgers (1975) described the importance of controllability saying, “Life can be viewed as a struggle against randomness - an attempt to acquire the freedom to make choices or exercise control” (p. 194). Overmier and co-workers (1980) explained the significance of the ability of control and said that control modulates the affective value of event; it enhances positive affective value and decreases negative value. Mandler and Watson (1966) on the other hand, suggested that when an organism has some control over an event (even if it is an unpleasant and potentially interrupting event), it gives him/her the opportunity to plan the sequence of events to occur and as the potential interruption becomes part of the plan it is no longer an interruption.

Another approach to show the significance of controllability is to describe the negative impact of lack of control. When an organism experiences uncontrollable events, it may undergo subsequent motivational, cognitive, and emotional disturbance. This disturbance would be likely to increase anxiety in the immediate sense, and to cause chronic anxiety following a history of uncontrollable events (Chorpita & Barlow, 1998). Similarly, a reduction in controllability (or predictability) appears to be the main cause of typical stress symptoms, as a reaction to uncertainty (Wiepkema, 1987).

An animal's early experience of control or lack of control may have serious implications for the welfare of the animal later in life (Mineka & Zinbarg, 1996). Snowdon and Savage (1989) argued that individuals who experienced some control over their environment would develop a sense of control, thus, would be more ready for the challenge of novel situations. Lewis and Goldberg (1969) argued that for human infants, the contingency between their behaviour and their mothers' response enables them to learn that their behaviour does have consequences. Further, they showed that when mothers responded more rapidly to infants' behaviour (infants had control over the event since their activities affected the probability of its occurrence), they tended to be more efficient in processing repeated signal information, hence, developed a sense of control and became readier to cope with novel situations. Similarly, Wheatley and co-workers (1977) showed that rats that had learnt to associate their response (contacting a food cup) to the delivery of food were faster to acquire the bar pressing response in a novel experimental chamber than naïve animals.

2.5.3 The relationship between controllability and predictability

There is a great confusion between the effects of controllability and predictability (Overmier et al., 1980), and different scientists view the link between the two in various ways. Mineka and Hendersen (1985) suggested that because control and predictability are very closely related a full understanding of the effects of the two can only be achieved by examining them both together. On the other hand, "the traditional view of control makes the assumption that control cannot be present without predictability - an event may be predicted without being controlled, but may not be controlled without being predicted" (review by Bassett & Buchanan-Smith, 2007). In contrast, Nickels and colleagues (1992), and Dess and colleagues (1983), presented a set of studies in which the effects of control and predictability were (according to the authors) clearly separated, showing the positive but different effects of controllability and predictability.

Overmier and colleagues (1980) and Bassett and Buchanan-Smith, (2007) presented several theories to explain the relationships and interactions between controllability and predictability. First, the effects of predictability and controllability are additive. Second, control is important to organisms because it provides predictability. Third, predictability is important because it allows efficient control. However, it is difficult to manipulate control and predictability independently for technical reasons and in addition, the three theories makes identical predictions for the outcome of experiments designed to separate the effects of the two factors. The greatest behavioural and physiological influence would be seen in animals that experienced neither control nor predictability over an event. Animals that could either predict or control the event should show intermediate influence, while animals that could predict and control the event are expected to show the least severe influence of the event (Overmier et al., 1980). In conclusion, it is very unlikely that researchers will ever be able to provide experimental evidence to support or negate any one of the above theories.

2.5.4 The study of control over aversive stimuli

Most of the research on controllability has examined control over aversive simuli (e.g. electric shock), and demonstrated that allowing control over aversive events improves the animal's welfare (Overmier et al., 1980). Many studies have been published on the effects of controlled and uncontrolled electric shock on the behaviour and physiology of rats (e.g. Maier et al., 1982; Williams & Leirle, 1986; Seligman et al., 1971; Weiss, 1968), and dogs (e.g. Dess et al., 1983) showing the detrimental effects of the exposure to uncontrollable electric shock. Weiss and co-workers (1975) showed similar effects of the exposure to an uncontrollable cold swim. Hanson and co-workers (1976) showed that allowing rhesus monkeys control over high intensity noise, resulted in lower levels of the stress hormone cortisol, relative to a yoked group that had no control. Conversely, Helmreich and co-workers (1999), and Maier and colleagues (1986) did not find large behavioural and neurochemical differences between rats that were exposed to escapable and inescapable tail shocks.

Some of the outcomes of exposure to uncontrollable aversive events are a reduction in activity and lack of reaction to consequent exposure to controllable aversive events (Anisman et al., 1978; Maier & Jackson, 1979; Overmier et al., 1980). Overmier and Seligman, 1967; Seligman, 1975) offered the 'Learned helplessness' theory to explain the detrimental outcomes of exposure to uncontrollable aversive events. According to this theory, these detrimental outcomes are the consequence of motivational, cognitive, and emotional deficits due to prolonged exposure to noncontingent events.

2.5.5 Effects of controllability on captive primates

Little research has been done on the effects of control over positive stimuli on the welfare of captive animals in general and of captive primates in particular. Previous research can be divided into three categories: control over the delivery of food, control over novel objects, and control over various aspects of the environment.

2.5.5.1 Effects of controllability over the delivery of food

Rhesus macaque peer-reared infants that were given control over delivery of food, water and treats showed increased exploratory behaviour, coped better after being separated from peers, and displayed less fear after being subjected to provocative events (Mineka et al., 1986). In a similar study, Roma and co-workers (2006) found that surrogate peer-reared (individually-housed with daily access to peer group) rhesus infants that were given control over food delivery (by lever pressing) were significantly more active (including locomotion and exploratory activities) and exhibited significantly lower cortisol reactivity compared to yoked monkeys, when exposed individually to a novel enriched environment. In addition, the amount of lever pressing in the home cage was positively correlated with behavioural activity in the novel environment, and negatively correlated with cortisol reactivity to the novel environment.

The importance of having such control was backed up by qualitative observations made by Markowitz (1982). He showed that gibbons (*Hylobates lar*) and Diana monkeys (*Cercopithecus diana*) preferred to earn their food rather than being dependent on the staff. Although no formal observations were carried out, Markowitz mentioned that the monkeys were more active and ‘alive’ in the presence of the enrichment. Similarly, Reinhardt (1993) found that rhesus monkeys preferred to work for their food (i.e. invest an effort in acquiring it), even when the same food was also freely available effortlessly. This behaviour was interpreted as a desire for control. Other researchers have had similar results for non primate species (Jensen, 1963; Stolz & Lott, 1964; Singh, 1970; Inglis & Ferguson, 1986; and see Osborne, 1977 for a review).

However, Sambrook and Buchanan-Smith (1997) argued that the animal's tendency to work for their food does not reflect a desire for control, as by performing the behaviour, the likelihood of reward occurring is actually lower than if the animal gets some of the free food available (i.e. some of the time that might be spent eating the freely available food is taken up with performing the behaviour necessary to control its delivery). In addition, whilst feeding captive animals in ways that best improve their welfare is critically important, allowing control over feeding has limitations as many captive animals are overweight. Furthermore, animals may become obsessed with the new feeding opportunity. Markovitz and Line (1989) found that rhesus macaques would touch a control switch several thousand times to receive a food reward. The desirability of such behaviour is questionable, and it could be considered as another type of stereotypic behaviour (Sambrook & Buchanan-Smith, 1997).

2.5.5.2 Effects of controllability over novel objects

Sambrook and Buchanan-Smith (1996) found that monkeys in captivity preferred responsive objects, which they could control in specific ways (i.e. to elicit noise), rather than non-responsive objects. Similarly, Videan and colleagues (2005), and Vick and colleagues (2000) also found that primates preferred objects that they could control, or in other words, objects that responded in reaction to the animals' behaviour, or were manipulable (see paragraph 2.2 for details). More research has been done on the effects of control over visual stimuli (computers, video sets) on the behaviour of primates in captivity; this research will be reviewed in Chapter 8.

2.5.5.3 Effects of control over aspects of the environment

Line and co-workers (1990a, 1991a; Markowitz & Line, 1989) gave adult rhesus macaques control over a supply of banana-flavored pellets and a radio set (turning it on and off) through manipulation of a device. The animals showed much interest in the device, and spent a quarter of their time using it (both feeder and radio set together). They continued to use the device throughout the whole study period (12 weeks). Additionally, negative behaviour patterns, such as cage manipulation, abnormal behaviour and autogrooming, decreased significantly. Furthermore, the monkeys exhibited lower cortisol levels and heart rate values in response to restraint, and the return to normal heart rate value after restraint was faster. Markowitz and Aday (1998) also mentioned in relation to the above study that the monkeys showed quicker physiological recovery from routine sources of stress in their everyday lives. More research on control of positive events to other areas of the animals' environment is required.

One of the difficulties in providing captive animals with a device that controls environmental variables (such as music) is that often only one member of the group will be able to control the device, while all other group members will be affected by the stimuli. The same problem affects primates housed in a colony room. If the control over the stimuli is given to members of only one cage, other individuals within the colony room have no ability to control it, which may be detrimental to their welfare (Buchanan-Smith, 1997b).

2.5.6 Effects of loss of control

A major problem with providing captive animals with control is that at some point the controlled device may have to be removed; hence the animals may be exposed to loss of control which might have negative consequences (Mineka & Hendersen, 1985; Overmier et al., 1980; Dantzer et al., 1980). Hanson and colleagues (1976) found that when rhesus monkeys experienced loss of control over high intensity noise, cortisol levels were significantly higher than when the same animals had control over the noise, and than monkeys who never had control over the noise. Similarly, Zimmerman and Koene (1998) showed that loss of controllability over light and food led to higher levels of gakel-calls (which serve as a sign for frustration) in laying hens, compared to control sessions. In contrast, Hodgson and Bond (1994) did not find any significant differences in the behaviour of rats that were exposed to loss of control over food delivery to that of individuals who were exposed to uncontrollable food delivery. Brady (1958) exposed monkeys (species was not mentioned) to brief electric shocks. In each pair of monkeys one (“executive” monkey) could stop the shock by pressing a lever, while the other one served as the yoked control (these monkeys had a dummy lever and they lost interest in it quite quickly). The study procedure comprised of several hours (the exact number was changed in each replication of the study) in which the monkey could control the shock, followed by several hours in which the animal had no control over the shock. Only executive monkeys developed ulcers;

some even died. It is likely that these physiological consequences were the outcome of the experience of loss of control that only the executive animals experienced.

2.5.7 The study of the effects of controllability in the present thesis

In the present thesis, I present the results of three studies that examined the effects of controllability over different aspects of the captive environment on the behaviour of marmosets. In the first study, the effects of controllability over additional illumination and heat (as the additional light produced heat) on the behaviour of family groups of marmosets is reported (Chapter 7). In the second study, family groups of marmosets were able to control a visual stimulus, i.e. the projection of coloured lights into their home cages (Chapter 8). In the third study, pair-housed marmosets in two tier caging system were able to control additional illumination and heat in their cages (Chapter 9). In the first two studies, groups that had control over the stimulus were compared to unaffected groups that had no treatment at all, while in the third study, groups (pairs in this case) that had control over the light in their cage were compared to both unaffected pairs and yoked pairs that had additional light but had no control over its operation.

2.6 SUMMARY- The Definitions of the Terms Complexity, Choice, and Control and the Confusion between Them

As has been discussed above, it is possible to distinguish between complexity, choice, and control, however clear definitions and boundaries are needed. It is important to emphasize that the division between the study of complexity, choice, and control, which was made above, is quite artificial, and some of the examples might reasonably have been placed in other sections of the review. When using any of these terms (especially complexity and control) it is essential to provide a clear definition of the term and to clarify its use.

The links between these three terms are extremely complicated, particularly those related to control. When animals are housed in a more complex environment they experience more opportunities to make choices. However, when can we argue that animals have control over their captive environment? Do they experience more control when they live in a more complex environment (as has been argued by Carlstead & Shepherdson, 1994)? Do they experience more control over the environment when they have more choice (as has been argued by Bayne, 1989b)? Alternatively, it may be that control is a completely separate aspect of captive environments.

2.7 DEFINITIONS FOR THE PRESENT THESIS

As mentioned above, it is important to define the terms to avoid ambiguity.
The following definitions are used in the present thesis:

Complexity will be separated into two forms: physical and social complexity.

Physical complexity: The physical complexity of the captive environment is composed of two environmental features. The first is the structural characteristics of the environment (e.g. cage size, cage height, materials of cage itself, etc.). The second feature is the furniture inside the cage (materials of the furniture, quantity of devices, etc.). The physical complexity is lower in barren enclosures and higher in larger and more equipped enclosures.

Social complexity: refers to the size and the composition of the social group (e.g. number of individuals, age and sex of the individuals, familial relationships between individuals, etc.).

Choice: Animals are considered as having choice when they are provided with at least two environmental options. In particular, in Study II in Chapter 4 the marmosets were able to choose between lower and upper parts of their home cage, and in Chapter 6 they were able to choose between their indoor home cages and outdoor cages, while they had free access between these two enclosures.

Control: Animals are considered as having control over their environment only if an overall aspect of their entire enclosure is changed as a consequence of their own response (in this case touching a touch sensitive button). The marmosets are not considered to have control if they can choose between different environments, or if they can manipulate a puzzle feeder or any other responsive object inside their enclosure.

2.8 GENERAL AIMS OF THE PRESENT THESIS

The central aim of the present thesis was to investigate the importance of physical and social complexity, choice, and control, together with the relative significance of each of these aspects, for the welfare of captive primates, using marmosets as the study species. In addition, as a result of the nature of the different studies, the effects of other environmental components are discussed. In Chapter 4, the effects of the level of the cage in a two tier housing system on the behaviour of pair-housed marmosets is discussed. In Chapter 6, the effects of exposure to outdoor conditions together with the effects of occasional access to an enriched cage are added to the effects of choice. Further, in Chapters 7 and 9, the effects of illumination on behaviour are discussed, and in Chapter 8, the effects of visual stimulus are added to the effects of control over this stimulus. A secondary aim of the thesis was to create a better understanding of the normal behaviour of captive common marmosets, particularly in relation to rates of locomotion, inactivity and scent marking.

Chapter 3

General Methods

3.1 THE COMMON MARMOSET

Common marmosets (*Callithrix jacchus*) are the study animals of the present thesis; hence, it is necessary to be familiar with the ecology of wild populations in order to get a better understanding of the behaviour of captive marmosets. Furthermore, the effects of group composition on behaviour are studied; therefore the social system of wild populations is relevant. The common marmoset is one of the six species of the genus *Callithrix* (Rylands et al., 2000). It is a diurnal, small monkey (around 317g for males, and 322g for females, in the wild, Araŭjo et al., 2000), with average body measurements of 25cm from neck to tail base, and a tail length of 28cm (Stevenson & Rylands, 1988). The pelage is brindled black, brown and dark yellow with large white ear tufts, and alternating dark wide and pale narrow bands on the tail (Plate 3.1), and there is no visual sexual dimorphism (Hershkowitz, 1977). The pelage of young and juvenile animals is brown, grey, and lacks the adult markings (Plate 3.2).

The common marmoset is found in northeast Brazil, and has been introduced into the state of Rio de Janeiro and several other parts of the southeast of Brazil. It inhabits a wide variety of habitats such as the lower strata of gallery forests, and secondary forests (but also goes to the top of tall trees on occasion), scrubs, swamps, and tree plantations (Hershwokitz, 1977; Stevenson & Rylands, 1988). It is arboreal, but has also been recorded on the ground to cross forest clearings, and to pick fallen fruits (Stevenson & Rylands, 1988). It is probable that the common marmoset is one of the most adaptable species of the genus, and is classified at Lower Risk by the

IUCN (Rylands et al., 2000). The home range of wild populations is 0.5-6.5ha, and the home range of neighbouring groups overlaps (Hubrecht, 1985; Stevenson & Rylands, 1988; Scanlon et al., 1989; Ferrari & Digby, 1996). It has been suggested that the home range is small, compared to that of other callitrichids because of the marmosets' ability to use the stable food resource provided by tree exudates (Hubrecht, 1985). The marmoset has specialized teeth for gouging trees (Coimbro-Filho & Mittermeier, 1976, 1977), and the exudates they consume are a major part of their diet; they also eat fruits and insects (Stevenson, 1978; Ferrari & Digby, 1996).

The social structure of wild populations is a relatively stable (Ferrari & Lopes Ferrari, 1989) extended family group with a group size of three to fifteen individuals (Hubrecht, 1984; Scanlon et al., 1989; Digby & Barreto, 1993; Pontes & Da Cruz, 1995), but sizes are varied as a result of immigrations (Hubrecht, 1984; Arruda et al., 2005), emigrations, births and disappearances (Ferrari & Digby, 1996; Digby & Barreto, 1993). In captivity social groups of common marmosets are usually monogamous (Poole, 1990; Gerber et al., 2002a, 2002b), and sexual behaviour is inhibited in subordinate females (Abbott, 1984; Evans & Hodges, 1984; Saltzman et al., 1997). However, some spontaneous departures from monogamy, resulting in polygyny, have been observed in captivity but the groups were often unstable (Rothe & Koenig, 1991). In wild populations, monogamous groups have been documented (Albuquerque et al., 2001); however, more (compared to captive populations) cases of two reproductive females in one group were reported (Digby & Ferrari, 1994; Digby, 1995; Ferrari & Digby, 1996; Roda & Pontes, 1998; Arruda et al., 2005; Sousa et al., 2005).

Plate 3.1: An adult common marmoset

Plate 3.2: Young common marmosets

These situations may indicate a stable polygynous mating system (Ferrari & Digby, 1996), but may also indicate a transitional state between two monogamous phases (Pontes & Da Cruz, 1995; Digby, 1999), especially when the offspring of the subordinate reproductive female do not survive (Arruda et al., 2005; Sousa et al., 2005). Further, extra-group mating is relatively common, but usually performed by subordinate females (Digby, 1999; Lazaro-Perea, 2001). There is no evidence for polyandry in common marmosets, although this mating system has been reported in other callitrichids (e.g. *Saguinus fuscicollis*: Terborgh & Wilson Goldizen, 1985).

Common marmosets reach sexual maturity at the age of 18-24 months (Hearn, 1982; Rensing & Oerke, 2005), and usually produce twins, which have better survival than singletons and triplets in both the wild and captivity (Hearn et al., 1975; Jaquish et al., 1991; Sousa et al., 1999). In captive groups, it is advisable to leave young in their natal group until the next set of offspring are born and weaned since previous experience has been found to be important for the development of good parental behaviour (Hearn et al., 1975; Tardif et al., 1984). All group members take part in the carrying of infants (Box, 1977a; Rothe et al., 1993; Yamamoto, 1993; Ximenes & Sousa, 1996), and adults often encourage the youngsters to carry the infants (Hearn et al., 1975). There is no breeding seasonality in captivity, and usually inter-birth intervals are five to six months (Epple, 1970a; Stevenson & Rylands, 1988). In the wild, the inter-birth interval is similar (Hubrecht, 1984), but births occur mainly at the beginning of the dry season, and near to the start of the wet season (Hubrecht, 1984; Sousa et al., 1999).

Common marmosets are used widely in biomedical research to investigate immunology, virology, teratology, endocrinology, neurobiology and behaviour (Deinhardt, 1971; Poswillo et al., 1972; Hearn et al., 1975; Boyd Group, 2002). There are many advantages to their use in laboratories from a practical perspective. Their small size (although captive individuals weigh more than their wild counterparts, Araŭjo et al., 2000), makes them relatively easy to handle and economical to maintain (Hearn et al., 1975; Poole & Evans, 1982). Further, under suitable conditions they will breed rapidly (Stellar, 1960; Epple, 1970a; Tardif et al., 1984), and although the life-span of wild individuals is 11.7 years (Ross, 1991), captive individuals may reach the age of 20 years (Kirkwood & Stathatos, 1992). All the marmosets used in UK laboratories are captive bred, mostly in the UK, as wild-caught marmosets are not available (Boyd Group, 2002). Further, over the last ten years there has been an overall downward trend in the number of callitrichids used in scientific procedures in Great Britain. For instance, 643 callitrichids were used in 2005 compared to 1060 in 2000 (Home Office, 2006, and 2001, respectively).

The common marmoset is used as the study animal in the present thesis for several reasons:

1) Its frequent use in captivity leads to wider application of findings.
2) A large sample size was available for the study.
3) The range of group compositions and enclosures in which it is housed in captivity allows the study of the effects of social and environmental complexity.

3.2 STUDY ANIMALS

Study animals were common marmosets housed at the Medical Research Council (MRC) Human Reproductive Sciences Unit, Bush Estate, Edinburgh, Scotland. It is standard for the marmosets at the MRC to wear a tag on a chain around the neck to aid identification; numbers on these tags are used in the thesis for the animals' identification. A total number of 238 common marmosets (all captive bred) were used for the different studies of the present thesis (see Table 3.1).

Table 3.1: Number of animals and group compositions in all studies

	Number and composition of study groups	Total number of animals
Chapter 4		
Study I	32 pairs	64
Study II	19 pairs	38
Study III	19 pairs	38
	8 small family groups	16 (adults only)
	12 large family groups	30 (adults only)
Chapter 5	1 large family group	8
Chapter 6		
Study I	4 large family groups	25
Study II	8 large family groups	46
Chapter 7	12 small family groups	43
Chapter 8	12 large family groups	44
Chapter 9	36 pairs	72
		Total number of animals-238

* Animals from the studies in Chapter 4 are not included in the total number of study animals as all animals in these studies were part of the studies in other chapters (see Chapter 4 for more details).

Animals were housed in pairs, small family groups (3-5 individuals), and large family groups (5-8 individuals). Animals were divided into two age groups of adults and youngsters. Youngsters were defined as less than 10 months (300 days) old, following Ingram (1977a, 1977b). Infants (younger than 45 days old) were not included in the study as they were still dependent on other group members and spent a considerable amount of time being carried. Although Ingram (1977a) defined infants as younger than eight weeks (64 days), youngsters older than 45 days were observed since captive common marmosets become independent earlier than their wild conspecifics (Stevenson & Rylands, 1988). On a few occasions animals were used for two different studies. When a whole group was used twice for the studies in Chapters 7-9, it used at least once as an unaffected group (no treatment), as repeated treatment of the same animal may markedly influence behaviour (Martin & Bateson, 1993). In a few cases a single animal was used twice, but as this was for different studies it was not considered to adversely impact on the results.

3.3 HOUSING AND HUSBANDRY

Marmosets were housed in different cage sizes according to the size of the group. Pairs were housed in single cages (one quarter of the quadruple cage, Figure 3.1, and plate 3.3), with the exception of pairs in Study II in Chapter 4 that were housed in double cages. Small family groups were housed in double cages (half of the large cage), and large family groups were housed in quadruple cages (a whole cage as seen in Figure 3.1, and Plate 3.4). The exact measurements of the cages are given in Table 3.2. Cages were furnished with wooden logs, a rubber shelf mounted on the front of the cage, a metal nest box, and sometimes a plastic shelf and/or a short bamboo bridge. The metal tray on the floor of each cage was filled with wood shavings to promote foraging, and to provide soft floor bedding. All quarters of the quadruple cages were similar and therefore, larger cages contained more furniture (but only one nest box was provided for each group, regardless of its size). Cages were positioned side by side in colony rooms while each colony room contained eight large cages, four along each opposite wall (see Figure 3.2). This housing system allowed visual contact between animals of opposite sides of the colony room. Some cages were fitted with mesh verandas which enabled the animals to be in visual contact with neighbouring groups. Marmosets had auditory, and sometimes visual contact with personnel while in the corridor or in other laboratory rooms.

Table 3.2: Measurements of all cage types used in the different studies

	High	**Width**	**Depth**
Single cage	1.15m	0.75m	1.1m
Double cage	2.30m	0.75m	1.1m
Quadruple cage	2.30m	1.50m	1.1m

Temperature in the colony room was maintained at 22-23ºC, and humidity at around 55%. The rooms were maintained on a twelve-hour light/dark cycle (700-1900h). Water was available *ad libitum*, and marmosets were fed once daily at around 1300h. The diet consisted of a mixture of New World primate pellets and fresh fruits (banana, apple, orange, grapes, tomato, and pears). Four times a week monkeys were also given dry fruits (dates, raisins), peanuts, and occasionally bread, and on the other three days, they were given ‘porridge’, consisting of yoghurt, baby rice and protein mixture with added vitamins and minerals. Food was served in paper ‘baking cases’ and was placed on the cage floor. Food leftovers were taken from cages daily, and colony rooms were cleaned daily between 800h and 1030h (excluding weekends). Wood shavings were changed weekly, and whole cages were replaced with clean cages every fourth week. During this procedure, used cages were cleaned in a cage washing machine. Any other experimental or husbandry routine procedures (e.g. weighing, blood sampling or manual palpation to detect pregnancy) were usually carried out before 1300h.

Figure 3.1: Schematic diagram of four single cages (not to scale)

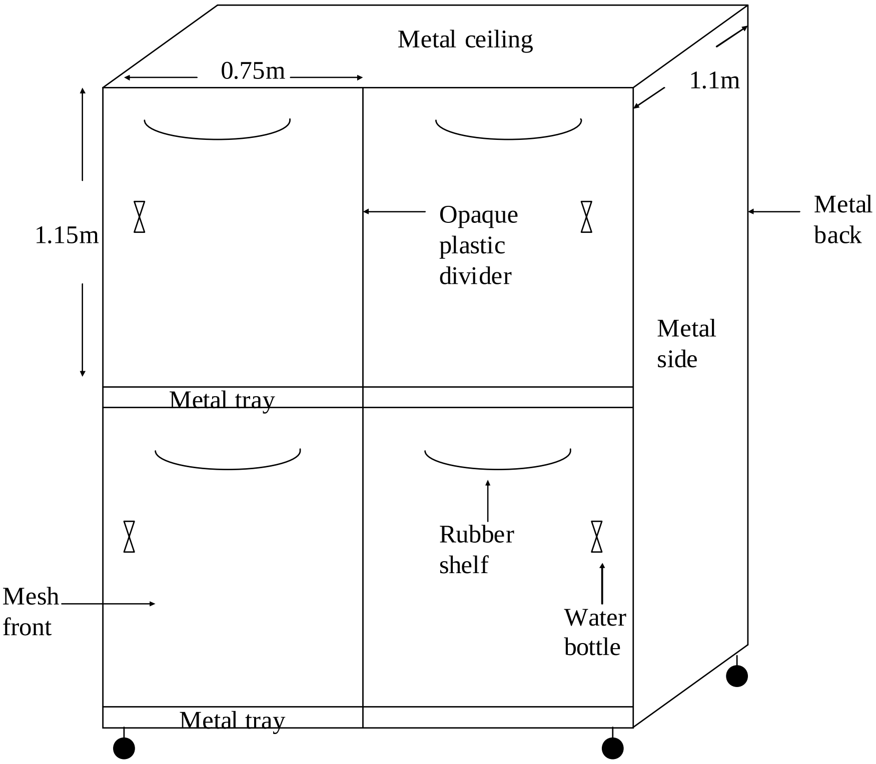


Figure 3.2: Schematic diagram of a colony room (not to scale)

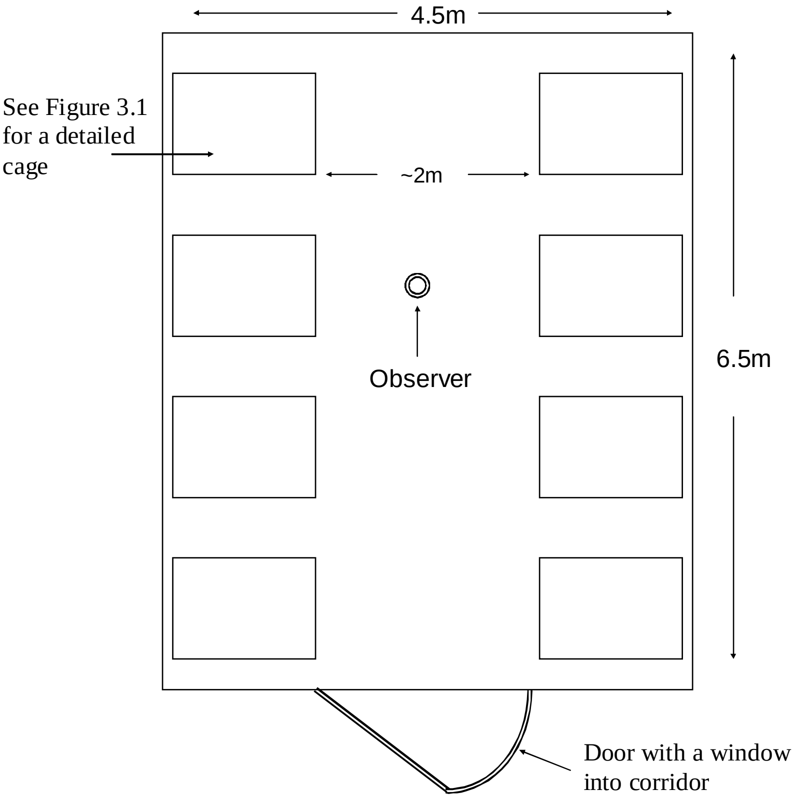


Plate 3.3: Single cage

Plate 3.4: Quadruple cage with dividers in place to create two vertical double cages

3.4 BEHAVIOURAL OBSERVATIONS

3.4.1 Observation protocol and data collection

Behavioural data were recorded in all studies and collected on a Psion Workabout (a hand-held computer) running THE OBSERVER 3.0 event recording computer programme (Noldus, 1995). I spent several hours inside the colony room over at least three consecutive days before the beginning of each study to allow habituation of the animals to my presence. However, as marmosets were never completely habituated to my presence, and tended to spend considerable amount of time watching me during observations, one of the recorded behaviours was ‘watching the observer’. During observations I sat on a stool around 1.5m from the front of the cage. Circadian rhythms in the behaviour of marmosets have been reported in captivity (e.g. Erkert, 1989, 1997; Menezes et al., 1993) and in the wild (e.g. Stevenson & Rylands, 1988). Observations took place between 1030h and 1600h (with a break between 1230h and 1400h to avoid feeding time) and were evenly distributed within and/or matched between groups to minimise this potential confound of time of day.

3.4.2 Sampling methods

Continuous focal animal sampling was used. Observation sessions for individual animals lasted four minutes in all studies, with the exception of the study described in Chapter 5, in which five-minute focal observations per animal were possible because of the small sample size (one family group). Observation length was based on three criteria. First, increasing the sample size improves statistical power and offsets the loss due to individual differences (Martin & Bateson, 1993). Second, thanks to the large number of marmosets at the MRC Unit, it was feasible to have a large sample size in each study. However, because of the large sample size, it was impossible to devote a large amount of time to the observation of each animal. Third, to ensure this was appropriate, a pilot study was carried out to examine whether there was a significant difference between a single four-minute focal animal observation session per day and two separate two-minute focal animal observation sessions per day.

In the pilot study nine adult female and nine adult male marmosets were studied and each individual was observed during three consecutive days. On each day, every animal was observed three times for a two-minute focal observation session. Two of the three sessions were continuous whereas the third was carried out either earlier or later in the day. Data from the two continuous sessions were combined, and data from one of these sessions were combined with data from the third session. Paired samples t-tests were performed for females and males separately. No significant differences were found between the two different data collection methods for any behaviour. Therefore, the more convenient data collection method of a single four-minute observation session was applied in all studies (with the exception of the study in Chapter 5).

In order to increase the reliability and the validity of the results, and to avoid possible influences of individual differences, data were collected in three phases for all studies: baseline phase, enriched phase (which was different in the various studies), and post-study phase. This method allowed the performance of within-subject comparisons in addition to the between-subject comparison when animals of different study groups were exposed to different treatments (see Table 3.3). The behaviour of each animal was likely to have been influenced by that of its cage mates, and so data from each individual could not be treated as independent. For this reason, statistical tests were carried out for all members of each group (adults and youngsters separately), i.e. each group was effectively treated as one individual in the analysis, with the exception of the studies in Chapter 6 (see details below). Further, when study groups were family groups comprised of adult and young animals (see Table 3.1), the effects of the study treatments could have been different for marmosets from different age groups. Therefore, statistical analyses were carried out for adults and youngsters separately (with the exception of Chapter 5). Here again, adults or youngsters from each group were effectively treated as one individual in the analysis.

Table 3.3: Types of analyses used for the different studies

	Within-subjects	**Between-subjects**	**Additional data**
Chapter 4			
Study I		✓	
Study II	✓		Preference for cage locations
Study III		✓	
Chapter 5	✓		
Chapter 6			
Study I	✓		Usage of outdoor cages
Study II	✓		"
Chapter 7	✓	✓	Preference for cage locations, duration and frequency of light usage
Chapter 8	✓	✓	"
Chapter 9	✓	✓	Duration and frequency of light usage

It was not possible to treat groups as separate data points in the studies in Chapter 6, because during the test phase of these studies (Outdoor phase), the marmosets had free access between their indoor home cages and the outdoor cages. For this reason different individuals were observed in every data collection session, and the number and identity of individuals which were observed were inconsistent. In these studies, data were analysed for each individual separately, and no analysis was carried out for whole groups. In addition, only marmosets that were observed at least three times outdoors were used for the behavioural analysis. In all studies, Kolmogorov-Smirnov tests were carried out to check whether the data were normally distributed, and when needed, log transformations were applied to allow parametric tests. Various types of ANOVAs and t-tests were applied as appropriate to the study questions and the data. In none of the statistical analyses was Bonferroni correction carried out as although they reduce the probability of Type I error, at the same time they increase the probability of Type II error (Caldwell et al., 2005).

The duration and frequency of all behaviours were recorded. Although Martin and Bateson (1993) distinguish between reporting longer duration states and short duration events, the results of all studies are presented as percentage duration, even when the behaviour was of relatively short duration (i.e. scent marking and scratching). However, for these two behaviours both the frequency and percent of time were analysed to ensure percentages correlated well with frequencies. To illustrate this, data from Chapter 9 are analysed and presented (scent marking: Pearson $r=0.98$, $P<0.001$; scratching: $r=0.95$, $P<0.001$, see Figures 3.3 and 3.4).

Figure 3.3: Scatter-plot of frequencies of scent marking against percents of time per four-minute observation session

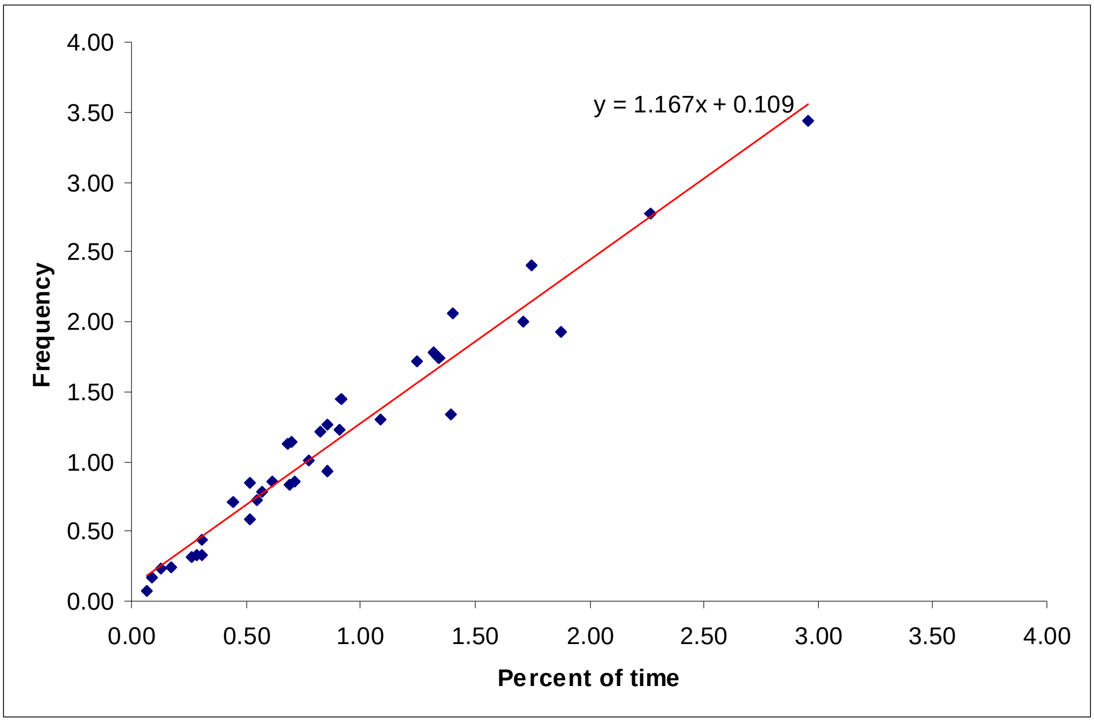
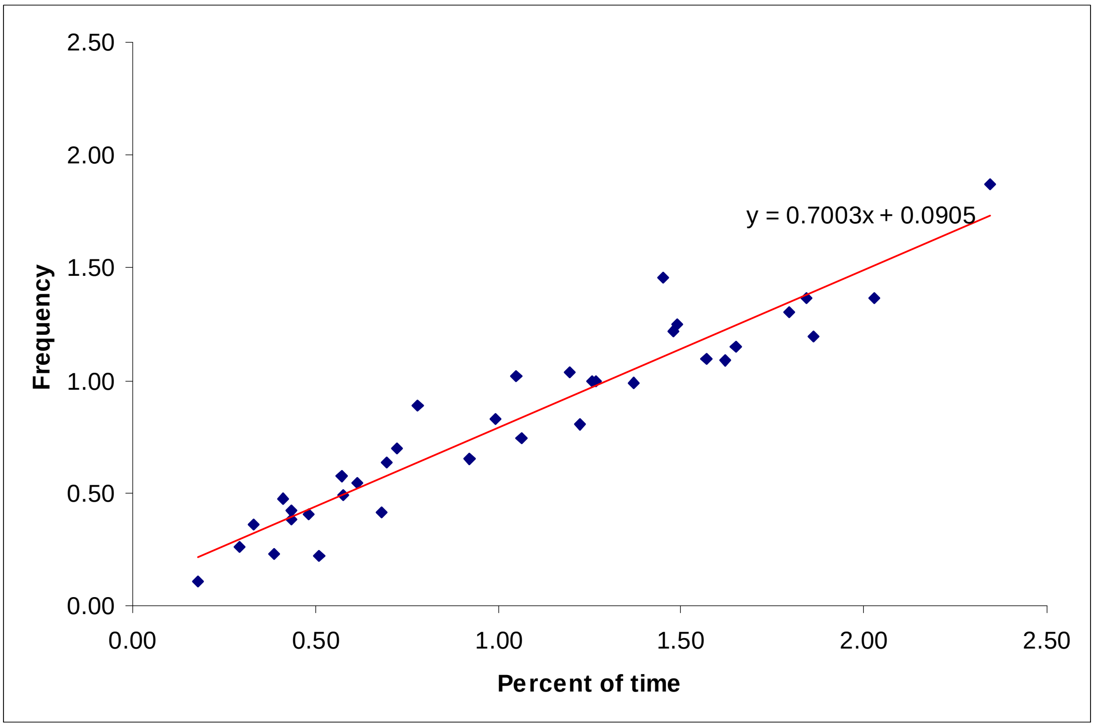


Figure 3.4: Scatter-plot of frequencies of scratching against percents of time per four-minute observation session



From these graphs, the relationship between the two measures can be calculated. For example, 1% of time spent scent marking means that the marmosets scent marked for a mean of 1.28 times per four-minute observation session (equivalent to a rate of 19.2 scent marks per hour). 1% of time for scratching means that the marmosets scratched for a mean of 0.79 times per four-minute observation session (11.85/hour).

3.4.3 Recorded behaviours

Since behavioural observations were the main source of information in all studies, it was important to obtain a wide range of different behavioural categories and types (see Table 3.4). Behaviours in each category were mutually exclusive. Additional behaviours such as aggression, stereotyped behaviour (e.g. moving rapidly in circles along a specific path), and time inside the nest box were observed and recorded. However, these behaviours were shown at such low levels and no significant differences between study conditions were found for any of them in any of the studies. Foraging behaviour (e.g. animal looking for food or eating) was recorded for relatively long durations, but no significant differences were found in any study, with the exception of the studies in Chapter 6, where a comparison between the study phases was not valid for this behaviour (see Chapter 6). Therefore, these behaviours will not be discussed. Vocalisation was very difficult to reliably record and therefore is not discussed.

The results of the statistical analyses are given in tables for all the behaviours noted in Table 3.4 in each experimental chapter. However, only behaviours in which a significant difference was found for the particular study are presented in figures.

Table 3.4: Behavioural categories and definitions used for all studies (based on Stevenson & Poole, 1976, and Cilia & Piper, 1997)

Category	Behaviour	Definition
Locomotion and Inactivity	**Agitated locomotion**	Animal moving between locations rapidly while its gait is not relaxed
	Calm locomotion	Animal travelling between locations by walking, running, climbing, or jumping and its gait is relaxed
	Inactive alert	Animal is stationary, awake and aware of the surroundings
	Inactive rest	Animal is stationary, usually the tail curled around the body or through the legs, with eyes open or closed
Individual behaviour	**Explore**	Animal investigating objects in its environment by sniffing, licking, biting, or handling the objects, or attending to them whilst walking around them
	Autogroom	Animal cleaning its own fur and/or skin with hand, or mouth
	Scent mark	Animal rubbing anogenital area along a substrate
	Scratch	Animal repeatedly moving its hand or foot whilst claws rapidly drawn across its fur and/or skin
	Solitary play	Animal hanging from or moving objects accompanied by rapid movement around the enclosure
	Tree gouge	Animal gnawing on wooden logs
	Watch obs.	Animal visually attending to the observer while stationary or moving
Social behaviour	**Allogroom**	Animal cleaning another animal's fur and/or skin with hand or mouth
	Contact	Animal is stationary and in physical contact with another individual
	Social play	Animal engaging in high activity interaction with other individuals, involving non-aggressive physical contact
*__Location inside the cage__	**Lower**	Animal is in the lower half of the double or quadruple cage
	Upper	Animal is in the upper half of the double or quadruple cage
Device orientated behaviours	****Close to device**	Animal sitting on the rubber shelf close to (almost touching) the light or coloured light box
	****Manipulate device**	Animal touching the light box and/or switching the light on or off, or trying to "catch" the coloured light's reflection
	*****Look at device**	Animal following the light's reflections on the cage's walls with its eyes

* Relevant to Chapters 4, 7, 8; ** Relevant to Chapters 7, 8, 9; *** Relevant to Chapter 8

3.4.4 The significance of the performance of behaviours

In order to understand the effects of the study treatments on the welfare of the marmosets, it is necessary to interpret the meaning of the performance of the various behaviours. However, it is also important to emphasize that the performance of a single behaviour has little meaning by itself, and it is necessary to consider the overall behavioural repertoire of an animal and the context before reaching any conclusions concerning the animal’s welfare state. Shepherdson (1989, 1990) suggested factors for judging the importance of a given behaviour for animal welfare:

1) The proportion of the behaviour in the activity budget of wild individuals
2) The short-term survival value of the behaviour in the wild
3) The degree of the internal (as opposed to external) stimuli to perform the behaviour
4) The consequences of performance of the behaviour on physiological health
5) The correlation of the behaviour with other welfare indicators

According to Shepherdson (1989), and under the above criteria, behaviours such as foraging, resting, locomotion, and social interaction are likely to be important to most captive animals. In addition, Poole (1988a) suggested that an increase in the animal’s behavioural repertoire (desirable behaviours in the right context) may indicate an improvement in welfare. Now I will describe the significance and functions of the behaviours that I recorded in the different studies. A summary list of desirable and undesirable behaviour is given in Table 3.5.

Locomotion and inactivity

Locomotor activity is a desirable activity that, together with other positive changes, may indicate better welfare for primates in captivity (Bayne, 1989a; Snowdon &

Savage, 1989; Buchanan-Smith et al., 2004). Conversely, large proportions of inactivity, in species that are usually active in the wild, are not desirable and are considered as indications of poor psychological well-being (Chamove 1989; Chamove & Anderson 1989; Broom & Johnson 1993). The mean daily path of wild common marmosets is 0.5-1.0km (Hubrecht, 1985), and locomotion activities occupy 35% of their time budget, while they are stationary for 53% of their waking time (Stevenson & Rylands, 1988). The achievement of a similar distribution between locomotion and inactivity is also desirable for captive populations, although different distribution may result from factors other than welfare condition (e.g. different data collection methodology, see section 1.2.3). It is also critical to distinguish between different types of locomotion and inactivity, in relation to the individual animal. For instance, when an animal is apathetic and inactive an increase in activity levels is desirable, but on the other hand, hyperactivity should be reduced (Poole, 1988a). Further, in the present thesis a distinction is made between calm and agitated locomotion (excluding play) and between inactive rest and alert. In welfare studies such discrimination between different types of locomotion and inactivity patterns is not common (but see Chamove & Rohrhuber, 1989; Johnson et al., 1996), and therefore the interpretation of results may be contradictory.

In general, it is desirable to increase levels of calm locomotion and inactive rest, and at the same time to decrease levels of agitated locomotion and inactive alert behaviours which may indicate a stressful situation. However, it is essential to be aware of other behavioural changes, as a reduction in agitated locomotion (or overall level of locomotion) and an increase in levels of inactive (both rest and alert) may indicate variation in physiological functioning which cannot be easily mapped onto welfare state. Further, Moodie and Chamove (1990; Chamove & Moodie, 1990) suggested that an exposure to brief threatening events (e.g. an exposure to over-flying bird model), which would increase levels of agitated locomotion and inactive alert, may be beneficial to captive primates, as it mimics elements from the natural habitat, and keeps the animals aroused (as opposed to bored). However, Chamove and Moodie's work (1990) received criticism (e.g. Roush et al., 1992), and the desirable levels of arousal in captive primates are not clear.

Explore

Exploratory behaviour is also usually judged as desirable for captive primates (Chamove & Anderson, 1989). The performance of exploratory behaviour may indicate lower levels of stress. For example, Barros and co-workers (2001) described an increase in exploration in marmosets after buspirone (an anti-anxiety agent) treatment. Further, the opportunity to perform investigative behaviour meets one of the basic internal animal needs of information-gathering, and has a significant influence on welfare (Wemelsfelder & Birke, 1997; Mench, 1998a). Complexity is one of the most important stimuli that elicit exploratory behaviour, as it provides more potential opportunities for responding (Berlyne, 1960; Dember & Warm, 1979; Hughes, 1997). Therefore, it could be concluded that higher levels of exploratory behaviour indicate a more complex environment. However, levels of exploratory behaviour may also be affected by factors other than the characteristics of the animal's environment. Kaplan and Rogers (1999) found that common marmosets that had received less anogenital licking by their mothers in early infancy were less likely to explore novel objects later in life. One explanation for this positive correlation may be that anogenital licking reduced stress levels in infants. The idea that stress inhibits exploratory behaviour was also suggested by van der Harst and co-workers (2003), when rats showed decreased levels of exploration while anticipating a negative stimulus (forced swimming). Barros and colleagues (2000) also found that common marmosets increased frequency of exploration only after an anxiolytic treatment, when they were exposed to a fearful situation (exposure to a stuffed natural predator).

Autogroom

Autogrooming behaviour is a natural behaviour of self-care; however, when autogrooming appears in high levels and/or out of context, it could be considered as a displacement activity which may indicate poor welfare or even stress (Maestripieri et al., 1992; Barros et al., 2000). Aureli and van Schaik (1991) found that long-tailed macaques increase levels of autogrooming after being the victim of an agonistic conflict, probably as a tension reduction strategy. Similarly, Schino and co-workers (1996) found that long-tailed macaques showed lower levels of autogrooming after being treated with anxiolytic drug. However, no evidence for autogrooming as a displacement activity in callitrichids has been found.

Scent mark

Scent marking is a well known natural behaviour of marmosets in captivity (Epple, 1975; Box, 1988) and in the wild (Lazaro-Perea et al., 1999), mainly performed by adults (Lacher et al., 1981; Stevenson & Ryland, 1988). Epple and colleagues (1993) studied the scent marks of saddleback tamarins (*Saguinus fuscicollis*) and found that these marks communicate a large body of information about the individual that produces them. Different functions have been offered for the performance of scent marking: orientation in the environment (Epple, 1972), marking important food sources (e.g. Lacher et al., 1981), intra-group communication (e.g. Epple, 1970a; Lazaro-Perea et al., 1999), inter-group communication such as territorial defence (e.g. Nogueira et al., 2001) and familiarization with other individual to form new groups (Epple, 1972). In captive callitrichids, scent marking frequently occurs when animals are highly aroused, but may also occur under conditions of normal or low arousal levels (Mack & Kleiman, 1978). Barros and co-workers (2001) found that scent marking disappeared after administration of buspirone, and Cilia and Piper (1997) labelled scent marking as an anxiety related behaviour, after they found that diazepam (another anti-anxiety agent) treatment reduced levels of this behaviour. Further, Bassett and colleagues (2003) found that common marmosets showed increased scent marking after being exposed to mildly stressful procedure (capture and weighing). In addition, Sutcliffe and Poole (1978) argued that close visual contact between marmoset groups may increase frequencies of scent marking. Similarly, Woodcock (1982) found that marmoset pairs which were visually isolated from other pairs showed no scent marking behaviour. Therefore, social tension may increase levels of scent marking, as a consequence of a stressful situation, or as a vestige of the natural behaviour of marking territorial boundaries.

Scratch

Scratching, although present in non-stressed individuals, is known to increase at times of stress (e.g. Chamove, 1996), and has been classified as a displacement activity; a behaviour that is irrelevant to the situation and may indicate stress (Cilia & Piper, 1997). Several researchers found levels of scratching to be reduced in response to anxiogenic agent treatments (*Macaca fascicularis*: Schino et al., 1991; *Callithrix jacchus*: Cilia & Piper, 1997; *C. penicillata*: Barros et al., 2000). Bassett (2003;

Bassett et al., 2003) found that the mildly stressful routine procedure of capture and weighing induced significant increases in amounts of self scratching in untrained common marmosets.

Tree gouge

Wild marmosets gouge holes in trees in order to gain plant exudate which provides a significant part of their diet (Stevenson & Rylands, 1988). A strong association has been found between scent marking and tree gouging, 40% of tree gouging bouts being immediately followed by scent marking (Stevenson & Rylands, 1988). However, Rylands (1985) argued that gouge holes attract scent marking only because they are certain to be visited by other group members. The only explanation I found in previous literature for the performance of gouging by (young) captive marmosets was to investigate objects in their environment (Stevenson & Poole, 1976). As tree gouging is a natural behaviour of wild marmosets, it may be viewed as desirable in captivity, indicating an increase in natural behavioural repertoire. It may also be seen as an expression of a proximate need of the marmosets, even though the ultimate need of avoiding death by starvation is not relevant in captive conditions (Dawkins, 1983). On the other hand, in captivity marmosets usually perform tree gouging out of context, as they do not gain gum out of the holes that they gnaw. Further, my observations showed that frequently the marmosets gouge wooden logs when they are agitated or in conflict with neighbouring groups. Hence, I would suggest that tree gouging may also be viewed as a displacement activity (based on Maestripieri et al., 1992 and Schino et al., 1991, 1996). To sum up, the function of tree gouging behaviour in captive marmosets is not clear and obviously further research in which the context is investigated is needed. Therefore, this behaviour will not be interpreted in terms of welfare state.

Watch observer

Caine (1990) found that red-bellied tamarins (*Saguinus labiatus*) reacted similarly to the presence of either familiar or unfamiliar observers; in both cases they delayed entry into their nest box, which could be explained as anti-predator behaviour. An increased amount of time spent watching the observer may also indicate boredom, and thus that the observer represents a positive stimulus. In either of these responses, the interpretation of this behaviour in terms of animal welfare is not clear.

Allogroom

Wild common marmosets spend 10-14% of their waking time in social activities (Stevenson & Rylands, 1988; Digby, 1995). Allogrooming has been also frequently observed in captive marmosets (Woodcock, 1978). Box (1975b) pointed out that social grooming is a frequent source of social interaction and maintenance of health. In addition, Cilia and Piper (1997) reported an increase in allogrooming in marmosets following diazepam (anxiogenic agent) treatment. It was also suggested that allogrooming may serve as a tension-reduction mechanism in other primates (Terry, 1970; Schino et al., 1988); however, there is no evidence for this in marmosets. Therefore, higher levels of allogrooming will be referred as an indicator of better welfare.

Contact

Social contact may be seen as a positive social interaction, as marmosets tend to rest in close proximity to each other (Stevenson & Poole, 1976), and in the wild they spend the whole night on a tree fork piled on top of each other (Stevenson & Rylands, 1988). On the other hand, Cilia and Piper (1997) reported a decrease in social contact following diazepam treatment. Further, Smith and co-workers (1998) noted that separated marmosets showed higher levels of close proximity (contact) upon reunion, and interpreted this behaviour as a method to reduce stress. The interpretation of social contact is difficult, as it may be seen as a positive natural social behaviour, but it may also serve as an indicator of a stressful situation.

Social and solitary play

Play behaviour is usually considered as an extremely desirable behaviour for captive primates. Lee (1983) argued that social play tends to appear in relaxed circumstances when stress is minimal. Play behaviour is also important for the development of young animals, and Chalmers and Locke-Haydon (1984) found that social play promoted specific skills (e.g. locomotor and social skills) in young common marmosets. Play was observed in wild marmoset populations at lower rates than in captive groups, and play patterns were more arboreal in the wild (Stevenson & Poole, 1982). In both wild and captive populations young animals tend to play more than adults (Voland, 1977; Stevenson & Poole, 1982), and adult animals were only occasionally observed playing with other adults (Stevenson & Poole, 1976).

Location inside the cage

Marmosets are arboreal monkeys, and tend to prefer the upper part of their captive enclosures (Ely et al., 1998; Buchanan-Smith et al., 2002). However, Poole (1988a) suggested that better utilisation of the captive environment, such as greater usage of the available cage space may indicate an improved welfare state. Therefore, in the present study, a more even utilization of the lower and upper parts of the cage will be referred to as desirable. As marmosets tend to spend significantly more time in the upper part of the cage, an increase of the amount of time spent in the lower part of the cage is desirable (as long as it is voluntary and they are not acting in a subordinate manner to conspecifics).

Although it is necessary to determine which behaviours we would like to promote and which behaviours we prefer to reduce or prevent in the behavioural repertoire of captive animals, what constitutes ‘normal behaviour’ for captive animals is thus far unclear. The terms ‘normal behaviour’ and especially ‘abnormal behaviour’ are consistently used in welfare studies, with no explicit definition. We usually compare the behaviour of captive individuals with the behaviour of their wild conspecifics, which we consider to be ‘normal behaviour’; however, we must take into account the environmental differences that may influence the frequency and/or duration of certain behaviours. In the General Discussion (Chapter 10) an attempt is made to establish a ‘normal range’ of frequencies/durations of several behaviours for captive common marmosets by comparing data from the present thesis with those of other studies on laboratory-housed and wild common marmosets. In addition, behaviours whose interpretation is unclear in terms of the welfare of captive marmosets are also discussed in the General Discussion.

Table 3.5: Desirable (elevated levels indicate positive changes in welfare) and undesirable (elevated levels indicate negative changes in welfare) behaviours for captive marmosets

Desirable	Undesirable	Interpretation is not clear in terms of welfare state
Calm locomotion	Agitated locomotion	Contact
Inactive rest	Inactive alert	Tree gouge
Explore	Scent mark	Autogroom
Allogroom	Scratch	Watch observer
Solitary play		
Social play		
Usage of lower part of the cage		

3.5 ADDITIONAL SOURCES OF DATA

In some of the studies further data were collected in addition to the behavioural observations (see Table 3.3). In the studies in Chapter 6, the amount of time that marmosets spent in the outdoor cages (in different weather conditions) was also important, in order to study their preferences regarding the outdoor cages, and the effects of weather conditions on these preferences. Therefore, outdoor cages were checked three to four times a day for animals' presence, during the Outdoor phase of the studies, and data on weather and temperature were taken each time.

In the studies in Chapters 7, 8, and 9, the frequency and duration of device usage were also collected. These data were obtained using an electronic counter (for frequency) and an alarm clock (for duration), which were connected to the device (Plate 3.5). The electronic counter recorded the overall amount of button presses, and the alarm clock measured the overall time in which the light was on. Further details regarding the device are given in Chapter 7 (light), and Chapter 8 (coloured light).

Plate 3.5: The light box (used in the studies of Chapters 7, 8, and 9) from its back (the outside-cage point of view)

Chapter 4

Choice and Complexity in Relation to Cage Level, Cage Size, and Group Composition

4.1 INTRODUCTION

Prior to discussing the effects of complexity, choice, and control on the behaviour of common marmosets, it is interesting to examine the effects of more basic aspects of the captive environment. In some cases the effects of these basic aspects seem obvious, so no experimental research has been done, and furthermore, legislation has been made based on no experimental data. For example, new European and U.K. legislation (Council of Europe, 2004; Home Office, 2005) bans the use of the two tier caging system, without being based on any experimental data to show the effects of cage height on the welfare of monkeys in captivity. Further, it is recommended that, whenever possible, callitrichids are housed in family groups. This recommendation is based on data from wild callitrichids; however, the captive environment is different to the natural habitat in many ways, and no study has been done on the effects of group composition on the behaviour and the welfare of callitrichids in captivity.

In the present chapter, the effects of some very basic aspects of the captive environment are discussed. The first aspect is the level of the cage, when common marmosets are housed in pairs in a two tier housing system. The second aspect is the size and the height of the cage, when pair-housed marmosets are moved from a two tier housing system (single cages) to full height cages (double cages). The third aspect is the composition of the group, when pair-housed adult marmosets are compared to family group-housed adults.

4.1.1 Effects of a two tier housing system on the welfare of captive primates

European and British legislation for captive conditions for primates in research bans the use of the two tier housing system (Council of Europe, 2004; Home Office, 2005). Nevertheless, research on this housing system is still important, as the United States' legislation allows the two tier housing method, and the impact of it on the animals' welfare is uncertain. Further, the United States' regulations have an internal contradiction, as they require uniform diffusion of lighting throughout animal facilities (United States Department of Agriculture, 1991), whereas several scientists have argued (Bellhorn, 1980; King & Norwood, 1989; Reinhardt et al., 1992; Reinhardt, 1997b; Reinhardt & Reinhardt, 1999, 2000) and shown that in two tier housing systems, light intensity in the lower tiers is much lower than that in the upper tiers (Scott, 1991; Schapiro et al., 2000). The impact of light intensity on activity levels (*Macaca mulatta*: Isaac & DeVito, 1958; Draper, 1965, *Saguinus oedipus*: Hampton et al., 1966; *Aotus lemurinus griseimembra*: Erkert & Gröber, 1986), reproduction (*Callithrix jacchus*: Heger et al., 1986) and depression (humans: Lewy et al., 1982) has been documented. However, there is little evidence regarding lighting needs for primates in captive environments, and guidelines for the care and management of primates in research facilities in the U.S., Europe and the U.K. are general and do not give specific recommendations for light intensity.

In addition to the variation in light intensity, other factors may differ between upper and lower tiers. When monkeys are housed in lower row cages, they are restricted to a more terrestrial life style (even though many monkey species are arboreal), and they are not able to show the vertical flee response. Further, it is less convenient for personnel to bend down to inspect them, so they tend to receive less attention than animals that are housed in upper tier cages (Reinhardt & Reinhardt, 1999; Reinhardt, 2004). Although the environmental conditions in the two housing levels are certainly different, the impact on the welfare of the monkeys is unclear, as findings from different studies are contradictory. Scott (1991) showed that common marmosets in lower tiers were significantly less active compared to marmosets in upper tiers, in the same colony room. In addition, Box and Rohrhuber (1993) found that cotton-top tamarins (*Saguinus oedipus*) housed in upper cages engaged in more close contact (huddling) and were less inactive than those housed in bottom cages.

Buchanan-Smith and colleagues (2002) studied the feeding height preferences of captive common marmosets, and the effects of cage level on these preferences. They found no effects of cage level on most study measures (e.g. number of visits to bowl, amount of eaten food, and use of enclosure). However, when they presented a single food bowl at one of two heights, there was a significant interaction between cage tier and bowl position. The lower tier monkeys spent less time at the bottom bowl and more time at the top bowl than upper tier individuals did. The authors concluded that cage level affected the monkeys differentially, and that lower tier marmosets were more reluctant to spend time on the floor. Additionally, Ely and co-workers (1997) found that common marmosets preferred the upper part of the cage compared to the lower part, although this preference reduced when the cage size decreased.

Most studies on the effects of two tier housing on the behaviour of singly housed macaques have found no impact of cage level on behaviour (*Macaca fascicularis*: Schapiro et al., 2000; *M. mulatta*: Schapiro & Bloomsmith, 2001; *M.*

nemestrina: Crockett et al., 1992, 2000; all three species: Bentson et al., 2004), nor cortisol levels (*M. fascicularis*: Crockett et al., 2000). However, Bentson and co-workers (2004) found that macaques (all the above species) in upper tiers spent a greater amount of time in the front third of their cage. Further, Woodbeck and Reinhardt (1991) reported that rhesus macaques housed in lower row cages spent significantly more time perching on PVC pipes compared to animals that were housed in upper cages.

From the above studies it appears that callitrichids are more affected behaviourally from the location of their cage than macaques, although macaques also prefer to be off the ground, and in a brighter position in their cage. However, the housing conditions of the macaques in both caging levels were worse than those of the callitrichids, as they were housed singly, and the relative size of their enclosures was smaller. Therefore, it is possible that the welfare of the macaques was poor in all cages and the level of the cage was irrelevant. More research is needed on the effects of two tier housing on callitrichid species, as previous research has presented the results of informal observations only (Scott, 1991) or has had a small sample size (Box & Rohrhuber, 1993)

4.1.2 Effects of cage size on the welfare of captive primates

Legislation for captive conditions for primates in research addresses the characteristics of the animals' enclosure, and determines minimum cage measurements (see Table 4.1). However, the stringency of the legislation differs between countries. United States' guidelines require primary enclosures that provide sufficient space to allow each nonhuman primate to make normal postural adjustments with adequate freedom of movement (USDA, 1991). U.K. guidelines also stress the importance of adequate enclosure height, which provides an additional sense of security for the animals (Home Office, 2005). European and International guidelines also require sufficient space to allow the animals to utilise as much of the cage volume as possible (Council of Europe, 2004; IPS, 1993).

Table 4.1: Legislation for minimum enclosure size for marmosets in captivity

	Minimum floor area for group housed animals (m^2)	**Minimum floor area per animal (m^2)**	**Cage height (m)**	**Minimum volume per additional animal over 5 months (m^3)**
U.K. (Home Office, 2005)	1.0 (8 animals maximum)	0.135	1.5 (minimum 1.8 above floor level)	-
Council of Europe (2004)	0.5 (1 or 2 animals plus offspring up to 5 months)	-	1.5	0.2
USDA (Animal Welfare Act, 1991)	-	0.15	0.508	-

There are many objections among scientists to the national guidelines and recommendations. The guidelines are not homogeneous between countries, they are far from ideal, and sometimes, different parts of guidelines of a particular country contradict each other. For instance, in some cases, the minimum cage sizes that are quoted in the guidelines are incompatible with statements regarding the behavioural needs of the animals, which should be met according to the same guidelines (Poole 1995). Further, all current guidelines based the minimum cage sizes for laboratory primates focus solely on the body weight of the animals and ignore their linear dimensions. This can result in a cage which is actually smaller in vertical dimension than the head to tail length of the animal (Poole, 1995; Buchanan-Smith et al., 2004; Wolfensohn & Honess, 2005). Additional physical and behavioural characteristics such as ecological factors, species differences, energy budgets, reproductive characteristics, activity patterns, individual temperament, sex and age of the animals, should also be considered when minimum cage sizes are determined (Buchanan-Smith et al., 2004; Prescott & Buchanan-Smith, 2004; Honess & Marin, 2006). The duration of stay of the animal in the particular cage is also relevant (Wolfensohn & Honess, 2005).

In addition to the argument that national guidelines for cage size are not appropriate, it is widely agreed among scientists that an increase in cage size alone cannot satisfy the physical and psychological needs of primates in captivity. The overall cage design is more important than the cage's measurements, as the influence of space on the animals' welfare depends on its quality rather than on its quantity. Appropriate cage furnishings allow better utilization of the entire cage space (Novak, 1989; Poole, 1990; Reinhardt et al., 1996; Buchanan-Smith, 1997a; Reinhardt & Reinhardt, 2001). Literature reporting the effects of cage size is presented in Table 4.2, which provides details on housing conditions and the primates' response to these conditions. A written summary of the main points is provided below. Studies are divided by social housing conditions since it might be expected that singly housed primates would be less affected by physical conditions than socially housed individuals as their welfare is already very poor.

Socially housed callitrichids

The effects of cage size on the behaviour of a range of captive primate species (especially *Macaca*) have been studied extensively, using various methods and conditions. The impact on the behaviour of callitrichids in particular has not been studied widely, but callitrichid studies have shown mainly positive effects of larger cage size on activity budget and social interactions (Box & Rohrhuber, 1993; Schoenfeld, 1989; Kitchen & Martin, 1996; Pines et al., 2002, 2003), cortisol levels (Pines et al., 2002, 2003), and heart rate (Kerl & Rothe, 1996).

Socially housed other primate species

When the effects of cage size on the behaviour of socially housed primates have been studied, the results of most studies have shown positive effects of a larger environment on social interaction (Southwick, 1967; Alexander & Roth, 1971; Demaria & Thierry, 1989; Elton & Anderson, 1997) and activity levels (Daschbach et al., 1982; Nash & Chilton, 1986). Conversely, in one experiment, pig-tail macaques (*Macaca nemestrina*) showed significantly higher levels of aggression in a larger enclosure. However, in this study, a comparison was made between the behaviour of the group when housed in one or two connected similar rooms, so it is possible that the very limited passage between the two enclosures was the cause of the aggressive encounters (Erwin 1977).

Individually housed primates

No research has been done on the effects of cage size on individually housed callitrichids. However, studies on the effects of cage size on the behaviour of other primate species, which are housed individually, have been inconsistent. Several studies have found a clear (Draper & Bernstein, 1963; Paulk et al., 1977; Brent, 1992; Kaufman et al., 2002) or minor positive behavioural effects of a larger enclosure (Crockett et al., 1992, 1993, 1995, 2000; Crockett & Bowden, 1994) on singly housed primates. Other studies have found no effects of enclosure size on the behaviour or heart rate of the monkeys (Line et al., 1989, 1990b, 1991a), or even negative effects of the larger enclosure (Bayne & McCully, 1989; Crockett et al., 1996).

Table 4.2: Effects of cage size on the behaviour of primates in captivity. (+)= positive effects of larger cage; (-)= negative effects of larger cage; (none)= no difference between cage sizes. The small number indicates specific behavioural changes; the key for these numbers is presented below the table.

Author	**Species**	**Housing (sample size)^a**	**Smaller cage ^{b}**	**Larger cage ^{b}**	**Time in each cage**	**Effects on behaviour (in brackets) and comments**
Draper & Bernstein, 1963	*Macaca mulatta*	Single (12)	$0.81m^2$ x 0.9m	$106m^2$ x 2.4m	10 x 5 min.	$(+)^{8,9,11}$ 3 cage sizes
Southwick, 1967	*M. mulatta*	Social (25 in 1 group)	$45.5m^2$	$91m^2$	Several days in small cage	$(+)^2$ Larger cage served as home cage
Alexander & Roth, 1971	*M. fuscata*	Social (84 in 1 group)	$186.7m^2$	$8058\ m^2$	3 x 4-6 days	$(+)^2$
Erwin, 1977	*M. nemestrina*	Social (14 groups)	$6.5m^3$	Two connected small rooms	One hour (14 groups)	$(-)^{15}$ Only females were affected
Paulk et al., 1977	*M. mulatta*	Single (24)	$0.8m^3$	$3.84m^2$ x 1.6m	20 hours	$(+)^{1,8}$
Daschbach et al., 1982	*Nycticebus coucang*	Pair (2 pairs)	$0.42m^3$	$8.75m^3$	1-3 months	$(+)^1$ Furniture in larger cage was more complex
Nash & Chilton, 1986	*Galago senegalensis braccatus*	Social (2 groups)	$6.9m^3$	$13.8m^3$	4 weeks	$(-\text{ and }+)^{3,4,5,15}$ There was also effects of new cage
Bayne & McCully, 1989	*M. mulatta*	Single (6)	$0.4m^2$	$0.55\ m^2$	2 months	$(-)^{14}$ Smaller cage served as home cage
Demaria & Thierry, 1989	*M. arctoiedes*	Social (1 group)	$10m^2$ and $18m^2$	$50000\ m^2$	Several months	$(+)^2$ Only smaller cage indoors

Continuation of Table 4.3

Author	Species	Housing (sample size)[a]	Smaller cage [b]	Larger cage [b]	Time in each cage	Effects on behaviour (in brackets) and comments
Line et al., 1989	*M. mulatta*	Single (6)	0.41m^2 x 0.81m	0.57m^2 x 0.81m	2 x one week	(none) Smaller cage served as home cage
Schoenfeld, 1989	*Callithrix jacchus*	Social (1 family group)	1m^3	160m^3	At least 45 days	(- and +)[1,18] 4 cage types, only the biggest one was outdoor and complex
Line et al., 1990b	*M. mulatta*	Single (10)	0.4m^2 x 0.81m	0.63m^2 x 1.1m x	2 weeks	(none) 3 cage sizes, smaller cage served as home cage
Line et al., 1991a	*M. mulatta*	Single (6)	0.4m^2	0.56 m^2	4 x one week	(none) Smaller cage served as home cage
Brent, 1992	*Pan troglodytes*	Single (4)	1.6m^2	4.5m^2		(+)[6,7,10]
Crockett et al., 1992; 1993; 1995; Crockett & Bowden, 1994	*M. fascicularis*	Single (20)	0.5m^2 x 0.36m	0.59m^2 x 0.84m	2 weeks	(none apart from locomotion)[1] 5 cage sizes
Box & Rohrhuber, 1993	*Saguinus oedipus*	Pair (17 pairs)	0.5m^2 x 0.7m	0.68m^2 x 1.7m	5-25 weeks	(- and +)[6,8,17] 3 cage sizes
Crockett et al., 1996	*M. fascicularis, M. nemestrina, Papio cynocephalus anubis*	Single (8)	0.41m^2 x 0.76m	0.36m^2 x 0.86m	One week	(-)[16]
Kerl & Rothe, 1996	*C. jacchus*	Pair (1 pair)	3.3m^3	10.7m^3	2 x 12 days	(none) 3 cage sizes
Kitchen & Martin, 1996	*C. jacchus*	Pair (12 pairs)	0.36m^2 x 0.82m	0.3m^2 x 1.95m	Several months	(+)[2,3,8,12,17]
Elton & Anderson, 1997	*P. anubis*	Social (13 in 1 group)	8m^2 x 3.04m	16m^2 x 3.04m	30-40 days	(+)[2,7] 4 cage sizes

Continuation of Table 4.3

Author	Species	Housing (sample size)[a]	Smaller cage [b]	Larger cage [b]	Time in each cage	Effects on behaviour (in brackets) and comments
Crockett et al., 2000	*M. nemestrina*	Single (8)	0.08 m^2 x 0.43m	0.59 m^2 x 0.84m	2 weeks	(none apart from locomotion)[1] 4 cage sizes
Williams et al., 2000	*Aotus* spp.	Social (?)	0.72m^3	9m^3		(– and +)[12,17]
Kaufman et al., 2002	*M. mulatta*	Single (8)	1.24m^3	6.8m^3	2 years	(+)[7,12] Larger cage served as home cage
Pines et al., 2002, 2003	*C. jacchus*	Social (18 in pairs or triplets)	4.6m^3	7.65m^3	5 hours x 3 days, or free access for 9 days	(+)[1,13] Smaller cage served as home cage

a) Number of individuals unless otherwise noted
b) A single m^3 figure indicates cage volume; m^2 + m figures indicate floor area plus cage height

<u>Key for the specific behavioural changes (arrows describe changes in rates in large cage as opposed to small cage):</u>

1) locomotion ↑
2) aggressive behaviour ↓
3) affiliative behaviour ↑
4) play ↑
5) resting ↑
6) inactivity ↓
7) abnormal behaviour ↓
8) stereotypy ↓
9) cage manipulation ↓
10) exploration ↑
11) vocalization ↓
12) foraging ↑
13) autogrooming ↓
14) abnormal behaviour ↑
15) aggressive behaviour ↑
16) cage manipulation ↑
17) affiliative behaviour ↓
18) scent marking ↑

From the results of the above studies, it is clear that an increase in the size of their enclosure has positive effects on the behaviour of socially housed primates. On the other hand, the results of some of the studies on the effects of cage size on the behaviour and welfare of individually housed primates are questionable. The cages in several experiments were unfurnished, so the animals could not use most of the additional space in the larger cages, and even if they could use some of it, they had neither reason nor encouragement to do so (Reinhardt & Reinhardt, 2001). In any case, further research on the effects of cage size on the behaviour and welfare of captive primates in general, and callitrichids in particular, is needed.

4.1.3 Effects of group composition on the welfare of captive primates

The social structure of wild common marmosets and the commonly held views concerning the optimum group composition of captive populations were discussed in Chapters 2 and 3. However, very little research has been done on the effects of group composition on captive callitrichids. Koenig (1995) studied the effects of group size and composition on reproductive success of common marmosets. Ingram (1978a; 1978b) compared families of wild born and captive born parents. However, no research has been done on the effects of group composition and size on the behaviour and welfare of captive callitrichid monkeys.

4.1.4 Aims of the present study

The aim of the present study was to examine the effects of three basic aspects of the captive environment on the behaviour of common marmosets. The effects of cage level on the behaviour of monkeys in captivity have been studied before (e.g. Crockett et al., 2000; Schapiro & Bloomsmith, 2001); however, little research has been done on callitrichid species (e.g. Scott, 1991). In addition, little research has looked at the effects of cage size and height on the behaviour of callitrichids in captivity (e.g. Kerl & Rothe, 1996; Kitchen & Martin, 1996), and no research at all has been published concerning the effects of group composition on the welfare of captive callitrichids.

The following questions were asked:

1) Does the behaviour of the marmosets differ in different cage levels when housed in a two tier housing system?
2) Does the size and the height of the cage affect the behaviour of pair housed marmosets?
3) Does the level of the previous cage affect the behaviour of pair housed marmosets when they are moved to a larger cage?
4) Does the group composition affect the behaviour of adult marmosets in captivity?

Based on previous literature (Scott, 1991; Reinhardt, 1999, 2004) it was hypothesized that the welfare of marmosets in upper tier cages would be better than that of their counterparts in the lower tier, and that the increase in cage size would improve the welfare of both lower and upper tier housed marmosets. In addition, as previous research has shown that wild marmosets live in family groups (e.g. Hubrecht, 1984; Scanlon et al., 1988; Digby & Barreto, 1993), it was hypothesized that adult marmosets would show signs of better welfare when housed in family groups with their offspring.

4.2 METHODS

The effects of various basic aspects of environmental conditions on the behaviour of common marmosets were looked at in three separate studies:

I. The effects of cage level on the behaviour of pair-housed marmosets.
II. The effects of cage size and height on the behaviour of pair-housed marmosets.
III. The effects of group composition.

Data for Studies I and III, as well as data for the first phase of Study II, were taken from baseline data of four different studies (Chapters 6, 7, 8, and 9). Figure 4.1 explains the relationships between the different studies.

4.2.1 Study I: Effects of cage level on behaviour

4.2.1.1 Study animals and housing

The study animals were 64 common marmosets housed in pairs in a two tier housing system. These pairs were part of the study on the effects of control over additional light in their home cage (see Chapter 9). In the study on the effects of control over light, four pairs were used twice; therefore, only data from the first time these pairs were observed were used in the analyses of the effects of cage level. Seventeen pairs were housed in lower tier cages, and 15 pairs were housed in upper tier cages.

No significant difference was found in mean age between individuals in lower and upper tiers ($F_{1,63}$= 1.81, P=0.183). All marmosets were over 300 days old; hence, no discrimination between age groups was made (see Table 4.3 for mean ages of all study groups, and Table 4.4 for pair details and individuals' ages and sexes). One male (72G) was used twice, when housed with two different cage mates. Animals were housed in single cages. Lower tier cages were located 20cm above floor level, and upper tier cages 1.35cm above floor level. In addition, illumination measures showed that the upper tiers were 1.5 times brighter than the lower tiers (for more housing details and husbandry routine see Chapter 3).

Figure 4.1: Sources of the data for the three studies of the present chapter, and the relationships between them

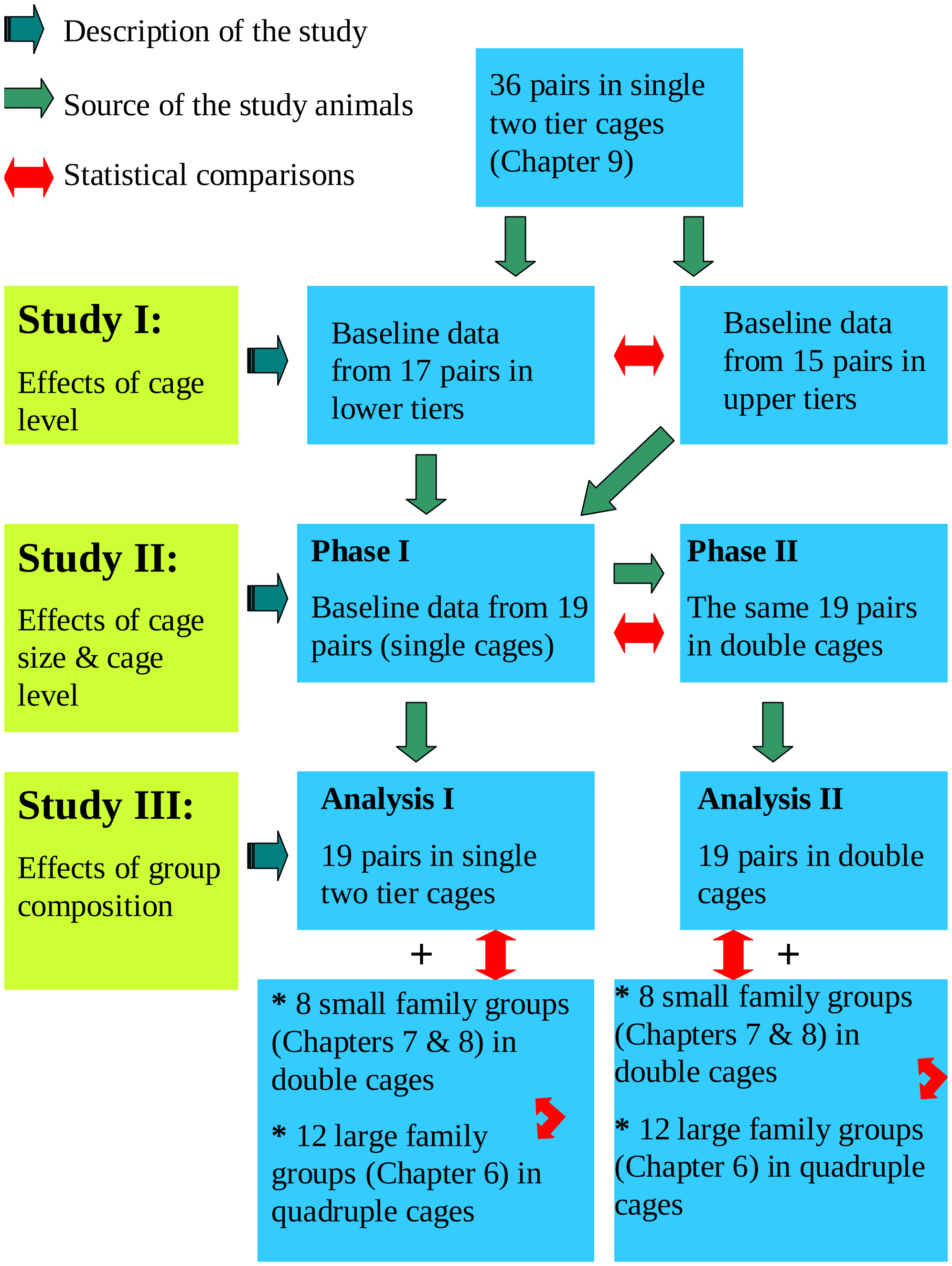


Table 4.3: Mean age for individuals in Studies I and II

	Study I 32 pairs			Study II 19 pairs		
	Mean age (days)	**S.E**	**n**	**Mean age (days)**	**S.E**	**n**
Lower tiers	1015	±113	34	1199	±159	20
Upper tiers	1271	±148	30	1413	±239	18

Table 4.4: Pair and individual details (sex, date of birth (D.O.B), age on first day of the study). Individuals used in Study II are marked in red.

Location	Pair identifier	Individual	D.O.B.	Age (days)
Upper tier	a-2RaU	111Y (♀)	19/12/2001	979
		184Y (♀)	13/03/2003	530
	a-3RaU	904R (♀)	22/7/1998	2225
		150Y (♀)	30/07/2002	756
	a-2RbU	104Y (♀)	09/11/2001	1019
		138Y (♀)	29/05/2002	818
	b-4RbU	215Y (♀)	09/08/2003	395
		211Y (♀)	04/08/2003	400
	c-2LaU	782R (♀)	22/08/1996	2996
		210Y (♀)	04/08/2003	458
	a-1RaU	131Y (♀)	16/04/2002	861
		156Y (♀)	18/09/2002	706
	a-1RbU	96Y (♀)	29/09/2001	1060
		123Y (♀)	03/04/2002	874
	6-2LbU	877BK (♂)	24/06/1999	1979
		6G (♂)	14/03/2002	985
	a-3RbU	95G (♂)	02/12/2002	631
		66G (♂)	22/05/2003	460
	6-2LaU	966BK (♂)	10/07/2001	1232
		7G (♂)	14/03/2002	985
	c-3LaU	4G (♂)	09/03/2002	971
		81G (♂)	04/08/2003	458
	b-4LbU	863BK (♂)	19/04/1999	1968
		84G (♂)	08/08/2003	396
	b-4RaU	676R (♀)	25/03/1993	4184
		5G (♂)	09/03/2002	913
	c-3LbU	959BK (♂)	05/06/2001	1248
		848R (♀)	05/09/1997	2617
	6-2RaU	55Y (♀)	02/01/2001	1421
		943BK (♂)	05/02/2001	1387
Lower tier	b-4RaL	20W (♀)	26/11/2000	1381
		176Y(♀)	26/02/2003	559
	c-1LbL	980R (♀)	21/09/1999	1871
		177Y (♀)	26/02/2003	617
	a-2RbL	137Y (♀)	29/05/2002	818
		173Y (♀)	24/02/2003	547
	b-1RbL	75Y (♀)	09/05/2001	1217
		187Y (♀)	11/04/2003	515
	b-3RaL	169Y (♀)	05/01/2003	611
		199Y (♀)	09/06/2003	456
	c-3RaL	192Y (♀)	03/05/2003	551
		193Y (♀)	03/05/2003	551
	a-2RaL	865BK (♂)	22/04/1999	1951
		78G (♂)	24/07/2003	397

Continuation of Table 4.4

Location	Pair identifier	Individual	D.O.B.	Age (days)
Lower tier	b-1RaL	822BK (♂)	18/06/1998	2273
		71G (♂)	09/06/2003	456
	b-4RbL	864BK (♂)	22/04/1999	1965
		72G (♂)	23/06/2003	519
	6-4LaL	72G (♂)	23/06/2003	442
		88G (♂)	20/08/2003	461
	6-4LbL	889BK (♂)	28/02/2000	1730
		943M (♂)	19/08/2003	462
	6-1LbL	122Y (♀)	13/03/2002	986
		53G (♂)	21/02/2003	641
	6-3LbL	981BK (♂)	09/11/2001	1110
		147Y (♀)	22/07/2002	855
	6-1LaL	870BK (♂)	04/05/1999	2030
		13Y (♀)	15/04/2000	1683
	6-3LaL	872BK (♂)	21/05/1999	2013
		160Y (♀)	02/10/2002	783
	a-4LbL	914R (♀)	03/09/1998	2182
		847BK (♂)	23/11/1998	2101
	b-3RbL	842BK (♂)	10/09/1998	2189
		134Y (♀)	16/05/2002	845

4.2.1.2 Experimental design, data collection, and statistical analysis

The 32 pairs were housed in four different colony rooms. Each animal was observed three times for four minutes (total observation time of 12 hours and 48 minutes), and each pair was effectively treated as one individual in the analyses. Further, single means were calculated for every study phase for each pair. Independent sample t-tests were carried out in order to examine the effects of cage level on the behaviour of pair housed marmosets in the two tier housing system (see Table 4.5 for details on all statistical analyses of the present chapter). This study was part of the study in Chapter 9 of the present thesis.

4.2.2 Study II: Effects of cage size on behaviour

4.2.2.1 Study animals and housing

The study animals were 38 common marmosets, from the 64 marmosets of Study I. Ten pairs were housed in lower tier cages and nine pairs in upper tier cages, before they were moved to the double cages. No significant difference was found in mean age between marmosets in lower and upper tiers ($F_{1,37}$= 0.58, P=0.452, see Table 4.3 for mean ages of all study groups, and Table 4.4 for pair details and individuals' ages and sexes). In the first phase of the study the monkeys were housed in the same cages as in Study I. In the second phase the marmosets were housed in double cages. The double cage did not contain any different furniture compared to the single cage, but the amount of regular furniture (wooden log, plastic shelf and rubber shelf) was doubled, as the two connected small cages were identical. However, the double cages contained a single metal nest box, as did the small cages.

4.2.2.2 Experimental design, data collection, and statistical analysis

In the first phase of the study the marmosets were housed in single cages in the two tier housing system. The data for this phase were part of the data of Study I. In the second phase (between one and two months after the beginning of the first phase), the marmosets (19 pairs out of the 32 pairs of Study I) were moved to double cages. Hence, the cages in the second phase of the study were larger and higher than the cages in the first phase. These cages also contained more furniture (although similar) and therefore, are considered more complex. Although complexity might be measured by the number of items per unit volume (which would be identical in single and double cages), as the marmosets had more opportunities for locomotion and more choice when housed in double cages than in single cages, the double cages are considered to be more complex. For each pair the space of the home cage was extended, thus they were familiar with one-half (lower or upper) of the larger cage. Observations were not carried out until the marmosets have been housed for at least 36 hours in their new cages. In common with Study I, during the second phase of the study, each animal was observed three times in the double cage (total observation time of 7 hours and 36 minutes). Two-way ANOVAs were carried out in order to examine the effects of cage size and cage level on the behaviour of pair-housed marmosets (see Table 4.5). The effects of single cage level on behaviour and preference for cage location were also examined when the marmosets were moved to the double cages, together with the interaction between cage level and cage size.

Table 4.5: Statistical analyses used in the three studies of the present chapter

Research question	**Statistical test**	**Factors**	**Levels**	**Analysis**
Study I: Effects of cage level (32 pairs)	Independent sample t-test	Cage level	Lower/upper	Between subjects
Study II: Effects of cage size, and cage level (19 pairs)	Two-way ANOVA mixed design	Cage size Cage level	Single/double Lower/upper	Within subjects Between subjects
Study III: Effects of group composition (pairs in small cages)	One-way ANOVA	Group composition	Large family/ small family/pair	Between subjects
Effects of group composition (pairs in large cages)	One-way ANOVA	Group composition	Large family/ small family/pair	Between subjects

4.2.3 Study III: Effects of group composition on behaviour

4.2.3.1 Study animals and housing

The effects of group composition were studied in two separate but identical analyses. In both analyses the same behavioural data were used for adults in family groups; however, in each analysis, pairs were housed in cages of different size. Data from four different studies were used for the comparison of behaviour of adult marmosets in various group compositions.

4) Pairs- data from the first (single cages) and the second (double cages) phases of Study II in the present chapter.
5) Small family groups in double cages- data from the Baseline phase of two different studies. Data from five family groups were taken from the study on the effects of additional light on the behaviour of small family groups of marmosets (Chapter 7). Data from three additional family groups were taken from the study on the effects of coloured light on the behaviour of small family groups of marmosets (Chapter 8).
6) Large family groups in quadruple cages- data from the Baseline phases of the studies on the effects of outdoor cages on the behaviour of large family groups of marmosets (Chapter 6).

Only family groups which consisted of two parents and at least one offspring were used. Small family groups consisted of two parents and one generation of offspring (one or two offspring). Large family groups consisted of two parents and at least two generations of offspring (between three and six offspring). Data from young offspring were not included in the study as the comparison was between adult animals only (as pairs do not have offspring). Some individuals in the pair condition were young adults (the youngest marmoset was 479 days old), as were some of the offspring of the family groups. Therefore, young adults (non parents) from family groups who were older than 450 days were used for the comparison of group composition. Mean age of individuals in pairs was 1332±138.1, mean age of marmosets in small family groups was 1490±139.4, and mean age of individuals in large family groups was 1715.2±112.8. No significant difference was found in mean age between animals of the three group compositions ($F_{2,83}$=2.29, P=0.107). For group details and individuals' ages and sexes see Table 4.4 (for pairs), and Table 4.6 (for family groups).

One pair of marmosets was used twice, once when housed in a family group with offspring (in the study of Chapter 7), and second, when housed as a pair with no offspring (in Study II of the present chapter). Marmosets in pairs were housed in two different cages; for the first analysis they were housed in single cages (data used were those from the first phase of Study II), for the second analysis they were housed in the same double cages as in the second phase of Study II. Animals in small family groups were housed in double cages. Animals in large family groups were housed in quadruple cages. Although the volume of the cage increased with the number of individuals housed in it, it was not always the same as regards to the available space per individual (see Table 4.7).

4.2.3.2 Experimental design, data collection, and statistical analysis

Data from the three different studies (see above) were used to compare the behaviour of adult marmosets housed in pairs (in single and double cages), small family groups, and large family groups. Each marmoset was observed three times. Animals in pairs were observed for a total of 7 hours and 36 minutes in each cage size. Adults in small family groups were observed for a total observation time of 3 hours and 12 minutes. Marmosets in large family groups were observed for a total of 4 hours and 48 minutes. One-way ANOVAs with group composition (between subjects) as a single factor were applied twice, once for pairs in single cages and once for pairs in double cages (see Table 4.5).

Table 4.6: Group and individual detail (sex, date of birth (D.O.B), age at first day of the study). Young adults who were not parents are marked in red, number of offspring in groups includes infants

Group type	Group identifier (number of young + infants)	Individual	D.O.B.	Age (in days)
Small family group	1Ra (2)	782R (♀)	22/08/1996	2703
		950BK (♂)	17/04/2001	1004
	1Rb (1)	21W (♀)	28/11/2000	1161
		866BK (♂)	23/04/1999	1746
	2Ra (1+2)	12W (♀)	11/01/2000	1595
		5BB (♂)	15/01/2000	1591
	2Ra (2)	55Y (♀)	02/01/2001	1126
		943BK (♂)	05/02/2001	1092
	3Lb (2)	94Y (♀)	13/09/2001	956
		868BK (♂)	29/04/1999	1824
	3Ra (1)	743R (♀)	16/08/1995	3075
		962BK (♂)	27/06/2001	933
	3Rb (2)	15W (♀)	02/02/2000	1444
		861BK (♂)	08/04/1999	1744
	4Ra (1)	1Y (♀)	28/02/2000	1547
		979BK (♂)	07/11/2001	929
Large family groups	22L(5)	4W (♀)	07/04/1999	1834
		816BK (♂)	08/06/1998	2137
	22R (5)	10W (♀)	08/09/1999	1680
		850BK (♂)	05/04/1998	2201
		136Y (♀)	23/05/2002	692
	2L2 (4+2)	853R (♀)	03/11/1997	2457
		792BK (♂)	01/01/1998	2398
		895BK (♂)	05/03/2002	874
	2R4 (3)	30Y (♀)	01/08/2000	1442
		844BK (♂)	30/09/1998	2113
		186Y (♀)	11/04/2003	459
	3L2 (3)	852R (♀)	26/10/1997	2452
		770BK (♂)	13/03/1997	2679
		65G (♂)	05/03/2003	496
	3R2 (3)	999R (♀)	27/02/2000	1611
		863BK (♂)	21/07/1998	2197
		113Y (♀)	25/12/2001	944
	44L (4+2)	26Y (♀)	29/06/2000	1390
		846BK (♂)	09/11/1998	1988

Continuation of Table 4.6

Group type	Group identifier (number of young + infants)	Individual	D.O.B.	Age (in days)
Large family groups	44R (3)	923R (♀)	30/09/1998	2028
		849BK (♂)	25/11/1998	1972
		141Y (♀)	16/06/2002	673
	4L1 (3)	847R (♀)	05/09/1997	2516
		872BK (♂)	21/05/1999	1893
	4L4 (6)	994R (♀)	31/12/1999	1669
		810BK (♂)	29/04/1998	2280
	4R1 (5)	25Y (♀)	29/06/2000	1475
		862BK (♂)	09/04/1999	1922
	4R4 (3)	37Y (♀)	02/09/2000	1410
		901BK (♂)	21/03/2000	1575

Table 4.7: Cage volume and available pace per individual in each housing condition

	Pairs in single cages	Pairs in double cages	Small family groups (double cages)	Large family groups (quadruple cages)
Cage volume	$0.91m^3$	$1.90m^3$	$1.90m^3$	$3.80m^3$
Available space per individual	$0.45m^3$	$0.95m^3$	$0.38\text{-}0.63m^3$	$0.48\text{-}0.76m^3$

4.3 RESULTS

The present study examined the effects of different aspects of the basic environmental conditions of pair and family housed common marmosets: cage level, cage size, and group composition.

4.3.1 Effects of cage level on behaviour

The effects of the level of the cage on the behaviour of marmosets housed in a two tier housing system were analysed twice. First, data from 32 pairs were analysed using independent sample t-tests (see above), and second, data from 19 of these pairs were analysed using two-way ANOVAs. In the analysis of 32 pairs, results showed that marmosets in lower tiers performed significantly more scratching behaviour compared to those in upper tiers, but no further differences were significant (see Table 4.8 and Figure 4.2 a and b).

Table 4.8: Results of t-tests of 32 pairs, and of ANOVAs of 19 pairs for the effects of cage level on behaviour (*** P<0.001)

	32	**Pairs**	**19**	**Pairs**
	t-	test	Three way	AVOVA
			d.f.=	1,17
	t	**P**	**F**	**P**
Agitated locomotion	-1.01	.319	0.07	0.794
Allogroom	-0.84	.407	2.21	0.155
Autogroom	-1.52	.259	3.17	0.093
Calm locomotion	-0.67	.507	0.00	0.968
Contact	.23	.817	0.43	0.519
Explore	-1.07	.295	1.596	0.180
Forage	.13	.895	0.10	0.760
Inactive alert	1.56	.130	0.0.02	0.886
Inactive rest	-0.05	.962	0.28	0.603
Scent mark	-0.45	.656	1.88	0.189
Scratch	6.64	<.001***	0.26	0.619
Social play	-1.07	.295	1.12	.305
Solitary play	-1.07	.295	No data	No data
Tree gouge	.19	.852	0.25	.623
Watch obs.	-1.01	.319	0.00	0.950

In the analysis of 19 pairs, neither significant differences, nor significant interactions between cage level and cage size were found between animals in the two cage levels, showing that the previous levels of the housing did not affect the response to the double cages (see Table 4.8).

4.3.2 Effects of cage size on behaviour

The effects of the size of the cage (together with the effects of its height) were analysed using two-way ANOVAs with cage size (within subjects), and cage level (between subjects) as factors, and showed significant results for several behaviours. The marmosets showed significantly more inactive rest and calm locomotion behaviours in the double cages as compared to the single ones. Further, they watched the observer significantly less and showed significantly less inactive alert, and agitated locomotion behaviours in the double cages (see Table 4.9 and Figure 4.3 a and b).

Table 4.9: Results of ANOVAs for the effects of cage size on behaviour of 19 pairs (*P<0.05; ** P<0.01; *** P<0.001)

	F d.f.= 1,17	**P**
Agitated locomotion	32.43	<0.001***
Allogroom	0.27	0.610
Calm locomotion	96.35	<0.001***
Contact	0.68	0.421
Explore	2.08	0.167
Forage	0.04	0.842
Autogroom	0.12	0.735
Inactive alert	13.02	.001**
Inactive rest	4.67	.045*
Scent mark	3.53	0.077
Scratch	3.11	0.096
Social play	1.70	0.210
Solitary play	No data	No data
Tree gouge	0.81	0.382
Watch obs.	4.67	0.045*

Figure 4.2: Mean percentage time (±S.E. bars) spent in behaviours for 32 pairs in two cage levels (*** P<0.001)

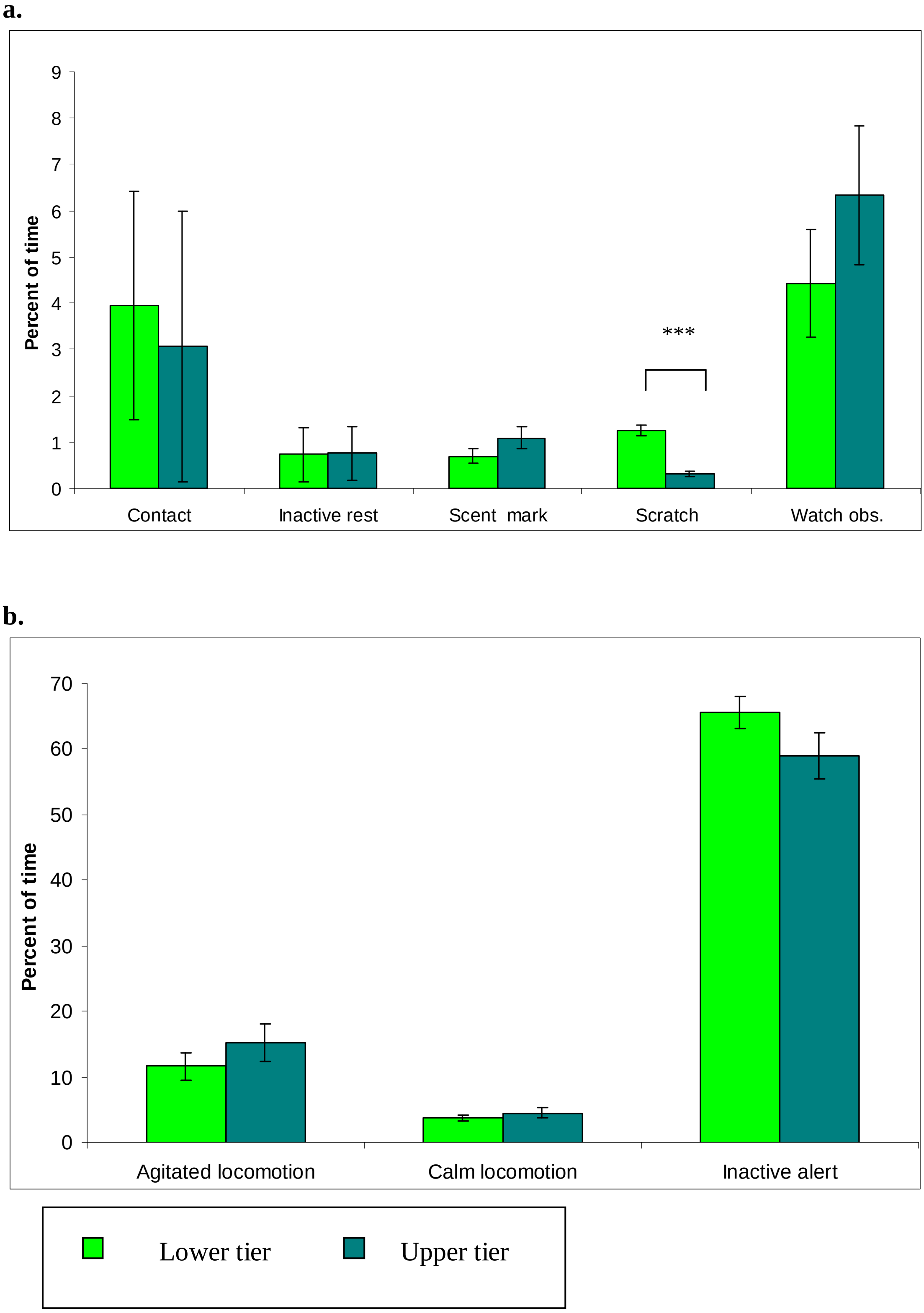
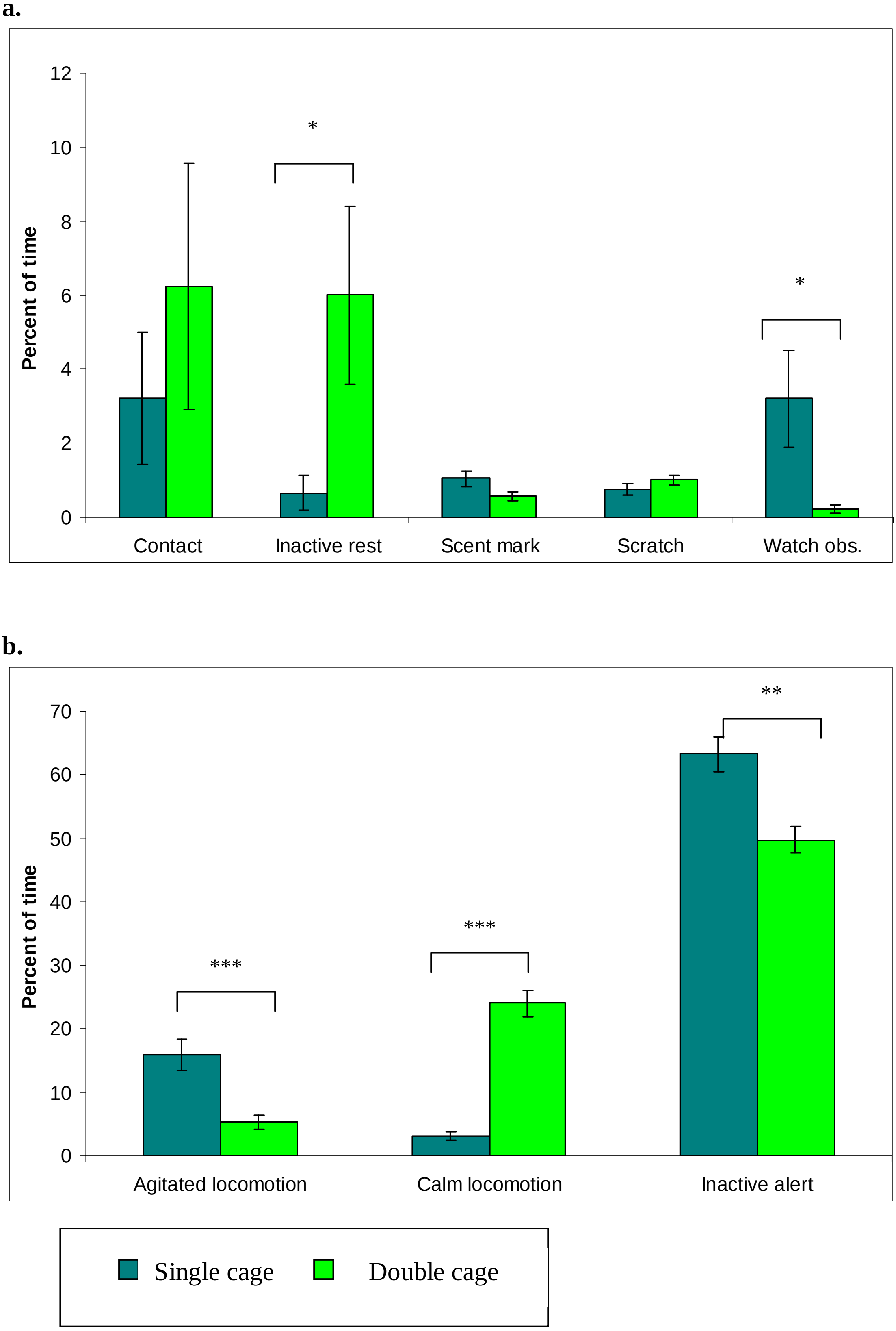


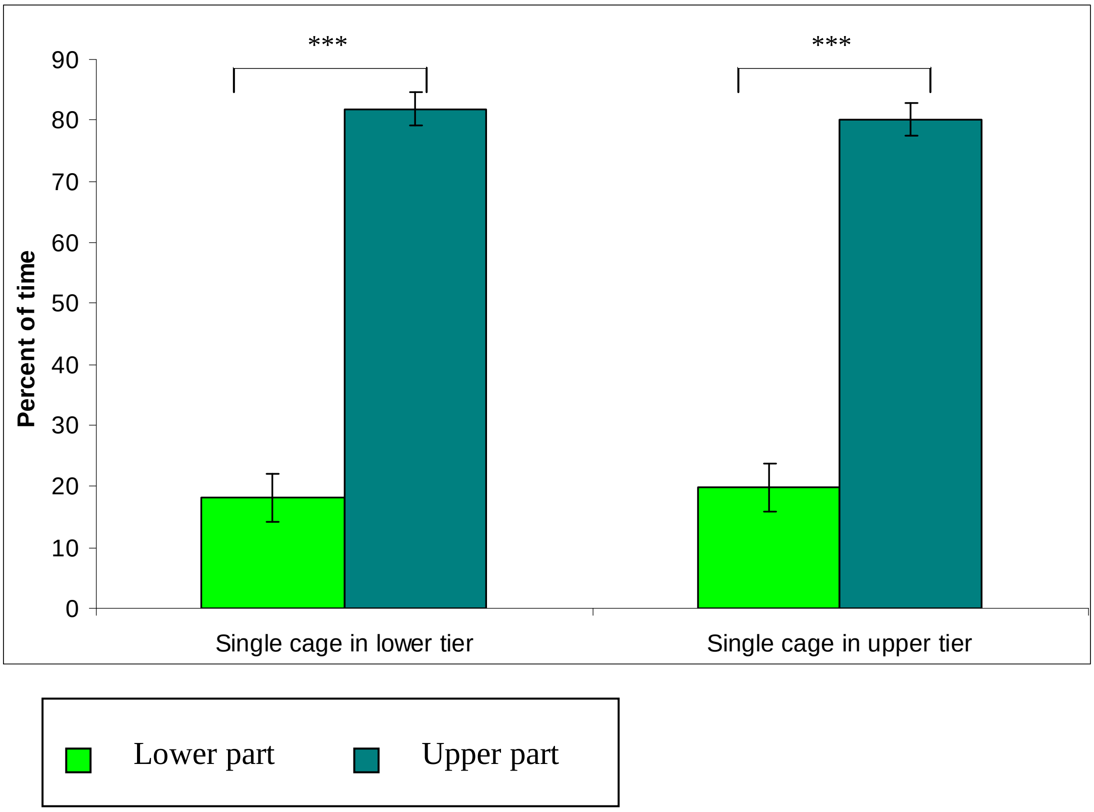
Figure 4.3: Mean percentage time (±S.E. bars) spent in behaviours for 19 pairs in two cage sizes (*P<0.05; **P<0.01; *** P<0.001)



4.3.3 Effects of level of single cage on location in double cage

In order to examine the effects of familiarity with one half of the cage on the preferred location in the double cage, a two-way ANOVA with cage size (within subjects) and cage level (between subjects) as factors was carried out. It was found that all marmosets spent significantly more time in the upper part of the double cage, regardless of the level of the small cage in which they were housed ($F_{1,17}$=174.41, P<0.001, see Figure 4.4). Further, no interactions were found between cage size and cage level for any other behaviours.

Figure 4.4: Mean percent of time (±S.E. bars) spent in the lower and upper parts of the double cage for 19 pairs (***P<0.001)



4.3.4 Effects of group composition on behaviour

One-way ANOVAs were used to examine the effects of group composition on the behaviour of marmosets in three different group compositions: pairs, small family groups and large family groups. When pairs were housed in single cages a significant main effect of group composition was found in calm locomotion, inactive rest, and scratching behaviour (see Table 4.10 and Figure 4.5 a and b). Tukey post-hoc tests showed no significant differences between small and large family groups. However, it was found that adults that were housed in pairs spent significantly less time scratching themselves and showed significantly less calm locomotion than adults in both small and large family groups. In addition, marmosets in pairs showed significantly less inactive rest behaviour compared to monkeys in small family groups (see Table 4.11 and Figure 4.5 a and b).

Table 4.10: Results of ANOVAs for effects of group composition on behaviour when pairs were housed in single cages (*P<0.05; ** P<0.01; *** P<0.001)

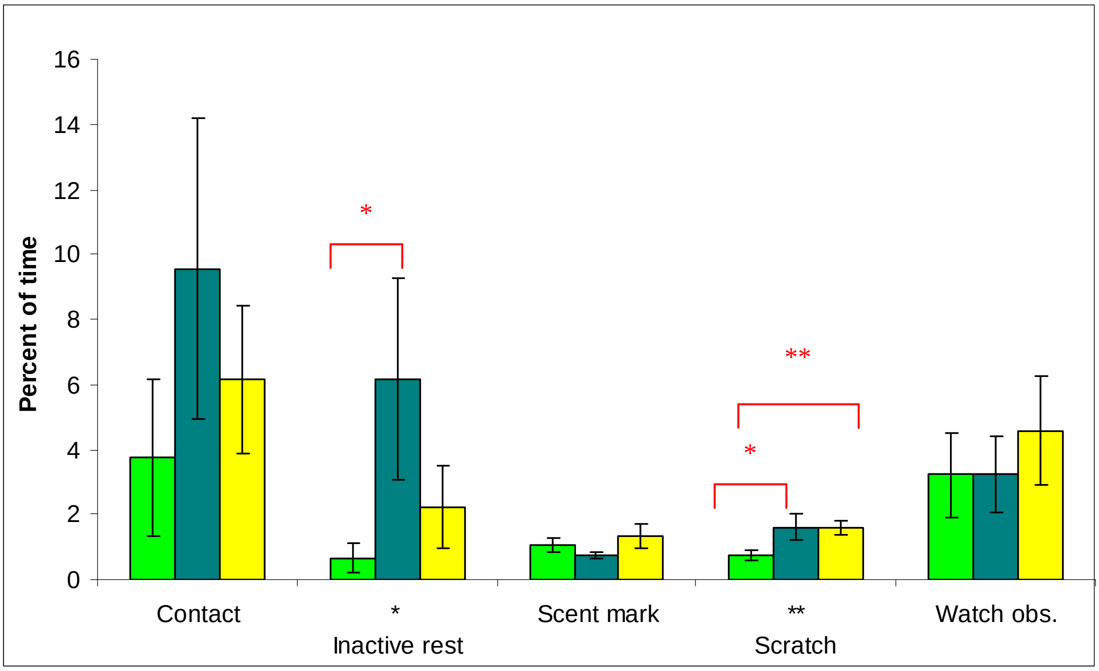
	F d.f.= 2,38	**P**
Agitated locomotion	2.35	0.109
Allogroom	0.14	0.869
Calm locomotion	9.31	0.001**
Contact	0.89	0.417
Explore	1.57	0.222
Forage	1.27	0.293
Autogroom	1.06	0.358
Inactive alert	1.74	0.190
Inactive rest	3.75	0.033*
Scent mark	0.87	0.426
Scratch	5.40	0.009**
Social play	No data	No data
Solitary play	No data	No data
Tree gouge	1.88	0.168
Watch obs.	0.28	0.759

Table 4.11: Results of Tukey post-hoc tests for effects of group composition when pairs were housed in single cages (*P<0.05; **P<0.01)

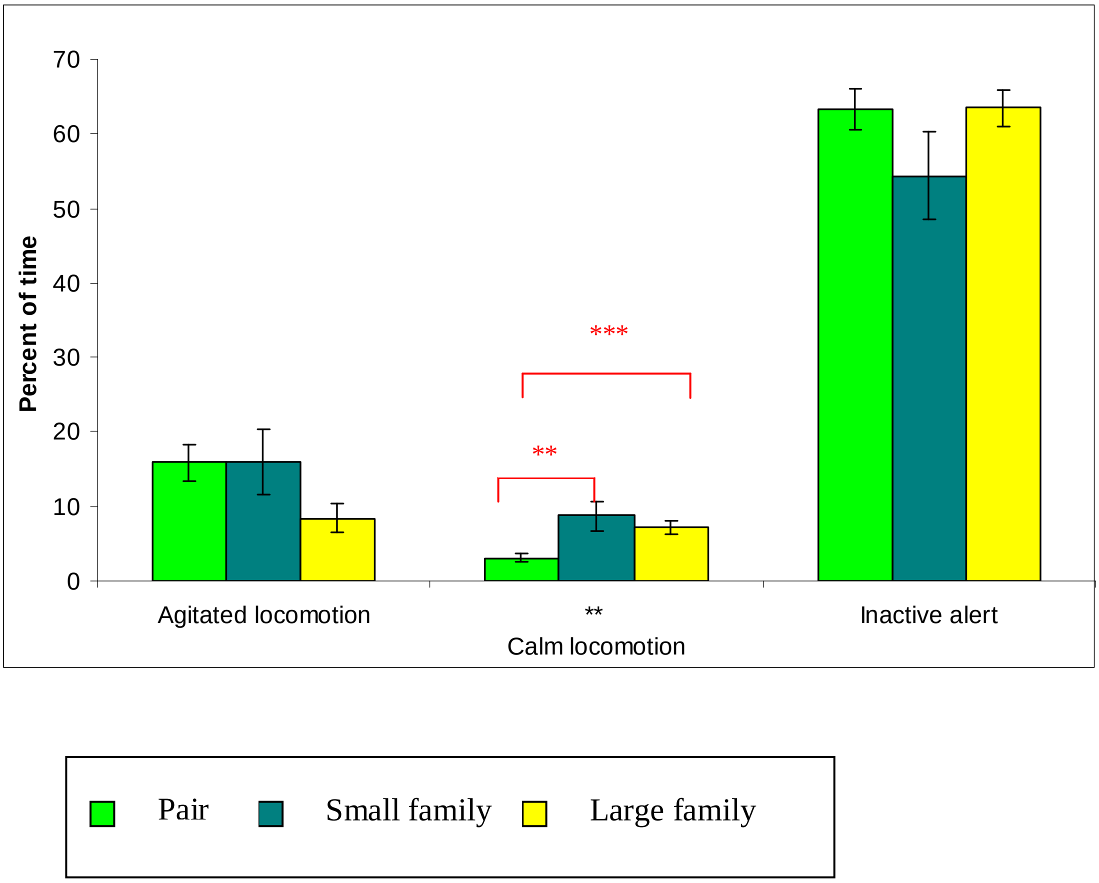
	Pairs vs.	**Small family groups**	**Pairs vs.**	**Large family groups**	**Small family groups vs.**	**Large family groups**
	t	**P**	**t**	**P**	**t**	**P**
Calm locomotion	3.68	0.001**	3.99	<0.001***	-0.76	0.457
Inactive rest	2.64	0.014*	1.38	0.178	-1.33	0.199
Scratch	2.50	0.020*	3.22	0.003**	-0.52	0.959

Figure 4.5: Mean percentage time (±S.E. bars) spent in behaviours in three group compositions when pairs were housed in single cages [one-way ANOVA (black marks) and Tukey post-hoc tests (red marks) *P<0.05; **P<0.01; ***P<0.001]

a.



b.



When marmosets in pairs were housed in double cages, a significant main effect of group composition was found in calm locomotion, agitated locomotion, inactive alert, scent marking and watching the observer behaviours (see Table 4.12 and Figure 4.6 a and b). The results of Tukey post-hoc tests show no significant differences in the behaviour of monkeys in the two different family compositions (small and large family groups). However, several significant differences were found between adults in family groups and adults in pairs. Adults in pairs watched the observer significantly less, and spent significantly more time in calm locomotion compared to adult marmosets in large and small family groups. Further, they spent significantly less time inactive alert, and scent marked significantly less compared to adults in large family groups. In addition, adults in pairs showed significantly less agitated locomotion compared to adults in small family groups (see Table 4.13 and Figure 4.6 a and b).

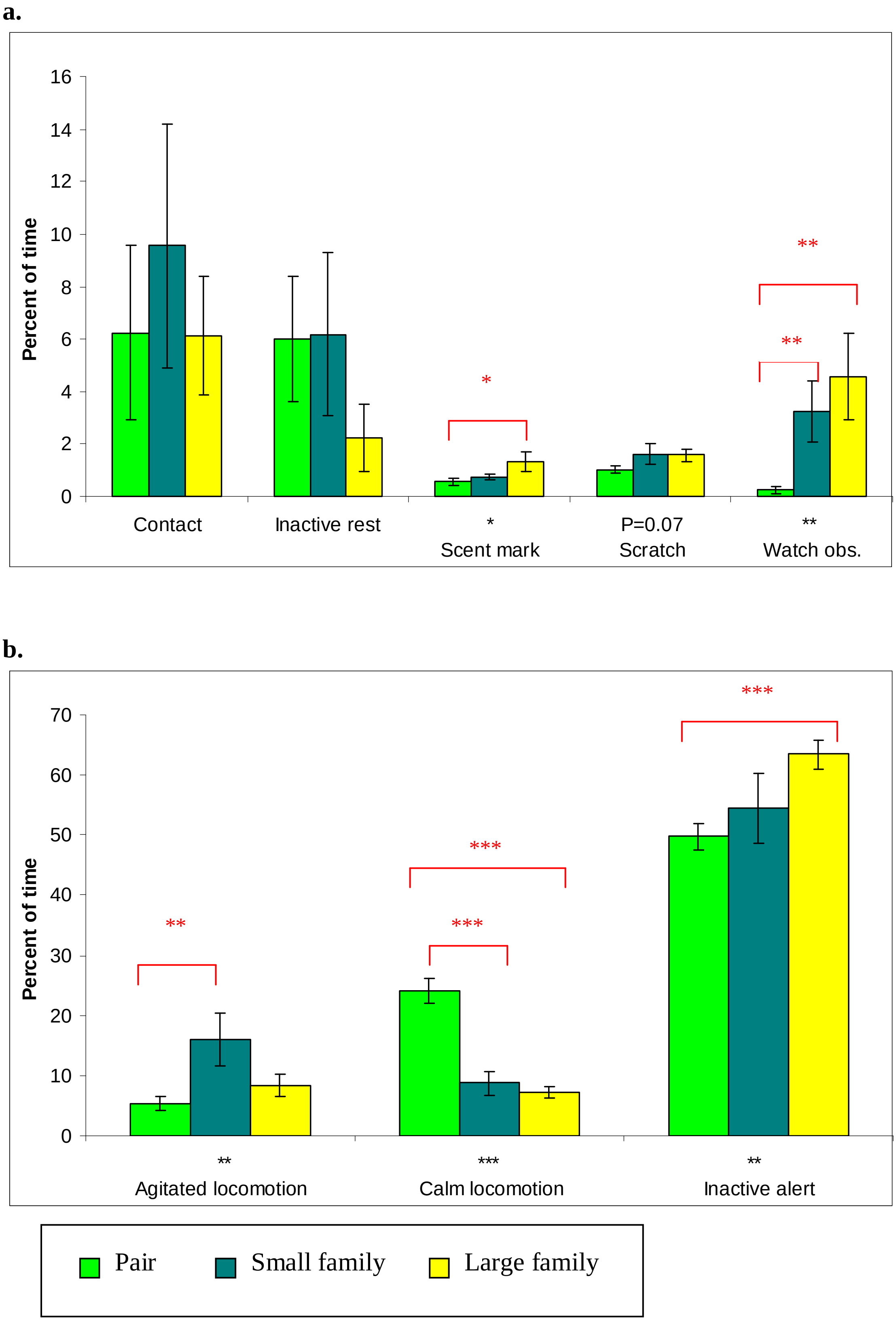
Table 4.12: Results of ANOVAs for effects of group composition on behaviour when pairs were housed in double cages (*P<0.05; ** P<0.01: *** P<0.001)

	F d.f.= 2,38	**P**
Agitated locomotion	5.56	0.008**
Allogroom	0.48	0.625
Calm locomotion	25.06	<0.001***
Contact	0.23	0.798
Explore	0.91	0.412
Forage	2.04	0.144
Autogroom	1.79	0.181
Inactive alert	6.03	0.006**
Inactive rest	0.80	0.459
Scent mark	3.33	0.047*
Scratch	2.76	0.077
Social play	0.67	0.516
Solitary play	No data	No data
Tree gouge	1.03	0.368
Watch obs.	6.10	0.005**

Table 4.13: Results of Tukey post-hoc tests for effects of group composition when pairs were housed in double cages (*P<0.05; **P<0.01;***P<0.001)

	Pairs vs.	**Small family groups**	**Pairs vs.**	**Large family groups**	**Small family groups vs.**	**Large family groups**
	t	**P**	**t**	**P**	**t**	**P**
Agitated locomotion	3.20	0.004**	1.43	0.163	-1.76	0.095
Calm locomotion	-4.37	<0.001***	-6.08	<0.001***	-0.76	0.457
Inactive alert	0.95	0.35	4.20	<0.001***	1.64	0.118
Scent mark	0.90	0.378	2.33	0.027*	1.25	0.226
Watch obs.	3.94	0.001**	3.32	0.002**	0.61	0.551

Figure 4.6: Mean percentage time (±S.E. bars) spent in behaviours in three group compositions when pairs were housed in double cages [one-way ANOVA (black marks) and Tukey post-hoc tests (red marks) *P<0.05; **P<0.01; ***P<0.001]



4.4 DISCUSSION

The results of the present study showed a minor effect of cage level when the marmosets were housed in a two tier housing system. Further, they showed positive effects of larger cage (and/or better lighting conditions) on the behaviour of pair housed common marmosets. In addition, in contrast to the initial hypothesis, the results suggest that adult marmosets are more relaxed when housed in pairs with no offspring (in double cages) than adults housed in family groups.

4.4.1 Effects of cage level on behaviour

The only significant difference between marmosets in lower and upper tiers in the present study was found in self-scratching behaviour, with monkeys in lower tiers scratching themselves more compared to those in upper tiers. Scratching is well known as a welfare indicator, with increased levels in poor welfare states (see Chapter 3). Nonetheless, as this was the only significant behavioural difference between animals in the two different cage levels, welfare does not appear to be severely affected by this housing factor. These results are similar to those of several earlier studies (Crockett et al., 1993; Schapiro et al., 2000; Crockett et al., 2000; Schapiro & Bloomsmith, 2001; Buchanan-Smith et al., 2002).

In contrast to the above, Scott (1991) found that common marmosets in upper tiers were significantly more active than their counterparts in lower tiers. Further, Box and Rohrhuber (1993) reported that cotton-top tamarins housed in upper tier cages showed significantly more close physical contact, and were more active compared to those that housed in lower tiers. In addition, Reinhardt (Reinhardt et al., 1992; Reinhardt, 1997b, 2004; Reinhardt & Reinhardt, 1999, 2000) argued that the welfare of nonhuman primates housed in lower tiers is much poorer than that of those housed in upper tiers, although the argument was supported by very little quantitative evidence. Effects of illumination on callitrichids have been shown (e.g. Hampton et al., 1966; Hegar et al., 1986); nevertheless, differences in light intensity between lower and upper tiers hardly affected the behaviour of the marmosets in the present study.

4.4.2 Effects of cage size and height on behaviour

The new European (Council of Europe, 2004) and U.K. (Home Office, 2005) legislation requires a minimum cage height of 1.5m for captive callitrichids. However, in all previous research on the effects of cage dimensions on the behaviour of callitrichid species the emphasis was mainly on the volume of the cage rather than on its height. In the present study, the cages in the two housing conditions were identical for all measures apart from volume and height, which was more than twice as high in the double cages. Further, cages in both conditions were furnished similarly; however, larger cages contained more furniture as they were made of two connected (upper and lower) single cages, and therefore were more complex and allowed the marmosets more choice.

Locomotion and inactivity

The results of the present study show that activity durations and patterns were affected by the increase in cage size. The marmosets showed significantly higher levels of calm locomotion and inactive rest behaviours when housed in the larger cages. Further, they showed significantly lower levels of agitated locomotion and inactive alert behaviours under the same housing conditions. The changes in locomotion and inactivity patterns in the present study may indicate a less stressful environment in the larger cages, as marmosets showed calmer patterns of activity (see Chapter 3).

Previous studies on callitrichids have found that monkeys show higher levels of activity in larger enclosures. Box and Rohrhuber (1993) found that cotton-top tamarins were significantly more active when housed in larger cages. Similarly, Schoenfeld (1989) studied the effects of cage size (together with its location and complexity; see Chapter 6) on the behaviour of a single family group of common marmosets. She found that a reduction in the size of the cage (and its complexity) resulted in a significant decrease in locomotion levels. Kitchen and Martin (1996) found an initial rise in activity levels of common marmosets after transfer to a larger cage. However, these levels reduced again three months after the marmosets were introduced to the larger cage. Pines and colleagues (2002, 2003) also found a positive impact of larger cage size on general activity levels in common marmosets. However, they stressed that the increase in activity levels may have been the result of novelty rather than the effects of the size of the cage. In the present study the larger cages were not all new for the marmosets, as each pair of marmosets was familiar with half of its double cage, with the room, and with conspecifics housed within it. Therefore, novelty alone is unlikely to explain the results.

Watch the observer

The marmosets watched the observer significantly more while housed in small cages than they did when housed in large cages. Two explanations are possible for these differences. First, the second phase of the study took place after I had observed the marmosets for at least one month. Therefore, the marmosets were more used to my presence in the colony room, and hence spent less time watching me. Second, it is possible that the marmosets were more confident and/or less bored in the double cage, and therefore spent less time watching me (a potential predator or a source of interest). Similar results were found in several studies in the present thesis and the alternative explanations are examined and discussed in the General Discussion.

4.4.3 Effects of level of the small cage on location in the larger cage

As each pair of marmosets was familiar with half of its double cage, it was interesting to examine the location of the marmosets in their “half novel” larger cages. The results show that all marmosets preferred the upper part of the double cage, with no impact of the level of their original cage. This preference is in line with previous research, which showed a preference of common marmosets for the upper part of the cage (Ely et al., 1997), as well as with the arboreal nature of wild marmosets (Stevenson & Rylands, 1988). These results, together with the results of the impact of the size of the cage on the behaviour of the marmosets in the present study, testify the importance of the changes in European and U.K. legislation regarding height of the cages for marmosets in captivity.

4.4.4 Effects of group composition on the behaviour of adult marmosets

The results of the present study are quite surprising, showing that pair-housed marmosets, when housed in double cages, appeared more relaxed than their counterparts who were housed together with their offspring. These results contradict the natural social character of common marmosets, which was discussed in Chapter 3. When pairs were housed in single cages, the behavioural differences between these adults and family-housed adults were inconsistent. When adults in pairs were housed in single cages, they scratched themselves significantly less than adults in both large and small family groups. In contrast, the same pair-housed individuals showed lower levels of calm locomotion compared to adults in small and large family groups. In addition, they rested significantly less than adults in small family groups. It is difficult to interpret these results, as they include internal contradictions. On the one hand, the differences in levels of scratching behaviour may indicate better welfare conditions of pair-housed monkeys than those in family groups. On the other hand, the differences in levels of calm locomotion and inactive rest behaviours may lead to the opposite conclusion (see Chapter 3).

Conversely, when marmosets in pairs were housed in double cages, the results were much more consistent. Monkeys in pairs showed lower levels of scent marking compared to monkeys in large family groups. Further, marmosets in pairs showed significantly lower levels of inactive alert and agitated locomotion behaviours, together with higher levels of calm locomotion behaviour. In addition, they watched the observer significantly less than marmosets in small and large family groups. These behavioural differences may indicate that adults in pairs were more relaxed than those in family groups.

Two different explanations may account for these differences in the behaviour of pair housed and family housed adult marmosets. Firstly, density within the cages differed between groups in different compositions, and between pairs-housed in single or double cages (sees Table 4.7). When marmosets in pairs were housed in single cages, the density was higher than that of family groups. However, when they were housed in double cages, the density was less compared to marmosets in family groups.

It is possible that density has significant effects on the behaviour and welfare of captive marmosets. Secondly, the significant differences between adults in family groups and adults in pairs in double cages may lead to the conclusion that adults are more stressed in captive conditions when housed with their offspring. They have to protect their offspring from every possible assailant, so they have to watch the observer carefully, and they cannot be relaxed while their offspring may be in danger. Although it is important for the young to remain in their natal group to learn how to take care of their own offspring (Box, 1975b; Ingram, 1978b; Tardif et al., 1984; Rothe et al., 1992; Röder & Timmermans, 2002), there is no evidence for the beneficial effects of parenthood (Young, 2003). It is logical that as parents have to assure the welfare of their offspring; their own welfare may be harmed. However, it is possible that the results were inconsistent when pairs were housed in single cages because their welfare was compromised by their small cages.

Although the effects of group composition on welfare have not been studied, some previous findings support the results of the present study. First, Box (1975b) found that as family groups of common marmosets grew larger, the adult pair associated with the group less than they had done previously, and the male especially showed poor behavioural variability, and was involved mainly in vigilant activities. Similarly, Koenig and Rothe (1991) found that the adult pair, in a family group of common marmosets, built a strong reciprocal relationship with no connection to their offspring. These results suggest that having offspring does not improve the welfare of the adult breeding pair. Second, it has been shown that in captive groups of callitrichids the adult pair (especially the female) was more aggressive towards intruders (*Saguinus oedipus*: Epple, 1978), and the number of helpers in the group was positively correlated with the levels of aggression exhibited by the breeding female (*Callithrix kuhlii*: Schaffner & French, 1997; *Leontopithecus rosalia*: French & Inglett, 1989). In contrast, in wild populations subordinate females participate more than reproductive females in territorial defence, and in non-agonistic interactions with individuals from other groups (Lazaro-Perea, 2001). These results suggest that breeding adults in captivity may be more stressed in large family groups. Finally, human studies have shown that adult couples report lower levels of happiness and marital satisfaction when they have children than they do before their first child is born and after their children have left home (Walker, 1977; Gilbert, 2006). In addition, women are less happy when taking care of their children than when they are involved in almost every other activity in their daily routine (Kahneman et al., 2004).

Additionally, studies have shown that the presence of helpers (older offspring) in family groups of callitrichids increases at least the physical well-being of the adult pair (Rothe et al., 1993; Snowdon, 1994; Snowdon, 1996), although findings concerning the contribution of helpers for infant survival are conflicting (Rothe et al., 1993; Bardi & Petto, 2002). However, the results of the present study suggest that the welfare of adult marmosets may improve when they are housed in pairs with no offspring. In addition, no significant effects of the size of family groups on the welfare of the adult pair were found. More research is needed in order to extend the findings of this preliminary study.

4.5 CONCLUSIONS

The studies in the present chapter examined the effects of physical complexity, social complexity, and choice on the behaviour of captive marmosets. Table 4.14 summarizes the results of the three studies.

The conclusions made from these studies are:

1) The levels of the cage in two tier housing system did not have significant effects on the behaviour of the pair-housed marmosets (with the exception of scratching).
2) An increase in the size of the cage had positive effects on the activity budget of pair housed marmosets. However, the result that the marmosets spent >80% of their time in the upper half of the cage suggests that the increased cage size, complexity and choice were not fully utilised. Further, it is possible that the increased cage size was of no real benefit for marmosets housed previously in upper tiers, which may explain some lack of real effects of the larger cage (only locomotion patterns were affected).
3) The results of Study III suggest that the welfare of captive adult marmosets may be improved when they are housed (in a reasonable cage size) without offspring, in other words, when the composition of the group is less complex and social interactions are less demanding of time and energy.

Table 4.14: Summary of the main results of Chapter 4

	Elevated levels	**Reduced levels**
Study I Effects of housing in upper tiers vs. lower tiers (32 pairs)		scratch
Study II Effects of housing in double cage vs. single cage*	Inactive rest Calm locomotion	Inactive alert Agitated locomotion Watch observer
Study III (Analysis I) Effects of pair housing (single cage) vs. family housing (small and/or large) on the behaviour of adults**		Inactive rest Calm locomotion Scratch
Study III (Analysis II) Effects of pair housing (double cage) vs. family housing (small and/or large) on the behaviour of adults**	Calm locomotion	Inactive alert Agitated locomotion Scent mark Watch observer

* All animals spent >80% of the observed time in the upper part of the double cage
** No significant behavioural differences were found between adults in small and large family groups

In the next chapter the effects of complexity and choice are examined again, however, the study animals are not adult pair-housed, but a family group of marmosets. Further, the enriched environment in the next chapter is much larger and much more complex, and allows the marmosets more choice. In addition, as the marmosets were moved back to a smaller and less complex environment on a few occasions during the study period, the effects of loss of complexity and choice are also examined.

Chapter 5

A Case Study: The Effects of Complexity and Choice, Together With the Loss of Them, on the Behaviour of a Family Group of Common Marmosets

5.1 INTRODUCTION

The effects of complexity and choice on the behaviour of pair-housed marmosets were discussed in the previous chapter. In the present chapter the effects of the same environmental contingencies are discussed again, however, in this study the study animals are a family group of common marmosets and the enhanced enclosure is bigger and more complex. As a consequence, the marmosets experience much more choice. Furthermore, the effects of the loss of complexity and choice on the behaviour of the marmosets are also examined.

In this study a family group of marmosets was moved to an enriched room, in which they were separated from other marmoset groups (other families were housed in the colony room where their previous enclosure was located). The proximity to other groups of conspecifics may have a significant influence on behaviour (Stevenson & Poole, 1976; Sutcliffe & Poole, 1978; Stevenson, 1983; Box, 1984b). In the present study, the effects of the proximity to conspecifics are confounded with other factors, such as the structural differences between the two enclosures. The aspects of proximity to other groups are addressed in the General Discussion. On a few occasions throughout the study period the marmosets were moved back to the colony room, and to a smaller and less complex environment. Therefore the effects of crowding in this small enclosure, together with the effects of loss of complexity and choice, are discussed.

Although the study animals in the present study are only one family group of marmosets, it is interesting to carry out the study as it has links to both the previous and the next chapters. Schoenfeld (1989) studied the effects of complexity and choice on the behaviour of a family group of marmosets; however, in Schoenfeld's study the marmosets were moved from a large and complex enclosure (in four stages) into a much smaller and less complex cage. In contrast, in the present study, the process was reversed; the marmosets were moved from a laboratory cage in a colony room into a larger and more complex enclosure (and back to the laboratory cage on a few occasions).

5.1.1 Effects of enclosure size and environmental complexity on the behaviour of captive callitrichids

The effects of cage size (see Chapter 4) and environmental complexity (see Chapter 2) on the behaviour of captive primates were reviewed earlier. However, this is the place to emphasize the importance of the complexity of the captive environment above the impact of its size. It has been argued that space is useless for captive monkeys if it is barren and/or inaccessible (e.g. Poole, 1990; Buchanan-Smith, 1997a). Further, the review in Chapter 4 showed that an increased cage size has no impact on behaviour when all cages are too small, and especially when they contain only minimal or no furniture at all. Previous studies on common marmosets showed a positive impact of environmental complexity and a larger enclosure on behaviour (Schoenfeld, 1989; Kitchen & Martin, 1995). However, two studies found greater effects of environmental complexity as compared to the effects of the available space. Kerl and Rothe (1996) found no effects of cage size on the behaviour of pair housed common marmosets (but there was an effect on heart rate), while they found positive effects of cage complexity on the behaviour of the same individuals. The marmosets explored their environment and were more active in the enriched cage compared to a less complex cage of the same dimensions. Similarly, Gaspari and colleagues (2000) studied family groups of common marmosets and found that monkeys increased levels of solitary play and exploratory activities, and reduced stereotyped behaviour in the enriched cages. However, they found no effects of the size of the cage.

5.1.2 Effects of crowding on the behaviour of captive primates

Only one previous study has been done on the effects of crowding on the behaviour of captive callitrichids. Schoenfeld (1989) found negative effects on the behaviour of a family group of common marmosets after they were moved from a large (10x4x4m), outdoor greenhouse, in several stages into a small (1m^3), barren, indoor cage. She found that the marmosets showed decreased levels of play, grooming, scent marking, and locomotion, and spent less time in close proximity to each other in the smaller cages.

More research has been done on the effects of crowding in other primate species, and results show negative effects of a considerable reduction in available space. In several similar studies, socially housed Japanese macaques (*Macaca fuscata*: Alexander & Roth, 1971), rhesus macaques (Southwick, 1967; Boyce et al., 1998), and chimpanzees (Nieuwenhuijsen & de Waal, 1982) showed a significant increase in aggressive behaviour after they were transferred from an outdoor large enclosure into a much smaller indoor cage. In addition, in Nieuwenhuijsen and de Waal's study (1982), the chimpanzees also showed decreased levels of social play and increased allogrooming in the smaller enclosure. In another study the cage space of socially housed baboons (*Papio anubis*) was reduced in four stages, until the troop had 50% of the original floor space. In this study, agonistic and sexual behaviours increased significantly with space reduction, and each decrease of available space appeared to cause stress and tension. The final result of crowding was social disintegration and individual pathology (Elton & Anderson, 1997). However, Demaria and Thierry (1989) increased enclosure space of stump-tail macaques (*Macaca arctoides*) from 10m^2 (indoors-baseline phase) up to 50,000m^2 (outdoors), in two steps, and then reduced it again to 10m^2. They found that aggression levels decreased in the largest enclosure, however, when the macaques were moved back to the 10m^2 enclosure (crowding), levels of aggression did not exceed the baseline levels.

5.1.3 Effects of loss of complexity and choice

The effects of loss of complexity and choice can be studied in two different ways. One way is for animals have free access between two different enclosures (e.g. home cage and exercise cage, or indoor and outdoor cages, see Chapter 6 for a review) and then lose this free access. The second way is when animals to experience a complex environment which allows them more choice, and then be transferred back to a smaller and less complex enclosure. Kessel and Brent (1995a, 1995b) studied the effects of limited access to an exercise cage on the behaviour of baboons (*Papio hamadryas anubis, P. h. hamadryas,* and *P. h. papio*). In addition to the positive effects of these improved housing conditions on behaviour, they found no significant differences in the monkeys' behaviour inside their home cage immediately before and after they had access to the exercise cage. This result indicates that there were no negative effects on the behaviour of the monkeys upon return to home cage and hence no effects of loss of complexity and choice. Bryant and co-workers (1988) in their study on the effects of an exercise cage on the behaviour of long-tail macaques stated that the beneficial effects of the exercise cage did not persist once the monkeys had returned to their home cage; however, they did not report any negative effects upon return to their home cage.

In one study (Seier & de Lange, 1996), vervet monkeys (*Cercopithecus aethiops*) were allowed free access between their home cage and an exercise cage; however, the effects of the blockage of this free access were not investigated. In addition, in several studies, monkeys of different species were allowed free access between their indoor home cage and an outdoor cage (Chamove & Rohrhuber, 1989; Crowley et al., 1989; Redshaw & Mallinson, 1991; O'Neill, 1994; O'Neill-Wagner & Price, 1995; Pines et al., 2002, 2003). However, the effects of loss of choice between the different environments were not investigated in any of these studies.

Therefore, further research is needed on the effects of loss of complexity and choice on the behaviour of captive primates, as their removal to smaller and less complex enclosures could have detrimental effects on welfare. Further, in most of the research on the effects of exercise cages, animals were transferred into and out of the exercise cages, while the effects of the ability to choose between the two different enclosures were hardly studied. In contrast, in many studies on the effects of outdoor environments, animals were allowed free access between indoor and outdoor enclosures; however, the effects of the loss of this free choice were not studied.

5.1.4 Aims of the present study

Although previous research has been done on the effects of cage size (e.g. Box & Rohrhuber, 1993; Pines et al., 2002, 2003) and environmental complexity (e.g. Schoenfeld, 1989; Kitchen & Martin, 1996; Kerl & Rothe, 1996) on the behaviour of callitrichids, it is interesting to examine this topic again, and under different environmental conditions. In most of the previous studies the monkeys were not moved to an entire room which was much larger and more complex than their home cage. In addition, in Chapter 6, the effects of larger and more complex outdoor cages on the behaviour of family groups of marmosets are discussed. In the studies in Chapter 6, the marmosets had free access between their home indoor cages and enriched outdoor cages, while in the present study the marmosets had no choice between different enclosures, as they were transferred into the enhanced enclosure and back into the smaller cage whenever necessary.

The following questions were asked:

1) How does a larger and more complex environment affect the behaviour of family group of common marmosets?
2) How does return to a small cage (crowding) affect the behaviour of the same individuals?

It was hypothesised that a larger and more complex environment would have positive effects on behaviour, while crowding would have negative effects.

5.2 METHODS

5.2.1 Study animals and housing

The study animals were a family group of common marmosets. The group was composed of eight animals, two parents and their offspring of five different generations. Only the youngest generation included both a male and a female twin, while for the other generations only one offspring remained with the family group (for more details about the study animals see Table 5.1).

Table 5.1: Individual details (sex, date of birth (D.O.B), and age at first day of the study)

Individual	D.O.B	Age (in days)
776R (♀, mother)	25/07/1996	2624
749BK (♂, father)	26/08/1996	2592
894BK (♂)	25/02/2000	1314
89Y (♀)	03/09/2001	758
119Y (♀)	11/02/2002	597
145Y (♀)	17/07/2002	441
Infants (♂♀)	28/08/2003	34

The monkeys were housed in three different enclosures during the three phases of the study. In Phase I the monkeys were housed in a quadruple cage (see Plates 3.4 and 5.1) within a colony room. In Phase II the marmosets were housed in an enriched room with brick walls, ceiling, and floor (covered with wood shavings). The enriched room measured 5m long, 2.7m wide and 2.5m high. Moreover, the room’s furniture was much more complex compared to the quadruple cage, and contained wooden logs of different types and sizes, bamboo bridges, ropes, natural plants, metal shelves and various feeding enrichment devices. The metal nest box was the only item that was transferred from the quadruple cage to the enriched room (see Plate 5.2).

Plate 5.1: Quadruple cage in which the marmosets were housed in Phase I

In Phase III the monkeys were housed in two linked quadruple cages, which were connected by a short (about 25cm) tube. In Phases I and III the cages were located in a colony room, which housed other family groups of marmosets. In contrast, in Phase II the family group was isolated from other marmosets; however, they could watch a family group of stump-tail macaques out of a glass window in the room's door.

Plate 5.2: Enriched room in which the marmosets were housed in Phase II

5.2.2 Experimental design

The study period was divided into three phases.

Phase I: one week in a quadruple cage in which the family group was housed for more than 18 months.

Phase II: four months in the enriched room.

Phase III: two separate days in two connected quadruple cages.

On the first day of Phase II the marmosets were encouraged to enter their nest box, and then the nest box was transferred into the enriched room and left in it (on a high shelf) to allow the marmosets to explore their novel environment at their own pace. Three times during the period of Phase II the marmosets were transferred (again in their nest box) back into the previous colony room to enable the cleaning of the enriched room. On the first occasion, the marmosets were housed in a quadruple cage and the behavioural reaction of the marmosets to this first transfer was severe. Therefore, on the following occasions the marmosets were given two connected quadruple cages.

5.2.3 Data collection

Focal animal sampling was used with five-minute of focal observations per animal. In Phase I, only six individuals were observed three times (total observation time of 1 hour and 30 minutes). The twin infants were not observed during this phase, as they were very young and were carried by other group members for almost 100% of the time. In the first week of Phase II all eight marmosets were observed five times, and from week 2 to 16 of Phase II, each individual was observed twice a week (total observation time of 15 hours). Although marmosets were transferred back three times into the smaller and less complex cage during the whole study period, they were observed under this condition on only two of these days (total observation time of 1 hour and 20 minutes). In Phases I and III of the study I observed the monkeys from within the colony room, while in Phase II, I observed them through a glass window. Because of the different situation, the behaviour 'watch the observer' cannot validly be compared across the study Phases and will not be discussed. However, it is noted that the time the marmosets watched the observer during Phases II and III was less than in Phase I. As this behaviour was mutually exclusive with other individual and activity behaviours (see Chapter 3), other behaviours must have increased during the last two phases.

5.2.4 Statistical analysis

One-way ANOVAs with study phase (within subjects) as a single factor with three levels were carried out twice: **1)** data from all eight individuals were used. **2)** data from six individuals were used. The reason for the second analysis was the fact that the two youngest infants were not observed during the Phase I of the study, as they were too young, and therefore, their absence in one of the analysis levels might affect the results. Although the behaviour of every individual in the study was likely to have been influenced by the other study animals, analysis was done at an individual level as the study included only a single family group. Further, no age differences were considered because of the small sample size. The results should be viewed with caution, as the data were not independent and considered only one family group.

5.3 RESULTS

Results of one-way ANOVAs and Tukey post-hoc tests for all eight study individuals and for six individuals only (when data fro the youngest twins were excluded from the analysis) are presented. Few data are available on the effects of the loss of complexity and choice, however, these data were analysed because of their importance, and the lack of previous research on this topic.

5.3.1 **Effects of complexity and choice on behaviour**

The results of one-way ANOVAs (for all eight individuals) revealed several significant main differences between the three housing conditions. These differences were in the amount of time marmosets spent exploring their environment, allogrooming and in contact with other group members. Further significant differences were in calm and agitated locomotion, and in the time marmosets spent inactive alert and inactive rest (see Table 5.2 and Figure 5.1 a, b and c).

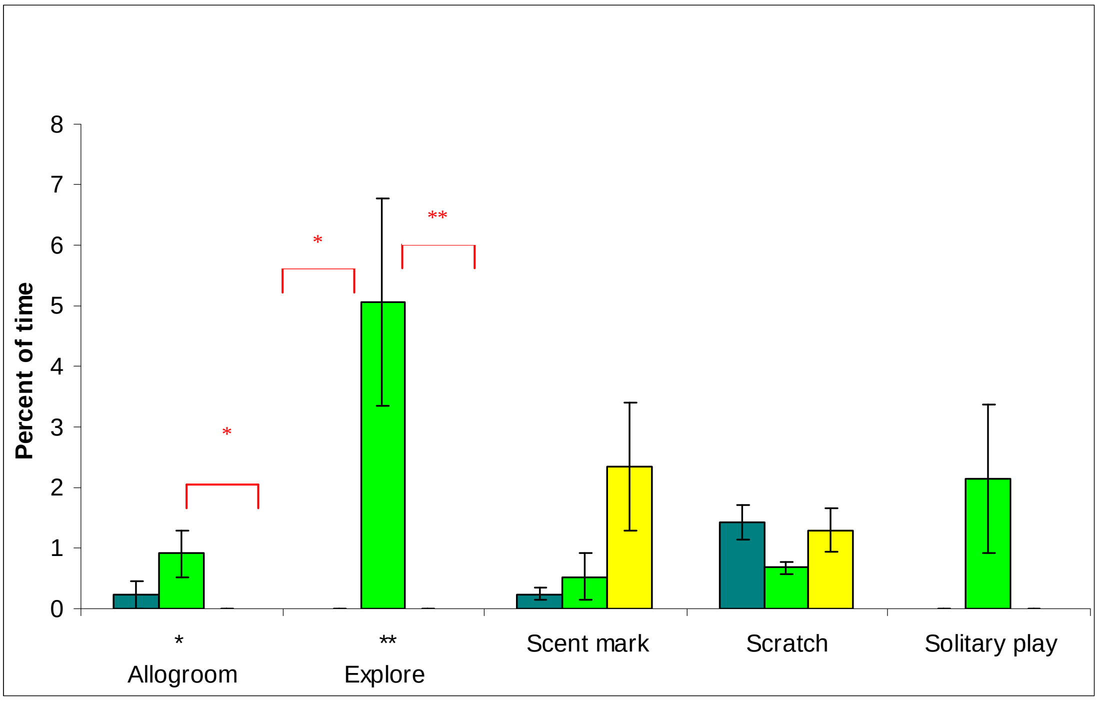
When data from six animals only were analysed, the results were similar to the above. However, main significant differences were found in two further behaviours, scent marking and solitary play, and no significant main effects were found in scratch and allogrooming behaviours (see Table 5.2 and Figure 5.2 a, b and c). The results of the Tukey post-hoc tests show significant effects of complexity and choice together with a significant impact of loss of complexity and choice.

Table 5.2: Results of ANOVAs for the effects of cage size and complexity on behaviour of 8 and 6 individuals (*P<0.05; ** P<0.01; *** P<0.001)

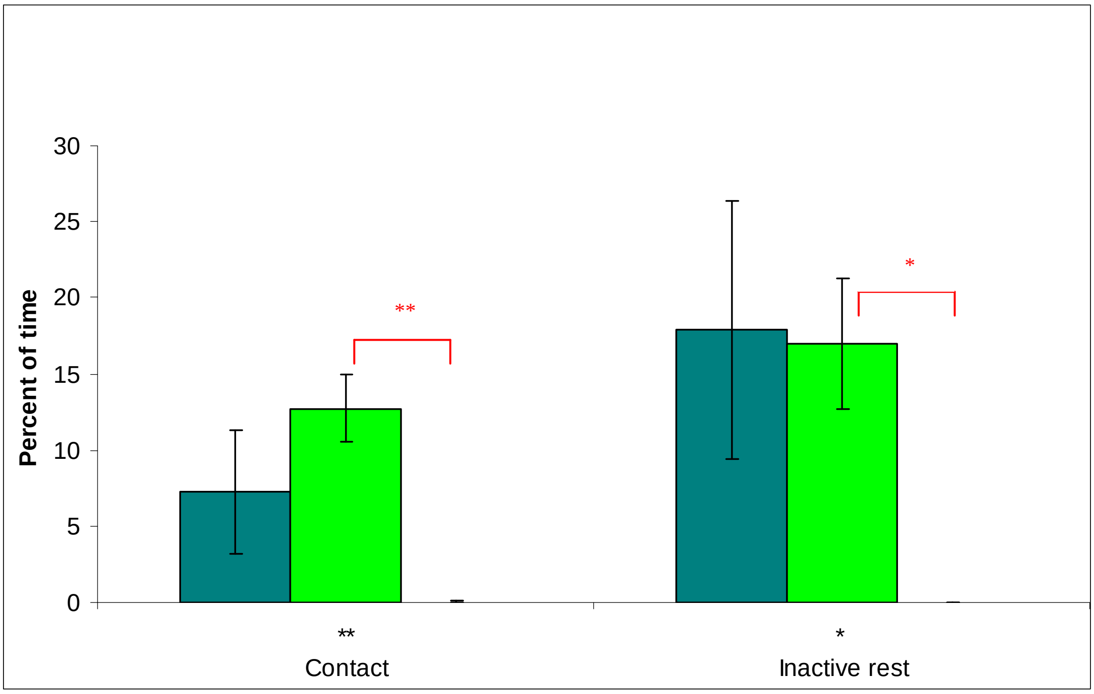
	8	**individuals**	**6** (no	**individuals** infants)
	One-way	AVOVA	One-way	AVOVA
	d.f.=	7,21	d.f.=	5,17
	F	**P**	**F**	**P**
Agitated locomotion	136.43	<.001***	114.93	<.001***
Allogroom	3.93	.048*	2.68	.117
Calm locomotion	25.50	<.001***	15.37	.001***
Contact	8.71	.005**	10.73	.003**
Explore	7.82	.007**	45.92	<.001***
Forage	2.15	.115	2.82	.139
Autogroom	1.07	.374	0.81	.473
Inactive alert	30.19	<.001***	32.11	<.001***
Inactive rest	4.92	.028*	4.27	.046*
Scent mark	2.43	.130	5.08	.030*
Scratch	2.28	.145	2.20	.162
Social play	2.29	.144	1.74	0.224
Solitary play	2.62	.112	6.63	.015*
Tree gouge	.92	.423	0.80	.477

Figure 5.1: Mean percentage time (±S.E. bars) spent in behaviours for eight individuals in three study phases [one-way ANOVA with repeated measures (black marks) and Tukey post-hoc tests (red marks), *P<0.05; **P<0.01; *** P<0.001]

a.



b.



c.

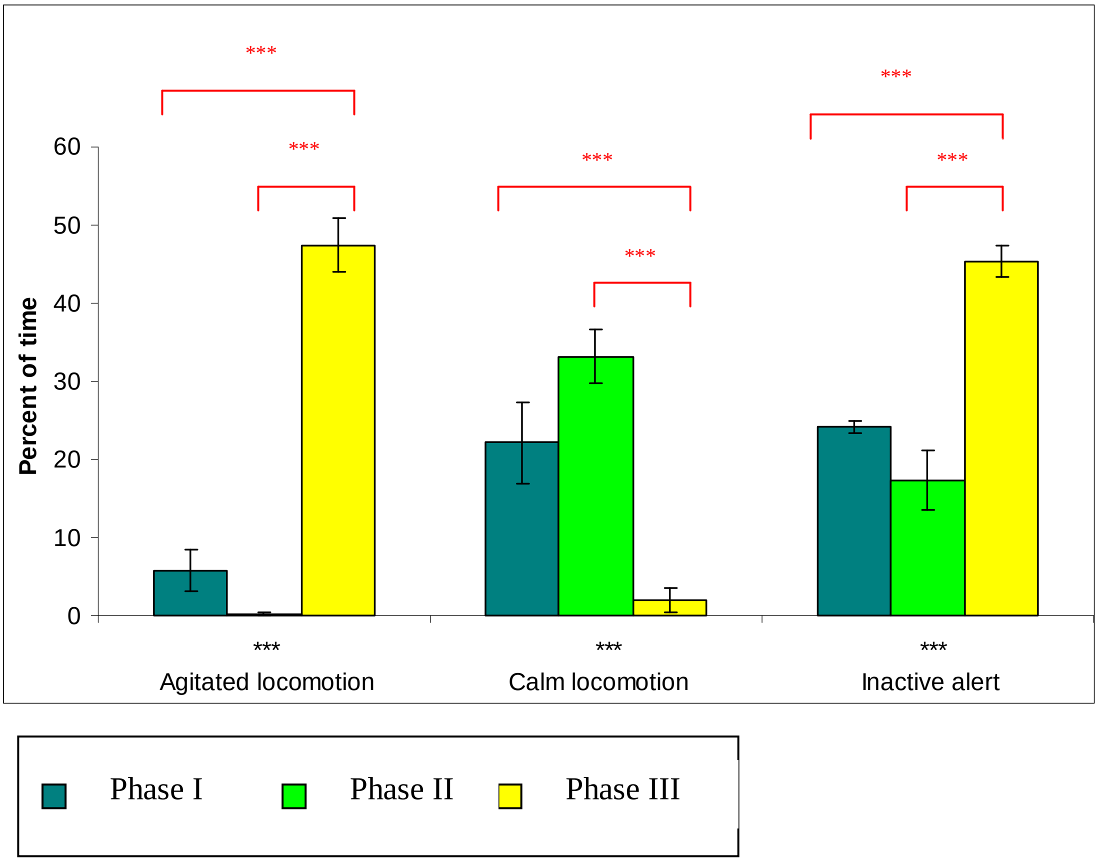
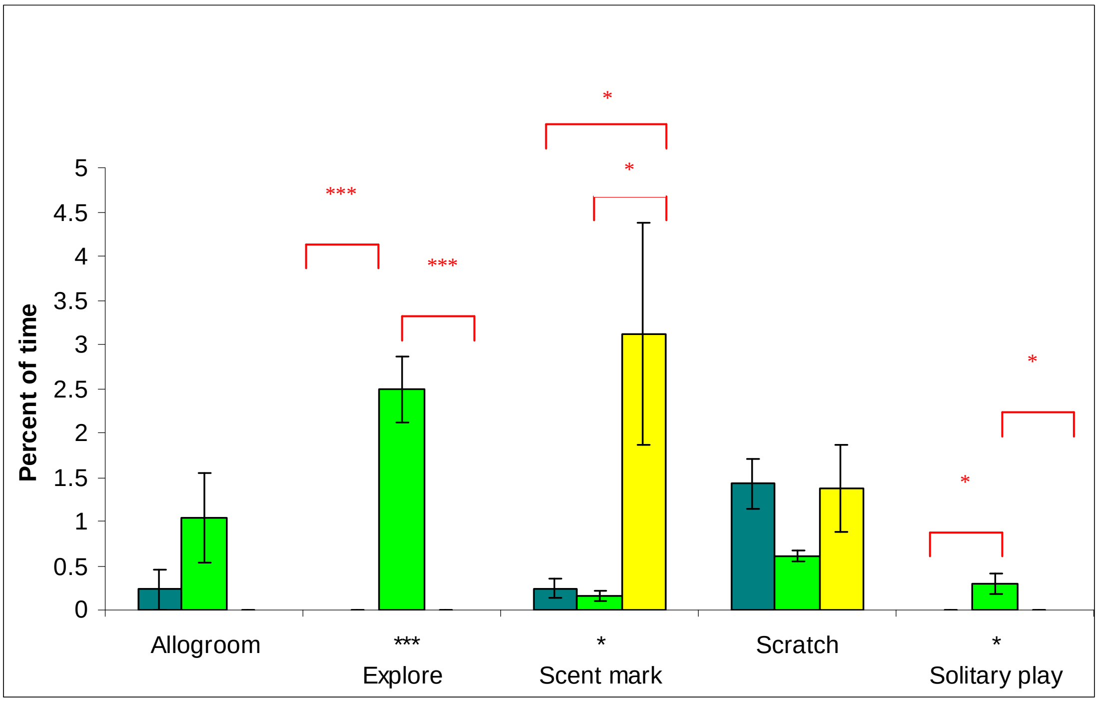

***
***
***
***
***
***
60
50
40
30
20
10
0
Percent of time
***
Agitated locomotion
***
Calm locomotion
***
Inactive alert
Phase I
Phase II
Phase III

Figure 5.2: Mean percentage time (±S.E. bars) spent in behaviours for six individuals in four housing conditions [one-way ANOVA with repeated measures (black marks) and Tukey post-hoc tests (red marks), *P<0.05; **P<0.01; *** P<0.001]

a.



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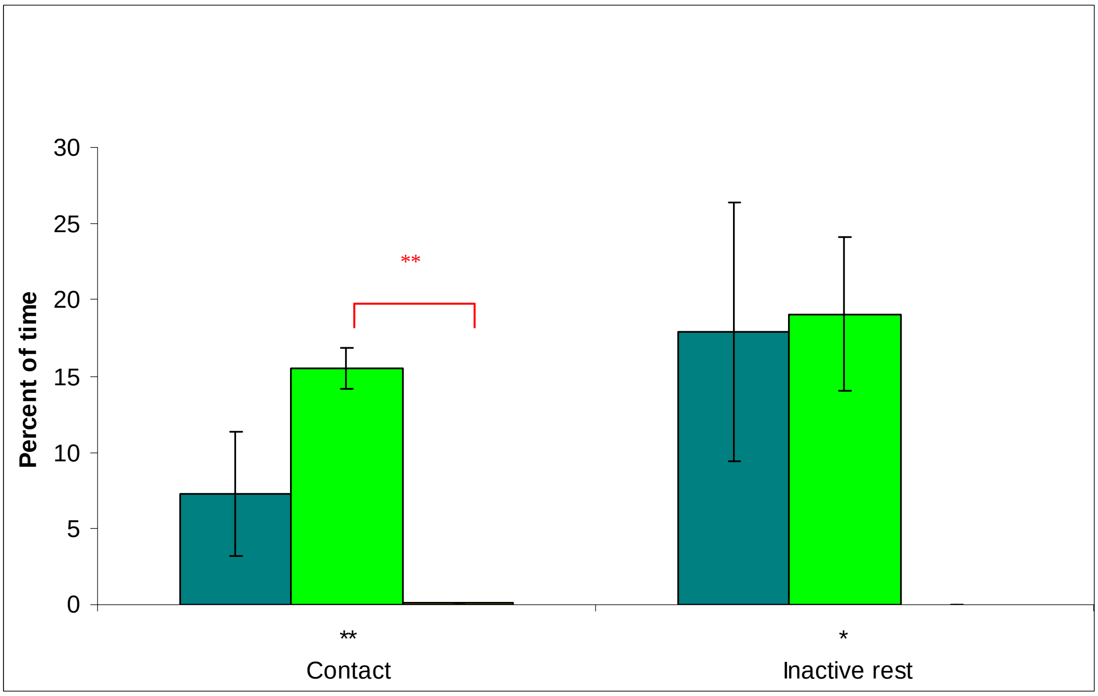
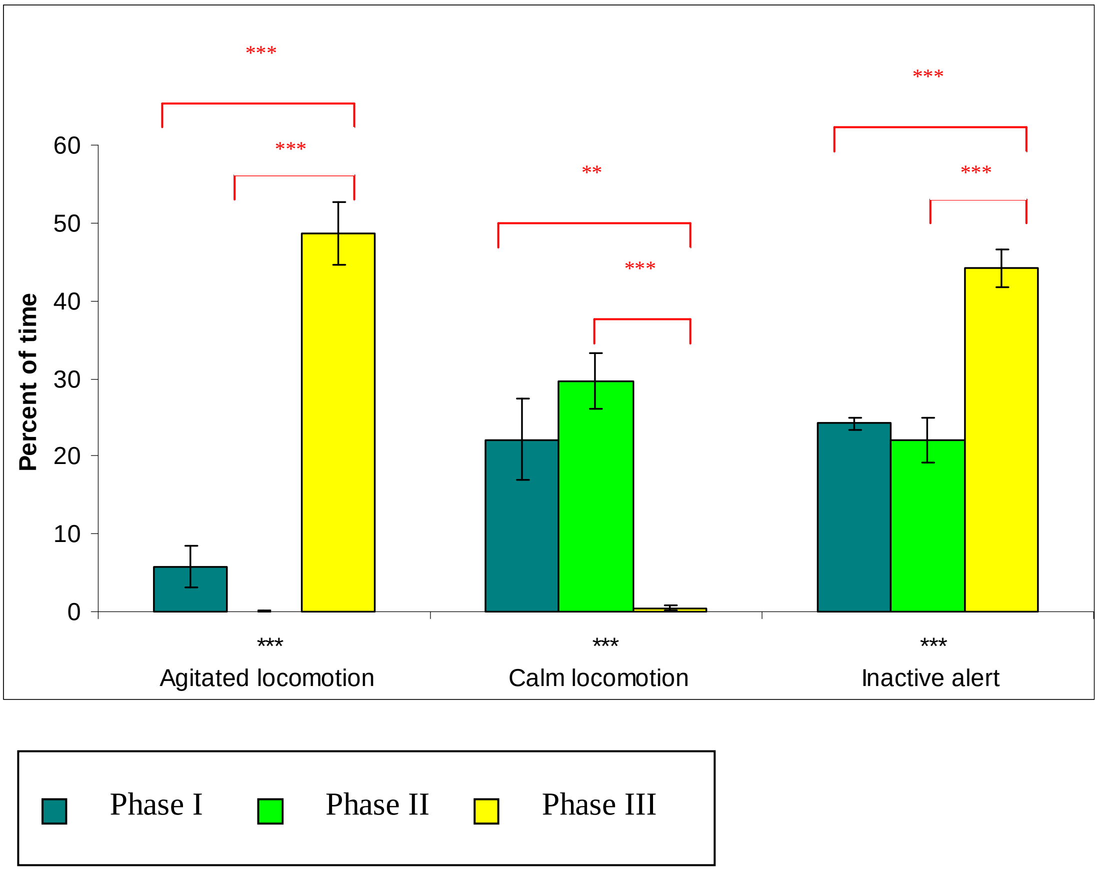


c.



5.3.1.1 *Effects of enhanced complexity and choice*

Certain behaviours were considered to be affected by complexity and choice only when significant differences were found between Phase II and Phase I. When data were analysed for eight individuals it was found that the marmosets explored the environment significantly more during Phase II compared to both Phases I and III (see Table 5.3 and Figure 5.1 a, b and c). When data were analysed for six animals it was found that the marmosets explored the environment significantly more and spent significantly more time in solitary play during Phase II compared to both Phases I and III (see Table 5.4 and Figure 5.2 a, b and c).

Table 5.3: Results of Tukey post-hoc tests (eight individuals) for effects of study phase on behaviour (*P<0.05; **P<0.01; ***P<0.001)

	Phase I vs.	**Phase II**	**Phase I vs.**	**Phase III**	**Phase II vs.**	**Phase III**
	t	**P**	**t**	**P**	**t**	**P**
Agitated locomotion	-1.48	0.333	12.27	<0.001***	15.38	<0.001***
Allogroom	1.77	0.221	-0.40	0.917	-2.68	0.046*
Calm locomotion	1.71	.242	-4.52	0.002**	-6.97	<0.001***
Contact	2.03	0.147	-1.70	0.246	-4.17	0.003**
Explore	2.66	0.050*	-0.87	-.667	-3.84	0.006**
Inactive alert	-1.20	0.474	5.42	<0.001***	7.40	<0.001***
Inactive rest	0.02	0.999	-2.50	0.067	-2.81	0.039*

Table 5.4: Results of Tukey post-hoc tests (six individuals) for effects of the study phase on behaviour (*P<0.05; **P<0.01; ***P<0.001)

	Phase I vs.	**Phase II**	**Phase I vs.**	**Phase III**	**Phase II vs.**	**Phase III**
	t	**P**	**t**	**P**	**t**	**P**
Agitated locomotion	-1.64	0.273	12.23	<0.001***	13.87	<0.001***
Calm locomotion	1.38	0.386	-3.96	0.007**	-5.34	<0.001***
Contact	2.48	0.076	-2.15	0.13	-4.63	0.003**
Explore	8.30	<0.001***	0	1.0	-8.30	<0.001***
Inactive alert	-0.72	0.755	6.55	<0.001***	7.27	<0.001***
Inactive rest	0.16	0.986	-2.45	0.080	-2.61	0.062
Scent mark	-0.8	0.997	2.72	0.052*	2.80	0.046*
Solitary play	3.15	0.025*	0	1.0	-3.15	0.025*

5.3.1.2 Effects of loss of complexity and choice

No formal observations were performed the first time the marmosets were moved back into a quadruple cage in the colony room. However, informal observations showed that levels of aggression, towards both family members and laboratory staff, were very high while the marmosets stayed in this cage. Formal observation during the next two transfers showed that the marmosets spent significantly more time in agitated locomotion and inactive alert behaviours, and less time in calm locomotion behaviour during Phase III compared to Phases I and II (data from either eight or six marmosets). When data were analysed for eight monkeys it was also found that the marmosets allogroomed less, spent less time in contact with each other and in inactive rest behaviour during Phase III compared to Phase II. When data were analysed for six individuals it was also found that the marmosets spent less time in contact with each other during Phase III compared to Phase II, and scent marked more during Phase III compared to both Phases I and II.

After approximately two and a half years in the enriched room, the group consisted of 17 individuals (a large family group compared to a maximum number of nine individuals in quadruple cages). Due to laboratory needs they had to be moved back to a colony room. No formal observations were carried out at this time, but a description of the removal process until a stable group was formed was given to me by the laboratory’s manager. In the first stage the group was moved to four linked quadruple cages (around half of the volume of the enriched room). Within a very short period (a few days) two marmosets had to be removed from the group due to fighting. After about three weeks two more individuals had to be removed again due to fighting. The group’s size was steadily reduced, ultimately to six individuals, which were housed in a quadruple cage, similar to other family groups in the colony rooms.

5.4 DISCUSSION

The results of the study show positive effects of enhanced levels of complexity and choice on the behaviour of family group of marmosets. Furthermore, the crowding situation, and the loss of complexity and choice had major negative effects on the behaviour of the marmosets.

5.4.1 Effects of complexity and choice on behaviour

In order to understand the effects of complexity and choice on the behaviour of family housed marmosets, a family group was moved from a quadruple cage into a much larger (almost nine times more volume) and more complex room, which allowed greater degree of choice. Surprisingly, only a few significant behavioural differences were found when the behaviour of the marmosets in Phase II of the study was compared to their behaviour in Phase I. The marmosets explored the environment significantly more in Phase II (when degrees of complexity and choice were increased) compared to Phase I, when data from eight or six marmosets were analysed. In addition, when data from only six monkeys were analysed (data from infants were excluded) it was found that the marmosets showed significantly higher levels of solitary play during Phase II compared to Phase I. The findings that the significant difference in levels of exploratory behaviour was similar in both analyses, and that the significant difference in levels of solitary play between the study phases was found only when the infants were excluded from the analysis show that no significant differences resulted from the fact that the infants were older and more active and independent in Phase II compared to Phase I, and it can be concluded that all behavioural differences resulted from the different housing conditions.

Despite the lack of more significant behavioural differences between Phase I and Phase II, a positive influence of enhanced levels of complexity and choice can be concluded as increased levels of both exploratory behaviour and solitary play are very desirable for captive marmosets (see Chapter 3). Previous research has also shown similar results. Kerl and Rothe (1996) and Gaspari and co-workers (2000) found that common marmosets explored their cages significantly more when the cages contained complex furniture. Further, Ventura and Buchanan-Smith (2003) studied the effects of the complexity of the cage on the development of infant common marmosets, as well as on the behaviour of caregivers. They found that both the infants and their caregivers explored the environment more when housed in a more complex cage. In addition, they found that infants started to explore their environment earlier when their home cage was more complex. In addition, Pines and colleagues (2005) found that common marmosets used climbing structures more, and were more active when wooden bars in the enclosure were located in a more complex position which provided the marmosets with more choice (vertical and horizontal, or at random compared to vertical only).

The results of the present study are similar to those of Study II in Chapter 4 which also showed a positive impact of enhanced complexity and choice on the behaviour of pair housed marmosets. Nevertheless, these positive effects expressed themselves differently in the two studies. In the present study, levels of exploratory behaviour and solitary play increased significantly with increased levels of complexity and choice, while in Chapter 4 only activity patterns altered. These differences between the two studies may result from two factors. First, in the present study a family group of marmosets was studied, while in the previous study only adult individuals were studied. It is possible that age differences were the cause for the behavioural variation between the studies. Second, in the previous study the marmosets were housed in single cages before they were moved to double cages and it is possible that in those single cages the activity possibilities were very limited. In contrast, in the present study, in Phase I the marmosets were housed in a quadruple cage which is four times bigger than the single cage and allows more options for locomotion (although the available space per individual was similar in the two housing conditions).

5.4.2 Effects of loss of complexity and choice on behaviour

Although few data are available on the effects of loss of complexity and choice, the results are discussed because of their importance for the welfare of captive primates. Further, since the marmosets were moved to the impoverished cage for very short periods of time, one may argue that these results are not relevant since it is possible that the marmosets' reaction was an immediate response to the transfer process which involved capture, and that they would settle down again if they were given more time. However, the response of the marmosets to the permanent removal into a colony room, although no formal data were collected and the conditions were different (a much larger group size, and slightly different housing conditions, see section 5.3.1.2) suggest that this response was a real reaction to loss of complexity and choice.

The results of both analyses show that levels of agitated locomotion and inactive alert increased significantly, while levels of calm locomotion decreased significantly in Phase III compared to those in Phases I and II. In addition, when data for eight individuals were analysed it was found that the marmosets allogroomed significantly less in Phase III compared to Phase II. Further, when data for only six marmosets were analysed it was also found that the marmosets scent marked significantly more during Phase III compared to Phases I and II, and spent significantly less time in contact with each other in Phase III compared to Phase II. These results show a detrimental influence of the loss of complexity and choice on the behaviour of the marmosets, and are in line with findings of previous studies on the influence of crowding in other primate species (Alexander & Roth, 1971; Demaria & Thierry, 1989; Elton & Anderson, 1997; Boyce et al., 1998). In contrast, Schoenfeld (1989) found that common marmosets showed lower levels of scent marking after they were moved to a smaller and less complex enclosure; however, similar to the findings of the present study, she also found that the marmosets showed decreased levels of play and locomotion, and presented fewer positive social interactions when the complexity of the enclosure and the degree of choice were reduced.

The effects of occasional exposure to a larger and more complex cage on the behaviour of primates when returned to their home cage have not been studied extensively. Two studies reported the lack of negative effects on the behaviour of baboons (Kessel & Brent, 1995a, 1995b), and long-tail macaques (Bryant et al., 1988) in their home cage after exposure to an exercise cage. However, in both studies the monkeys stayed in the exercise cages for a very limited time (2 days monthly, and 1 hour daily, respectively), whereas in the present study the marmosets were housed continuously in the larger enclosure around a month and a half between transfers to the impoverished cage. Therefore, it may be suggested that, if permanent access to an enhanced enclosure in not possible, occasional and shorter exposure to an enhanced enclosure may improve the welfare of captive primates. This idea, together with the significance of the techniques used to transfer the monkeys between different enclosures, are discussed in Chapter 6, in which family groups of marmosets are given free access between their indoor home cages and outdoor and more complex enclosures.

5.5 CONCLUSIONS

The effects of complexity and choice together with the effects of loss of these environmental contingencies, on the behaviour of a family group of marmosets were studied and the results are presented in Table 5.5.

The conclusions made from this study are:

4) Enhanced levels of complexity and choice have a positive influence on the behaviour of family-housed common marmosets.
5) The loss of complexity and choice has detrimental effects on the behaviour and the social interactions of family-housed marmosets.

Table 5.5: Summary of the main results of Chapter 5 (analyses of 6 and 8 individuals together)

	Elevated levels	**Reduced levels**
Effects of enhanced complexity and choice	Exploratory behaviour Solitary play	
Effects of loss of complexity and choice	Agitated locomotion Inactive alert Scent marking	Calm locomotion Allogroom Contact

In the next chapter, family groups of marmosets are given free access from their indoor home cages to outdoor, larger and more complex cages. In two separate studies the marmosets are given long term access and occasional short term access to the outdoor cages. The influences of outdoor enclosures and occasional access to improved enclosures are discussed, and further, the results are compared with the results of the present chapter.

Chapter 6

Effects of Free Access to Outdoor Cages on the Welfare of Family Housed Common Marmosets

6.1 INTRODUCTION

The effects of complexity and choice, and the effects of the loss of them, on the behaviour of captive common marmosets were described in Chapters 4 and 5. In the present study, common marmosets could choose how to distribute their time between their indoor home cage and a much more spacious and complex outdoor cage. The effects of choice on the welfare of captive primates, together with the differences between choice, control and complexity, were discussed in Chapter 2. However, little research has been done on the effects of choice *per se* on the behaviour of captive primates. In previous research, choice has been studied mainly in preference tests, and in this type of study, the important outcome is the animals' preference (choice), rather than the effects of being able to make that choice (e.g. Bayne et al., 1992b; Fraser & Matthews, 1997).

More research has been done on the effects of environmental complexity on the welfare of captive primates (e.g. Williams et al., 1988; Kitchen & Martin, 1996). A complex environment enables its occupants to make more choices; hence, studies on the effects of environmental complexity may also be considered to be studies on the effects of the ability to make choices.

Two separate studies were used to investigate the effects of continuous and occasional access to outdoor cages on the behaviour of family groups of common marmosets. In the first study, four family groups had free access to outdoor cages for a period of eight consecutive weeks. In the second study, eight family groups had free access to outdoor cages for three consecutive days, every second week. In both studies, the outdoor cages differed from the indoor cages in several respects. Apart from the different locations, the outdoor cages were larger and more complex than the indoor cages. Further, in the second experiment, the outdoor cages were available to the marmosets on a rotational basis. All these factors could affect the behaviour of the marmosets, both in their home cages and in the outdoor cages.

6.1.1 Effects of outdoor environments on the behaviour and physiology of captive primates

European legislation for the use of primates for scientific purposes emphasizes the advantages of access to outdoor enclosures. It points out that “Where possible, nonhuman primates should have access to outdoor enclosures”, as outdoor enclosures “can include many features of the natural environment” (Council of Europe, 2004). International Guidelines mention the benefit of access to outdoor enclosures, and argue that these enclosures can allow the animals to experience a degree of climatic variability (IPS, 1993). Both European and International guidelines stress the importance of free access to warm indoor or sheltered facilities whenever outdoor enclosures are used (Council of Europe, 2004; IPS, 1993).

Among scientists, opinions concerning the benefits and disadvantages of outdoor enclosures are contradictory. One basic advantage of free access to outdoor enclosures is the extension of available space; hence, while outdoor cages are available, the indoor cages may be smaller (Magere & Griede, 1986), but should still meet the values specified in legislation (Council of Europe, 2004). Additionally, partition of the available space into two separate enclosures may reduce stress, because of the increased opportunities for avoidance of aggressive encounters (Novak & Suomi, 1988). Another benefit of outdoor enclosures is exposure to seasonal fluctuations in light and climate which produce physiological and behavioural changes and may contribute positively to the animals' welfare (Novak & Suomi, 1988; Poole, 1991b; Buchanan-Smith, 1994, 1998). This is in contrast to the very stable and narrowly ranged temperature, humidity, and light conditions inside laboratory holding rooms. In addition, outdoor enclosures provide the animals with more sensory stimulation, and usually more complex environments, which provide greater opportunities for exploration and manipulation (O'Neill et al., 1991; Honess & Marin, 2006).

Despite the considerable benefits of outdoor enclosures, there are several practical disadvantages. First, stress might be intensified by seasonal events during the breeding season (Novak & Suomi, 1988). Further, outdoor enclosures provide potential risk of air pollution and disease transmission from outside vectors (Novak & Suomi, 1988; Honess & Martin, 2006; Wolfensohn & Honess, 2005). In addition, the opportunity for foraging behaviour is also likely to be restricted in outdoor enclosures, since there may be limitations for providing deep litter in these enclosures, as it could become soaked by rain or become bedding for vermin and therefore promote disease (Wolfensohn & Honess, 2005). Wolfensohn and Honess (2005) also stress that outdoor accommodations “do not in any real way liberate the animals, but simply offer access to a controlled external space” (p. 22). They even liken outdoor enclosures for captive primates to prison yards for human beings, and point out that the quality of the accommodation and the handling of the animals matter much more than the location of it. While these points are all valid, the risks may occur at very low frequencies and the other disadvantages may be outweighed by positive behavioural changes.

There have been a number of studies examining the effects of outdoor enclosures on the behaviour of captive primates (see Table 6.1). Many of these have been carried out in zoos rather than laboratories, as space and security are less restricted in zoos compared with laboratory environments. Therefore, although the present study concerns monkeys in laboratories, and although many aspects of laboratory conditions are different to those in zoos, some zoo studies are also discussed.

Effects of weather on usage of outdoor enclosures

Few studies have examined the effects of weather on usage of outdoor enclosures. Suchi and Rothe (1999) studied the effects of abiotic factors on the activity of semi-free ranging common marmosets. One of their findings was that the marmosets tended to sleep outdoors when the temperature was high and the wind velocity was low. Similarly, O’Neill (1994) found that rhesus macaques showed the highest rates of indoor enclosure use when the outdoor temperature was under 3.9ºC, and lower rates when the temperature was 32ºC or above. Further, during the birthing and breeding seasons (spring and autumn, respectively) the rates of indoor enclosure use were the lowest. When Japanese macaques were given the choice between indoor and outdoor enclosures, they spent nearly all day outside in any type of weather, but they usually slept indoors (Crowley et al., 1989). Clearly, more research is needed on this subject, as the value of access to outdoor enclosures during seasons of extreme weather conditions is limited if the monkeys are not using them (although it may still allow escape from aggressive encounters). Further, the effects of seasonal events on the behaviour of primates in indoor/outdoor enclosures have not been studied.

Callitrichid species

The only study that has isolated the impact of indoor/outdoor conditions from other housing conditions has been on common marmosets. Marmosets were allowed free access between their home cages and larger indoor or outdoor cages. These larger cages were the same size as each other and identically furnished; the animals had access to them at different times. The marmosets initially spent 60% of their time awake in the indoor larger cages. However, this decreased rapidly, even during the first three days of the study to 30%. Conversely, when the marmosets were allowed free access to outdoor cages, they spent 80% of their time outdoors until final (ninth) day of the study (Pines et al., 2002). In contrast, Redshaw and Mallinson (1991) allowed golden-lion tamarins free access between outdoor and heated indoor enclosures, and the tamarins spent about 70% of their time indoors. When the behaviour of callitrichids in indoor and outdoor cages has been studied, behavioural changes have always been found. However, while in some studies the changes have indicated a positive influence of the outdoor enclosure (Redshaw & Mallinson, 1991; Pines et al., 2002, 2003), in others they have been more difficult to interpret in relation to welfare (Schoenfeld, 1989; Chamove & Rohrhuber, 1989).

Other primate species

The effects of outdoor enclosures on the behaviour of macaques have been studied in different settings. In most studies the monkeys have been socially housed, however, when singly housed rhesus macaques were moved as a group to an outdoor or indoor playroom with peers, no significant differences in behaviour were found between the two conditions (O'Neill, 1989a, 1989b). Most of the studies on socially housed macaques have shown positive effects of an outdoor enclosure (O'Neill et al., 1991; O'Neill, 1994; Novak et al., 1992, 1995; Boyce et al., 1995). When macaques had the option, they always preferred to sleep indoors (Crowley et al., 1989; O'Neill, 1994). Further, it was found that outdoor housed macaques gained more weight, and showed higher pregnancy ratios compared to their indoor counterparts, although survival rates of both groups were similar (Banerjee & Woodard, 1970). However, no differences were found in morphological development patterns of indoor and indoor/outdoor macaques (Faucheux et al., 1978).

The effects of outdoor enclosures on the behaviour of great apes have been studied mainly in zoo settings. Orang-utans (*Pongo pygmaeus*) housed in a zoo showed no significant behavioural differences between indoor and outdoor enclosures (Forthman et al., 1993). In contrast, zoo housed lowland gorillas (*Gorilla gorilla*: Hoff et al., 1994, 1997) and chimpanzees (Neiuwenhuijsen & de Waal, 1982), and laboratory housed chimpanzees (Baker & Ross 1998) showed a positive influence of outdoor housing.

Table 6.1: Effects of outdoor enclosures on the behaviour of primates in captivity.

(+)= positive effects of outdoor cage; (-)= negative effects of outdoor cage; (?)= effects of outdoor cage were unclear; (blank)= behavioural effects were not mentioned, see key below the Table.

All animals were socially housed unless otherwise stated

Author	**Species (sample size)**[a]	**Indoor**		**Outdoor**		**Effects on behaviour (in brackets) and comments**
		Size [b]	**Period**	**Size** [b]	**Period**	
Banerjee & Woodard, 1970	*Macaca mulatta* (individually housed indoors only, 6)		1 year	4.9m in diameter	1 year	Outdoor monkeys gained more weight
Faucheux et al., 1978	*M. arctoides* (10 outdoors, 7 indoors)	2 cages- 70.56m^3	Free access [c]	450m^2	Free access [c]	Similar morphological development
Nieuwenhuijsen & de Waal, 1982	*Pan troglodytes* (22)	378m^2	Winter	7000m^2		(+)[1,2,4,13] Outdoor was more complex
Chamove & Rohrhuber, 1989	*Callithrix jacchus* (1 group)	8.82m^3	Free access [c]	1920m^2	Free access [c]	(?) Outdoor more natural
Chamove & Rohrhuber, 1989	*Saguinus oedipus* (2 groups)	26.25m^3	Free access [c]	1215m^2	Free access [c]	(?) Outdoor more naturalistic
Crowley et al., 1989	*M. fuscata* (9)	Varied	Free access [c]	Ellipse ~1280m^2	Free access	(+)[1,3,4,5,10] Spent nearly all day outdoors
Schoenfeld, 1989	*C. jacchus* (1 group)	16m^2 x 10m	At least 4 years	16m^2 x 10m	45 days	(?)[3,17,18, 19] Outdoor more naturalistic
Novak et al., 1992	*M. mulatta* (2 groups indoors, 1 group outdoors)	6.34m^3	Winter	0.02km^2		(?)
Forthman et al., 1993	*Pongo pygmaeus* (11)	47m^2- 120m^2		1515m^2- 3030m^2		(?) Outdoor more naturalistic
Hoff et al., 1994	*Gorilla gorilla* (6)	2 x 25 m^2		1500 m^2		(+)[4,10,13] Outdoor more naturalistic
O'Neill, 1994; O'Neill-Wagner & Price, 1995	*M. mulatta* (troop of 21)	~ 35 m^2	Free access [c]	0.02km^2	Free access [c]	(?) Indoor usage increased when temperature was <3.9ºC and ≥32ºC

Continuation of Table 6.1

Author	**Species (sample size)**[a]	**Indoor**		**Outdoor**		**Effects on behaviour (in brackets) and comments**
		Size [b]	**Period**	**Size** [b]	**Period**	
Novak et al., 1995	*M. mulatta* (3 groups indoors, 1 group outdoors)	2.8 m^2 x 2.06m or 5.6 m^2 x 2.06m		0.02km^2		(+)[1,7,8,12,13] Outdoor more naturalistic
Hoff et al., 1997	*G. gorilla* (3 groups)	Varied		Varied		(+)[2,3,6,12,13] Outdoor more natural and bigger
Baker & Ross, 1998	*P. troglodytes* (2 groups of 12-13 individuals)		Indoor only		Indoor + outdoor	(+)[1,7,13]
Boyce et al., 1998	*M. mulatta* (troop of 36)	91 m^2		0.02km^2		(+)[2] Inhibited monkeys were affected the most
Pines et al., 2002	*C. jacchus* (18)	4.6m^3	Home cage	7.65m^3	Free access [c] for 9 days	(+)[4] Monkeys spent 80% of the time outdoor
Pines et al., 2003	*C. jacchus* (18)	7.65m^3 (+ home cage)	5 hour x 3 days	7.65m^3	5 hour x 3 days	(almost none)[4] Home cage was smaller. Play and prey catching only outdoors

c) Number of individuals unless otherwise stated
d) A single m^3 figure indicates cage volume; m^2 + m figures indicate floor area plus cage height
e) Permanent free access between indoor and outdoor enclosures

<u>Key to specific behavioural changes (arrows describe changes in rates in outdoor enclosure compared to indoor enclosure):</u>

1) locomotion ↑
2) aggressive behaviour ↓
3) affiliative behaviour ↑
4) play ↑
5) resting ↑
6) inactivity ↓
7) abnormal behaviour ↓
8) stereotypy ↓
9) cage manipulation ↓
10) exploration ↑
11) vocalization ↓
12) foraging ↑
13) autogrooming ↓
14) abnormal behaviour ↑
15) aggressive behaviour ↑
16) cage manipulation ↑
17) affiliative behaviour ↓
18) scent marking ↓
19) locomotion ↓

These studies on the effects of outdoor cages on the behaviour of primates in captivity vary in many different respects. However, the overall impression is that the outdoor environment has a positive impact on the behaviour and the welfare of captive primates. Most studies on the effects of outdoor enclosures include many confounding factors. Usually, outdoor enclosures are larger, more complex, contain more natural elements, and expose the primates to various weather conditions. Only in Pines and co-workers' studies (2002, 2003), were the indoor and outdoor enclosures similar. Additionally, species, age groups, and previous housing conditions and experience could influence responses to outdoor environments. Further, local aspects such as climate may also affect the usage of outdoor enclosures. Therefore, more research is needed on the effects of outdoor enclosures on more primate species, housed in different conditions.

6.1.2 Effects of occasional access to enriched cages on the behaviour of captive primates

Cage size has a significant impact on the welfare of primates in captivity (see Chapters 2, and 3); nevertheless, in numerous research and breeding facilities, primates are housed in small cages because of lack of space and/or budget. International Primatological Society guidelines recommend the provision of a large complex area to which the primates can have regular, but limited access (IPS, 1993). No previous research has been carried out on the effects of occasional access to an exercise cage on the behaviour of captive callitrichids; however, several studies have been done on other primate species (see Table 6.2). Although the conditions were very different between the various studies, the conclusion of all of them has been a positive influence of the exercise cage on the behaviour of the primates.

The studies differed from each other in several respects. In some studies the monkeys were individually housed both in their home cage and in the exercise cage, which was located inside the colony room, thus, all animals in the colony room could see the individual inside the exercise cage (Blackmore, 1989; Kessel & Brent, 1995a, 1995b; Tustin et al., 1996; Storey et al., 2000). In other studies, the exercise cage was used to provide individually housed monkeys with social experience (O'Neill, 1989a; Wolff & Ruppert, 1991; Seier & de Lange, 1996). Another method was to locate two exercise cages in the same room when the monkeys were either individually (Bryant et al., 1988) or socially (Salzen, 1989) housed. However, when the exercise cage was separated from other cages, and the monkeys were housed socially, both in the home cage and in the exercise cage, the effects of exposure to the exercise cage were still positive (O'Neill, 1989b). Furthermore, O'Neill (1989a) exposed rhesus macaques to an enriched and to an empty exercise room, and showed that the complexity of the exercise enclosure was essential to its positive influence. The period of time that the monkeys spent in the exercise cage, together with the interval between exercise sessions, differed between studies. The time spent inside the exercise cage ranged from 15 minutes to two days, and the time between sessions ranged from 24 hours to one month.

Table 6.2: Effects of exercise cage on the behaviour of primates in captivity. (+)= positive effects of exercise cage; (blank): behavioural effects were not mentioned, see key below Table 6.1

Author	**Species (sample size)**[a]	**Home cage size**[b]	**Exercise cage size**[b]	**Time in exercise cage**	**Housing**	**Location of exercise cage**	**Effects on behaviour (in brackets) and comments**
Bryant et al., 1988	*Macaca fascicularis* (6)	$0.52m^3$	$1.92m^3$	1 hour, 4 days a week, 3 weeks	Single	View to another exercise cage	(+)[1,6,8,10] No effects on behaviour in home cage
Blackmore, 1989	*Macaca* (not given)		$5.5m^2$ x 2.1m and $4.9m^2$ x 2.1m	1 x 8 hours	Single	2 in a colony room + 2 in a separate room	(+)[2] Affected the behaviour of all monkeys in the colony room
O'Neill, 1989a	*M. mulatta* (8)	$0.35m^3$	$12.5m^3$	1 hour a day, 5 days a week	Single in home cage, social in exercise cage	Separate room	(+)[7]
O'Neill, 1989b	*M. mulatta* (8)	$2.82m^3$	$12.5m^3$	1 hour a day, 5 days a week	Social	Separate room	(+)[7]
Salzen, 1989	*Saimiri* (not given)	$0.42m^2$ x 1m; 1, 2, or 4 connected cages	$3.24m^2$ x 2m	24 hours, once a week	Social	2 cages in a separate room	(+)[8]
Wolff & Ruppert, 1991	*M. mulatta, M. fascicularis Cebus* sp. (19)		$5.67m^3$	4 hours per week	Single in home cage and social in exercise cage	Separate room	Old and young monkeys did not adjust to the new conditions

Continuation of Table 6.2

Author	**Species (sample size)**[a]	**Home cage size**[b]	**Exercise cage size**[b]	**Time in exercise cage**	**Housing**	**Location of exercise cage**	**Effects on behaviour (in brackets) and comments**
Leu et al., 1993	*M. fascicularis* (20)		1.1m^2	15 minutes per day, for 36 days	Single		(+)[1,8]
Kessel & Brent,	*Papio hanadryas anubis, P. h. hamadryas, P. h. papio*	0.74m^2	3.31m^2	2 days per month	Single	In the colony room	(+)[1,6] Positive effects on behaviour in home cage
1995a,	(12)						
1995b	(9)						
Seier & de Lange, 1996	*Cercopithecus aethiops* (22 females, 74 males)	0.36m^2 or 0.72m^2 x 0.8m	0.36m^2 or 0.72m^2 x 2m	24 hours every 6 days	Single in home age, with partner in exercise cage	Exercise cage was connected to home cage (monkeys had free access between cages)	(+)[1] Exercise cage with a female in it was connected to a male home cage
Tustin et al., 1996	*M. fuscata* (4)	0.3m^3	2m^3	One day	Single	In colony room	(+)[3,6,8,12,13]
Lynch & Baker, 1998; Lynch, 1998	*M. fascicularis* (34)	0.41m^2 x 1.96m	41m^2	1.5 hours at least once every 10 days	Limited access to a partner in home cage, with partner in the exercise cage	In a separate room	Exercise cage was used as part of the process of pairing animals
Storey et al., 2000	*M. mulatta* (20-30)	0.47m^3	1.62m^3	Several hours daily	Single	In the colony room	(+)[7]

a) Number of individuals unless otherwise stated
b) A single m^3 figure indicates cage volume; m^2 + m figures indicate floor area plus cage height

Another difference between the studies was the methods they used to transfer the monkeys from their home cage to the exercise cage and vice versa, and some of these methods may be stressful in themselves (Rennie & Buchanan-Smith, 2004b). In some studies, the transfer was done using a pole and a collar (Tustin et al., 1996; Storey et al., 2000). In Wolff and Ruppert's study (1991), the monkeys were also caught to be moved between cages; however, the exact method was not described. In other studies, transfer cages were used (Salzen, 1989), sometimes with favoured foods in them to encourage the monkeys to enter these cages (Lynch & Baker, 1998; Lynch, 1998). Another method for transferring the monkeys between the home and the exercise cages was to attach the monkeys' home cage to the exercise cage, open the doors between them and coax the monkeys from one to the other using food and praise (Kessel & Brent, 1995a, 1995b). In only one study (Seier & de Lange, 1996) was the exercise cage connected to the home cage by tunnels during the whole exercise session, so the monkeys could move freely between cages. However, the exercise cages were connected only to the males' home cages, while the females, who used the exercise cages simultaneously with the males, were transferred into the exercise cages at an earlier stage.

When the impact of exercise cages on behaviour has been studied, only positive changes have been found (e.g. Bryant et al., 1988; O'Neill, 1989a, 1989b). Further, positive (Kessel & Brent, 1995a, 1995b) or no effects on the behaviour in the home cage have been reported (Bryant et al., 1988). However, no research has been done on the effects of occasional access to exercise cage on the behaviour and welfare of callitrichid species.

6.1.3 Aims of the present study

The aim of the present study was to investigate the effects of complexity, choice, and exposure to outdoor conditions, together with the effects of occasional exposure to these conditions, on the behaviour of captive common marmosets. Although the effects of the location of the enclosure (outdoor/indoor, e.g. Pines et al., 2002, 2003), as well as the effects of the complexity of the cage have been studied before (see Chapters 4 and 5), the findings are contradictory and additional research is needed. In addition, in Chapter 5 it was found that loss of choice and complexity has detrimental effects on the behaviour of captive marmosets. In the present study the effects of loss of these contingencies are studied again; however, in these studies the less complex environment was still used as the home cage for the marmosets throughout the whole study, and the marmosets were able to roam freely between the two enclosures. Further, the effects of climate and temperature on the marmoset’s preferences have not been previously studied. In the present study, the enclosures differed in their location, size, and complexity; therefore, the effects of all of these aspects on behaviour are studied.

The following questions were asked:

1) Do weather and temperature affect the amount of time that the marmosets spend in the outdoor cages?
2) What factors influence usage of outdoor enclosures by different study groups?
3) Does the behaviour of the marmosets differ between the two enclosures?
4) Does loss of choice and complexity affect the behaviour of the marmosets?

5) Does occasional access to outdoor cages affect the behaviour of the marmosets in their home cages?

It was hypothesized, based on previous research (see above), that access to the outdoor cages would positively affect the behaviour of the marmosets. Further, as prior to the beginning of this study the marmosets were housed in the very controlled and stable laboratory environment, and in addition, rain and wind might be unpleasant, it was hypothesized that the weather would affect their attendance in the outdoor cages.

6.2 METHODS

Two separate studies were carried out in order to study the effects of free access to outdoor cages on the behaviour of family groups of common marmosets. Indoor and outdoor conditions were identical in both studies, while the study design was different. Results of both studies were very similar, therefore the methods and results for Study I are described briefly and only Study II is discussed in detail.

6.2.1 Study I

The first study examined the effects of continuous access to outdoor cages on the behaviour of four family groups (25 individuals). Indoor and outdoor cages were different from each other in several respects; these differences are presented in Table 6.3, and illustrated in Plates 6.1 and 5.1. The study period was divided into three phases: Baseline (3 days), Outdoor phase (8 weeks), and After phase (3 days). Data collection methods and statistical analyses were similar to those of Study II (see Table

6.6). However, the effects of the location of the cage inside the colony room on usage of outdoor cages were not examined in Study I.

Table 6.3: Characteristics of indoor and outdoor cages

	Indoor cages	**Outdoor cages**
Cage size	1.5m (l) x 1.1m (w) x 2.3m (h)	5m (l) x 1.5m (w) x 2.5m (h)
Cage features	Metal cage with wire grid on one side only	Wooden frame with metal mesh walls on all four sides, and transparent plastic on the roof
Furniture	Wooden logs, rubber shelves, plastic shelves, metal nest box, sometimes short bamboo bridges, thick layer of wood shavings on the floor	Wooden logs, bamboo bridges, natural plants, wooden shelves, stones, swing, stone floor with no covering
Feeding options	Regular food (see General Methods Chapter) and water were available at all times	Natural plants and insects, no water supply
Temperature	22-23ºC	7-22ºC
Weather	Not relevant, although some natural light entered rooms	All types of Scottish spring and summer, from rainy and windy to sunny and warm
Cage surroundings	Laboratory room with limited view to the technicians' corridor	Open roof, where the marmosets could see the sky, feel the fresh air, get wet by the rain, warm up in the sunshine, and hear and/or see wild animals
Neighbouring marmoset groups	There were at least 8 family groups in each colony room (4.5m x 6.5m), with visual, auditory and olfactory contact with each other	There were no more than 4 groups simultaneously in the outdoor cages, with unlimited auditory and olfactory access, while the visual contact between the groups was very limited

Plate 6.1: An outdoor cage

6.2.2 Study II

The second study examined the effects of occasional access to outdoor cages on the behaviour of eight family groups.

6.2.2.1 Study animals and housing

The study animals were 46 common marmosets housed in eight family groups. Two marmosets died two weeks after the beginning of the study, and therefore they were excluded from the study (deaths appeared to be unrelated to the outdoor cages). Each family group contained four to eight marmosets, which included adults, sub- or young-adults (non-parents, over 300 days old), youngsters (45-300 days old), and infants (less than 45 days old on the first days of the study). For the exact composition of each study group and further details regarding the study animals see Tables 6.4 and 6.5.

It is important to point out that the mark of each group has a meaning. The first digit (**2**L2) stands for the number of the colony room, and the middle letter (2**L**2) indicates the side of the room in which the cage located (L for left and R for right). The last digit (2L**2**) shows the location of the home cage in relation to the room's door (1- shortest distance from the door, 4-longest distance from the door). When the indoor home cages were connected to the outdoor cages, the length of the connecting tube was similar to the distance of the home cage from the colony room's door. Both indoor and outdoor cages and housing conditions were similar to those in Study I. The only difference was that ropes were added to the outdoor cages before Study II began.

Table 6.4: Number of individuals of each age group in the eight study groups, and mean age of each age group

Group identifier	**2L2**	**3R2**	**4L1**	**4L4**	**2R4**	**3L2**	**4R4**	**4R1**	**Mean age (in days)**
Parents	2	2	1	2	2	2	2	2	1971.5±110.1
Young-adults	2	3	3	2	1	1	2	1	504±51.9
Youngsters	3	0	0	4	2	2	1	4	177.1±21.1
Infants	0	0	0	0	1	0	0	0	
Total number	7	5	4	8	6	5	5	7	

Table 6.5: Group and individual details (sex, date of birth (D.O.B), and age on first day of the study), monkeys marked in red died and have been excluded from the study

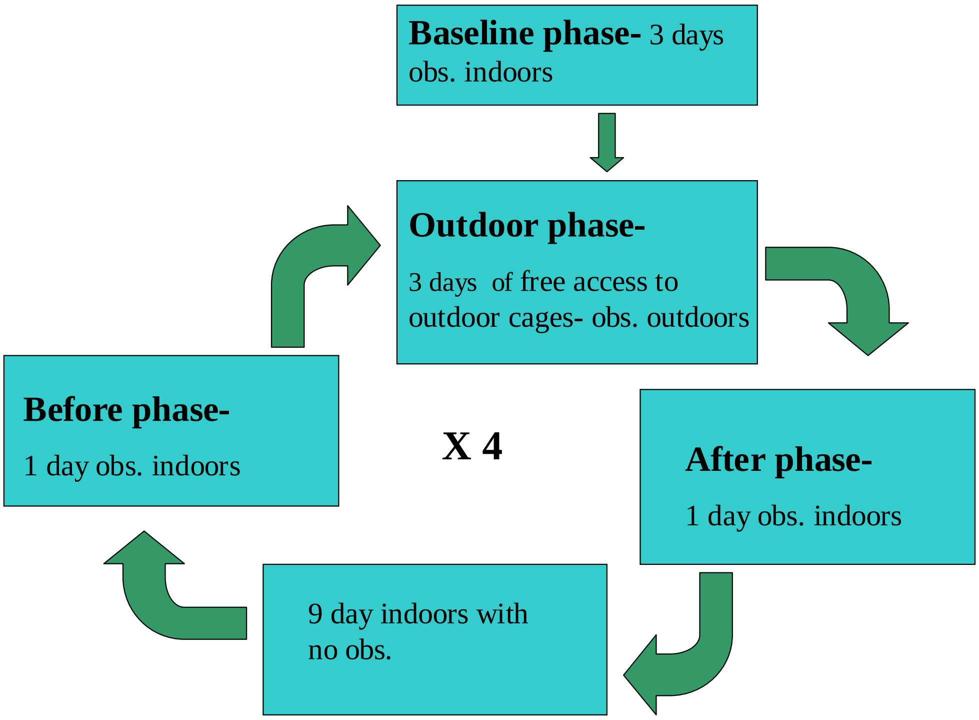
Group identifier	Individual	D.O.B	Age (in days)
2L2	853R	03/11/1997	2457
	792BK	01/01/1998	2398
	895BK	05/03/2002	874
	125Y	02/05/2002	815
	♀♂	02/01/2004	206
	♀♂	06/06/2004	50
3R2	999R	27/02/2000	1611
	836BK	21/07/1998	2197
	113Y	25/12/2001	944
	216Y	18/08/2003	343
	217Y	18/08/2003	343
4L1	847R	05/09/1997	2516
	872BK	21/05/1999	1893
	64G	01/05/2003	452
	191Y	01/05/2003	452
	♀	24/09/2003	306
4L4	994R	31/12/1999	1669
	810BK	29/04/1998	2280
	200Y	18/06/2003	404
	201Y	18/06/2003	404
	233Y	18/11/2003	251
	92G	18/11/2003	251
	♀♂	16/05/2004	71
2R4	30Y	01/08/2000	1442
	844BK	30/09/1998	2113
	186Y	11/04/2003	459
	♀♂	20/02/2004	144
	♀	26/07/2004	-13
3L2	852R	26/10/1997	2452
	770BK	13/03/1997	2679
	65G	05/03/2003	496
	228Y	19/10/2003	268
	229Y	19/10/2003	268
4R4	37Y	02/09/2000	1410
	901BK	21/03/2000	1575
	62G	27/04/2003	443
	63G	01/05/2003	439
	227Y	07/10/2003	280
4R1	25Y	29/06/2000	1475
	862BK	09/04/1999	1922
	204Y	23/06/2003	386
	234Y	21/11/2003	235
	94G	21/11/2003	235
	♂♂	27/04/2004	77

6.2.2.2 Study design

The present study was divided into four phases: Baseline (3 consecutive days), Before (3 x 1 day), Outdoor (4 x 3 consecutive days), and After (4 x 1 day), see Figure 6.1. The Baseline phase took place when all study animals were held in their indoor home cages, before they were given access to the outdoor cages. On the morning of the fourth day, the indoor home cages were connected to the outdoor cages for three consecutive days and marmosets were given access to outdoor enclosures for the first time ever. Home cages were connected to the outdoor cages by a plastic tubing system (20cm in diameter), allowing free access between indoor and outdoor cages. The length of the connecting tubes outside the colony room were similar for all groups (~5m indoors, from colony room to skylight + 2.5-3m outdoors, from skylight to outdoor cage); however, the tubes' length inside the colony room was affected by the location of each home cage and ranged from 2-4m (see Plates 6.2 and 6.3).

On the morning of the eighth day, access to outdoor cages was blocked, and then the After phase started (one observation per individual). Nine days later, each monkey was observed once again in his/her indoor home cage (Before phase), a day before the access to the outdoor cages was opened again. The Baseline phase took place only once, whereas the Outdoor and After phases were repeated four times. The Before phase was repeated only three times (instead of four) as it measured the behaviour of the monkeys on the day before they were given access to the outdoor cages, but it also showed their behaviour 10 days after the access to the outdoor cages was blocked, which was not possible in the first repetition.

Figure 6.1: Study design for Study II



6.2.2.3 *Data collection*

During the Baseline phase, each marmoset was observed three times for four minutes (total observation time 9 hours 12 minutes). During the Before phase, again each marmoset was observed three times (total observation time 9 hours 12 minutes). During the Outdoor phase only monkeys that were present in the outdoor cages were observed (total observation time 15 hours 32 minutes), and during the After phase each monkey was observed four times (total observation time 12 hours 16 minutes). During the Outdoor phase, the outdoor cages were checked five times a day (between 0900h and 1630h) for animals' attendance. The number of samples for the different groups varied as a result of cleaning days and times (2L2-71 samples; 3R2-68; 4L1-

65; 4L4-64; 4R4-64; 4R1-63; 2R4-58; 3L2-61). These data were used to examine the usage of the outdoor cages.

6.2.2.4 Statistical analysis

Two different sorts of data were collected. The first type of data was the behaviour of the marmosets, which was observed in the three study phases. The second type was the amount of usage of the outdoor cages, during the Outdoor phase of the study. Statistical analyses for all behaviours, and for location inside the cage, were calculated using percentages of total observation time. Statistical analyses for usage of the outdoor cage were calculated using percentages of all available samples (every time the outdoor cages were checked for animals' attendance).

Although the behaviour of each animal was likely to have been influenced by that of its family members, group means were not calculated for behavioural data. During most of the Outdoor phase days, not all marmosets in each study group were seen outdoors (some monkeys hardly accessed the outdoor cages at all). Therefore, if only days on which all group members were observed outdoors were used there would have been insufficient data for analysis. In addition, only individuals who were observed at least three times during the Outdoor phase were used for the behavioural analysis. Therefore, 16 individuals were excluded from the analysis (5 adults, and 10 young monkeys); all of them were members of groups 2R4, 4R4, and 4L4. Behavioural data were analysed for adults and young individuals (youngsters and young-adults together) separately, as age is known to impact on behaviour.

Plate 6.2: Tubing system indoors

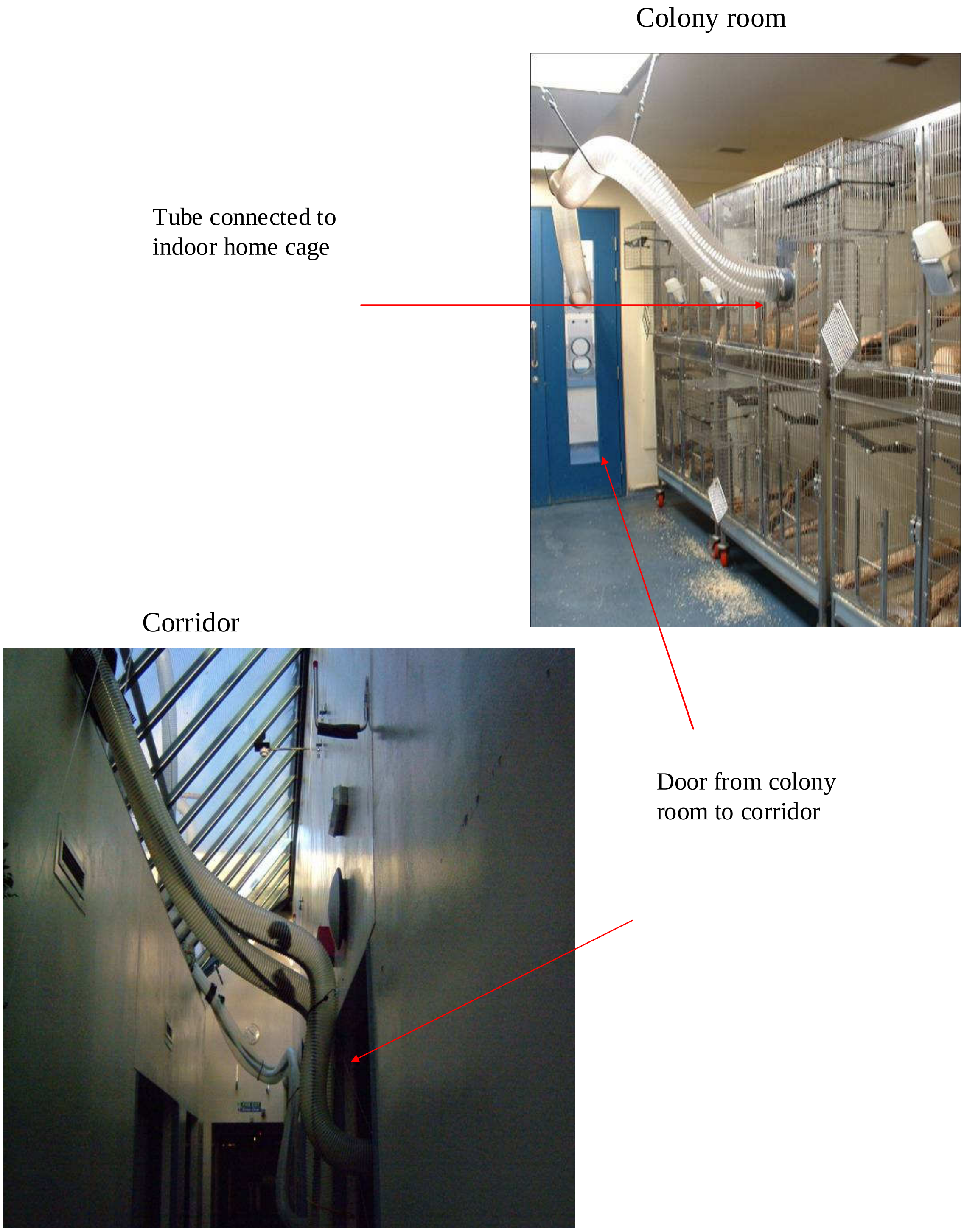
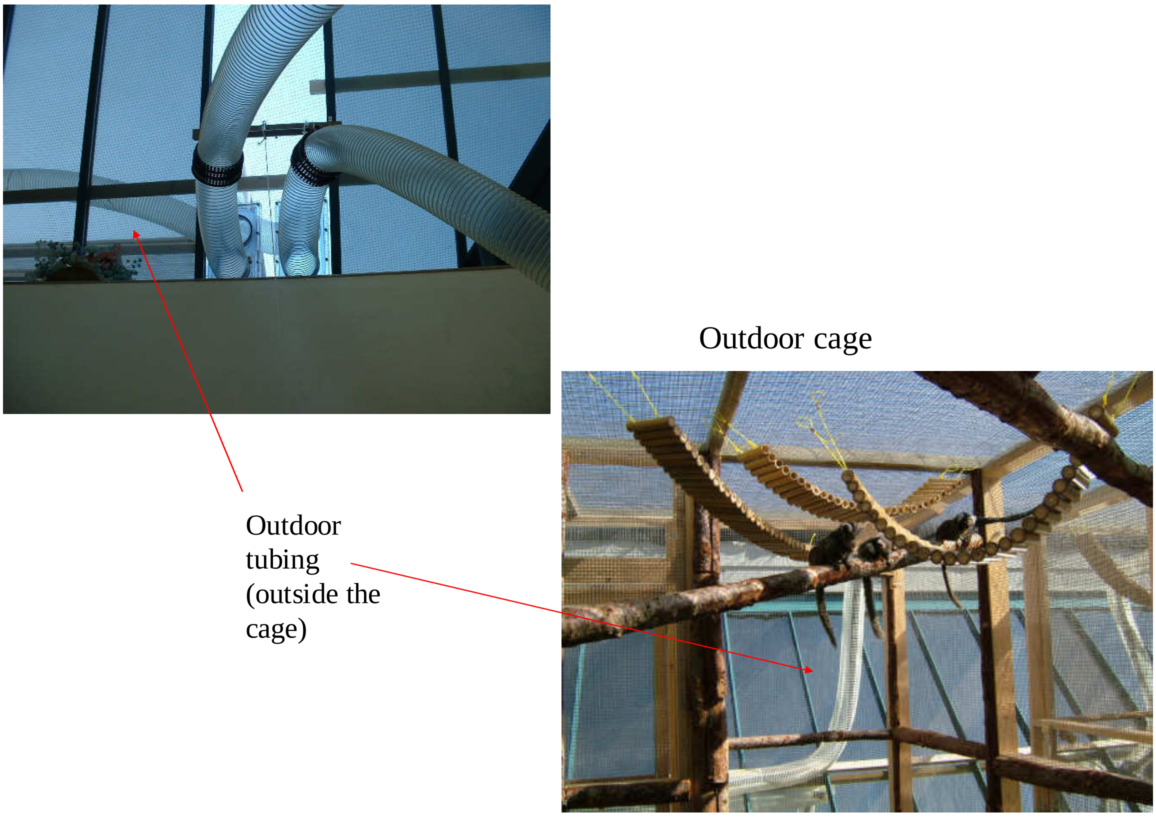


Plate 6.3: Tubing system outdoors



Skylight from an indoor perspective

Outdoor cage

For the analyses of outdoor cage usage, data from all individuals were used. Further, means were calculated for six different types of weather (rainy, cloudy windy, cloudy, partly cloudy windy, partly cloudy, and sunny), and for different temperature categories, under 18ºC, and above or equal to 18ºC. These temperatures were chosen as in Pines and co-workers' studies (2002, 2003) common marmosets were allowed to use outdoor cages only when the temperature was 18-32ºC. In addition, because of the very low rates of attendance of members of groups 2R4, 4R4, and 4L4, further analyses were carried out to examine reasons for this variation (see Table 6.6).

Separate statistical tests were carried out in order to examine effects of the different factors of the study (see Table 6.6).

Table 6.6: Statistical analyses used in Studies I and II

Topic	Research question	Statistical analysis	Factors	Levels	Analysis
Studies I + II					
Cage usage	Effects of weather	One-way ANOVA, repeated measures	Weather type	Six different types of weather	Within subjects
	Effects of temperature	Pair-sample t-test	Temperature	<18ºC/≥18ºC	Within subjects
Behaviour	Effects of outdoor cages on adults	One-way ANOVA	Study phase	Base/Before/Out/After*	Within subjects
	Effects of outdoor cages on young marmosets	One-way ANOVA	Study phase	Base/Before/Out/After*	Within subjects
Study II only					
Cage usage	Effects of cage location in the colony room	One-way ANOVA	Group (cage)	Eight different study groups	Between subjects
Cage usage of marmosets from groups 2L2, 3R2, 4L1, 4R1, 3L2	Effects of weather	One-way ANOVA, repeated measures	Weather type	Six different types of weather	Within subjects
	Effects of temperature	Paired-sample t-test	Temperature	<18ºC/≥18ºC	Within subjects

* The level ‘Before’ was used only in Study II

The comparison of levels of foraging between the Outdoor phase and the Indoor phases is not valid since no food was supplied outdoors (although a few unsuccessful attempts at prey capture were observed). Therefore, foraging behaviour is not discussed in the present chapter. However, it is important to mention that no undesirable behaviours compensated for the absence of foraging behaviour outdoors.

6.3 RESULTS

The results show the effects of outdoor cages on captive marmosets from several aspects:

1) Amount of usage of outdoor cages in different conditions
2) Effects of outdoor cages on behaviour
3) Effects of loss of complexity and choice
4) Effects of occasional access to outdoor cages

6.3.1 Study I

The results of Study I show that the marmosets used the outdoor cages for a mean of 48.32% (n=25, SE=±3.74) of time. Further they preferred warm and sunny weather and avoided wind and rain. Both adults and youngsters were positively affected by the exposure to outdoor cages. Adults and young showed higher levels of calm locomotion and exploratory behaviour together with lower levels of inactive alert behaviour during the Outdoor phase compared to both indoor phases of the study. Young marmosets also showed less scent marking and scratching during the Outdoor phase compared to at least one of the indoor phases. No consistent effects of loss of complexity, choice and access to outdoor cages were found for either youngsters or adults. Behaviours returned to levels which were not significantly different from baseline levels.

6.3.2 Study II

6.3.2.1 Marmosets' usage of outdoor cages

All individuals from all eight groups accessed the outdoor cages for a mean of 24.91% (n=45, SE=±3.12) of the available time. However, different factors affected their presence in the outdoor cages.

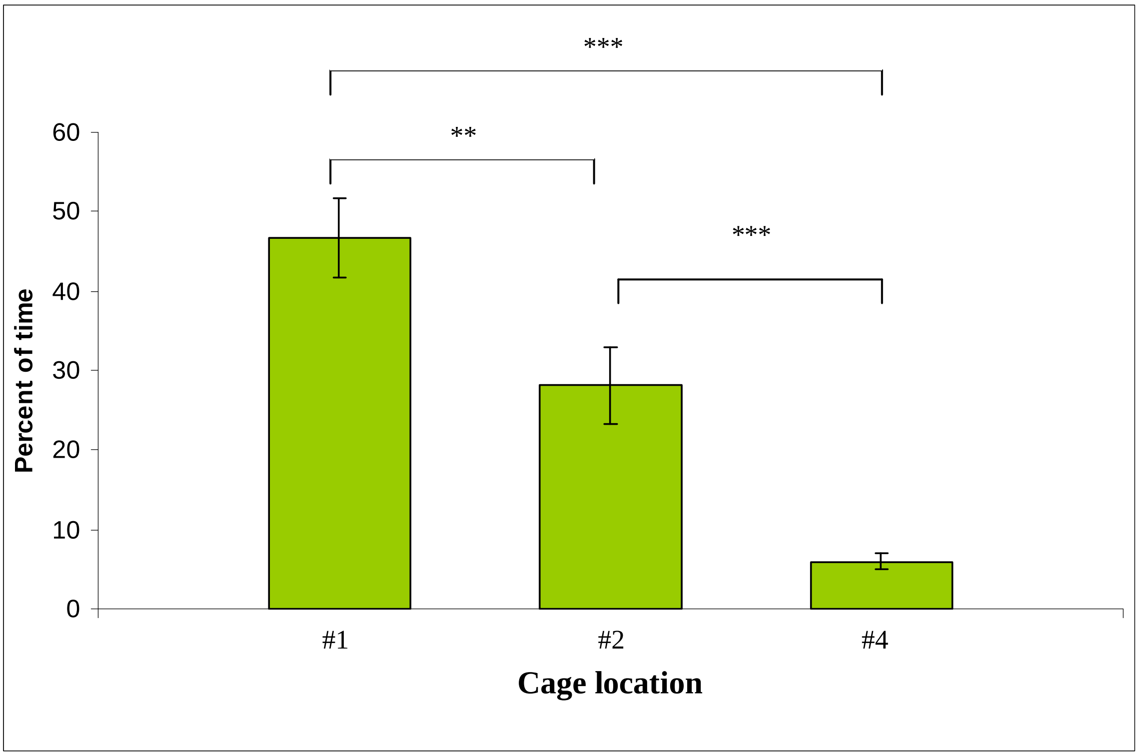
Cage location inside the colony room

The location of their indoor home cage inside the colony room had a great impact on the amount of time that the marmosets spent in the outdoor cages. A one-way ANOVA (with cage location as factor, between subjects) revealed a significant main effect of cage location ($F_{2,45}$=42.38, P<0.001). Tukey post-hoc tests showed that groups housed in cages number one (closest to the room's door) used the outdoor cages significantly more than groups that were housed in cages numbered two and four. Further, groups housed in cages numbered two, used the outdoor cages significantly more than those groups that housed in cages numbered four (see Table 6.7, and Figure 6.2), i.e. the further from the door the home cage location, the less the animals used the outdoor enclosure. When groups furthest from the door (number four) were taken out of the sample, the overall mean of outdoor cage usage was 37.16% (n=28, SE=±3.14).

Table 6.7: Results of Tukey post-hoc tests for effects of indoor cage's location on usage
of outdoor cages (**P<0.01; ***P<0.001)

		Cage #2	Cage #4
Cage #1	t	19.86	43.37
	P	0.001**	<0.001***
Cage #2	t		23.51
	P		<0.001***

Figure 6.2: Mean percentage of time (±SE bars) monkeys housed in different locations indoor spent in outdoor cages (**P<0.01; ***P<0.001)



On account of the considerable variation between the different groups regarding the amount of time they spent in the outdoor cages, the following analyses (in section 6.3.2.1) were carried out twice, once for all eight groups, and once only for the five groups that were located closest to the door in the colony room (cages numbered 1 and 2). However, the results of the two different analyses were similar (for the effects of weather and temperature on the marmosets' attendance of outdoor cages). Therefore, only the results of the analysis of all eight groups are presented.

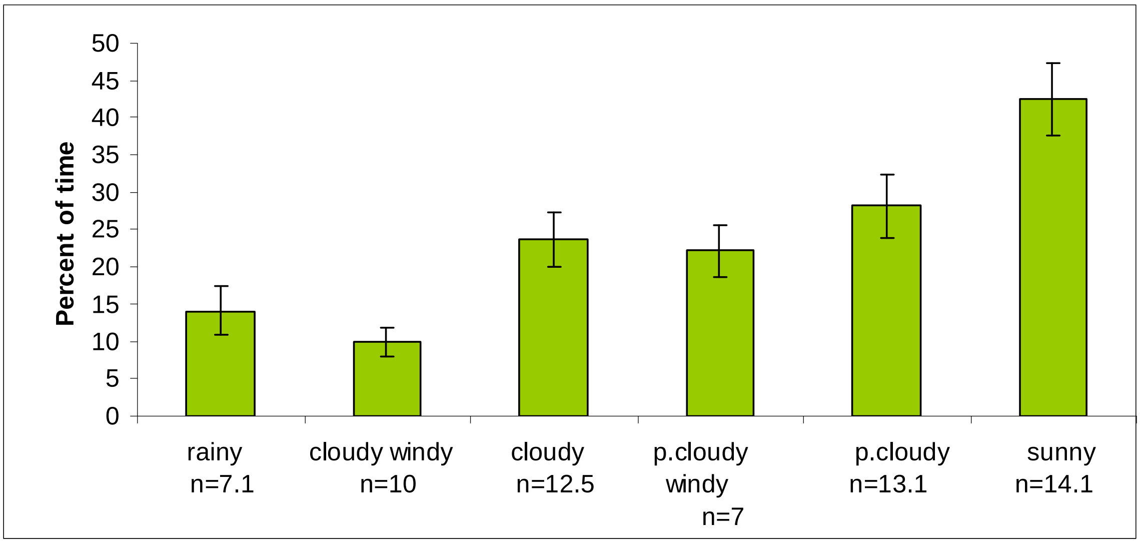
Weather

The one-way ANOVA showed a significant main effect of weather type ($F_{5,225}$=29.18, P<0.001). Tukey post-hoc tests again showed a significant preference for sunny weather, and avoidance of rainy and windy weather (see Table 6.8, and Figure 6.3).

Table 6.8: Results of Tukey post-hoc tests for the effects of weather on the usage of outdoor cages Emboldened significant effects indicate that the column weather condition is significantly greater than the row weather condition

		Cloudy windy	**Cloudy**	**Partly cloudy windy**	**Partly cloudy**	**Sunny**
Rainy	t	-1.38	**3.18**	2.71	**4.69**	**9.47**
	P	0.742	**0.021***	0.078	**<0.001*****	**<0.001*****
Cloudy windy	t		**4.56**	**4.08**	**6.07**	**10.85**
	P		**<0.001*****	**<0.001*****	**<0.001*****	**<0.001*****
Cloudy	t			-0.48	1.51	**6.29**
	P			0.99	0.66	**<0.001*****
Partly cloudy windy	t				-1.99	**6.77**
	P				0.35	**<0.001*****
Partly cloudy	t					**4.78**
	P					**<0.001*****

Figure 6.3: Mean percentage of time (±SE bars) marmosets spent in outdoor cages in different types of weather (P. means partly, numbers under columns indicate mean number of sessions per group)



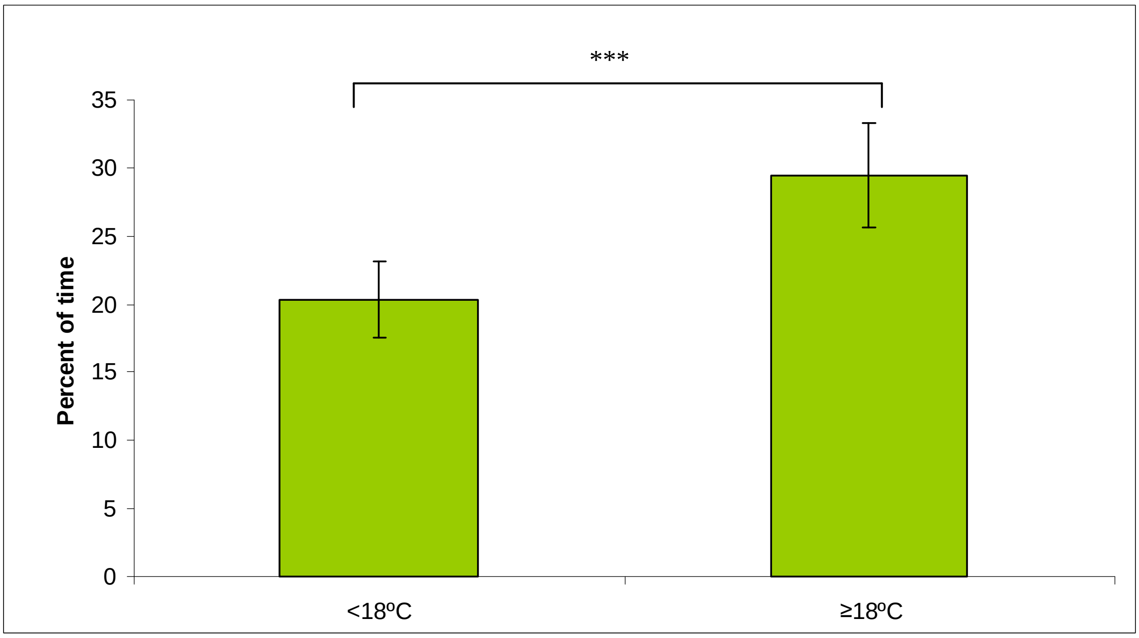
Temperature

In the present study, temperature significantly affected the amount of time marmosets spent in the outdoor cages (t=-3.77, P<0.001). Mean temperatures and ranges are given in Table 6.9. The marmosets preferred to use the outdoor cages in warmer temperatures than colder ones (see Figure 6.4).

Table 6.9: Basic statistics of temperature conditions in Study II

	<18ºC	**≥18ºC**
Mean	15±0.2ºC	20±0.1ºC
Maximum	17ºC	26ºC
Minimum	10ºC	18ºC
Number of sessions	24±0.4	40.63±0.7

Figure 6.4: Mean percentage of time (±SE bars) all monkeys spent in outdoor cages in different temperatures (***P<0.001)



6.3.2.2 Effects of occasional access to outdoor cages on behaviour

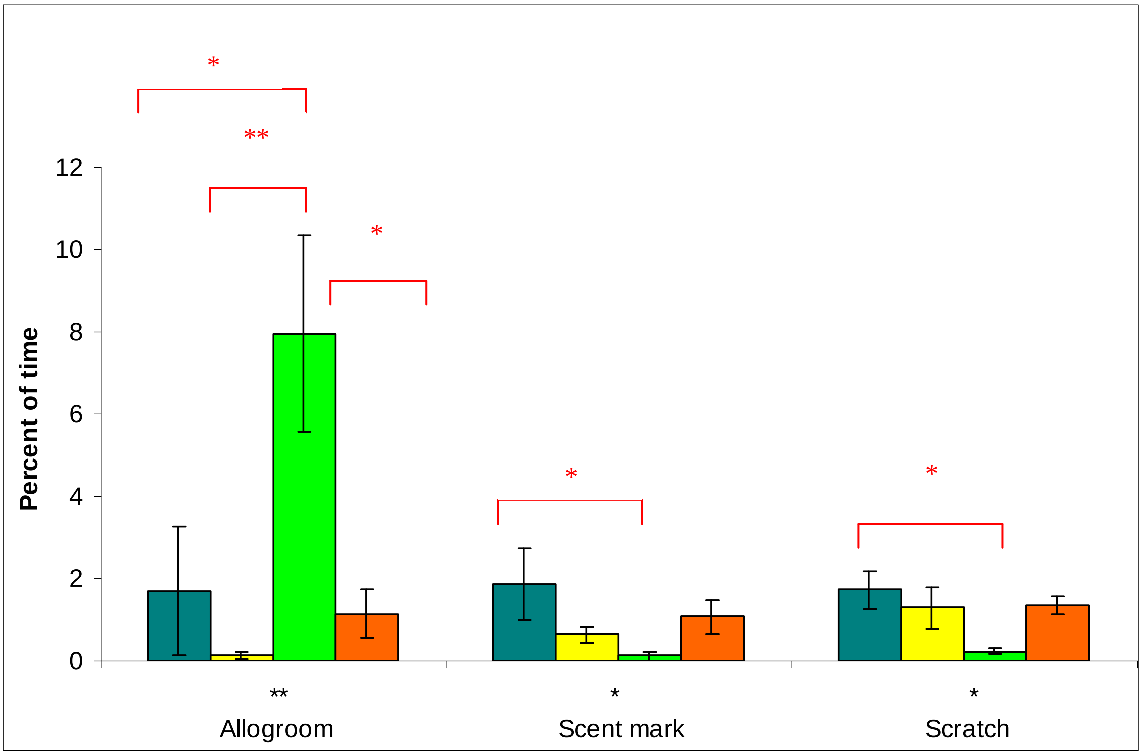
The behaviour of both adults and young was affected considerably by the outdoor cages. For adults, a significant main effect of study phase was found for scratching, scent marking, allogrooming, and exploratory behaviour. Further, a significant main effect was found for calm and agitated locomotion, as well as for inactive alert and inactive rest behaviours (see Table 6.10 and Figure 6.5 a, b, c and d). Tukey post-hoc tests revealed that for most of the behaviours, the significant main effect resulted from significant differences between the Outdoor phase and the three indoor phases. Adults spent significantly less time inactive alert, and more time inactive rest during the Outdoor phase of the study compared to all three indoor phases. Further, they spent significantly more time in calm locomotion, exploring the environment, and allogrooming other group members during the Outdoor phase compared to all three indoor phases. In addition, they scratched themselves more, scent marked more, and showed higher levels of agitated locomotion during the Baseline phase of the study compared to the Outdoor phase. It is important to emphasize that no significant differences were found in the levels of these three behaviours between the Outdoor phase and the Before or After phases (see Table 6.11 and Figure 6.5 a, b, c and d).

Table 6.10: Results of ANOVAs for the effects of study phases on behaviour of adults and young (*P<0.05; **P<0.01; ***P<0.001)

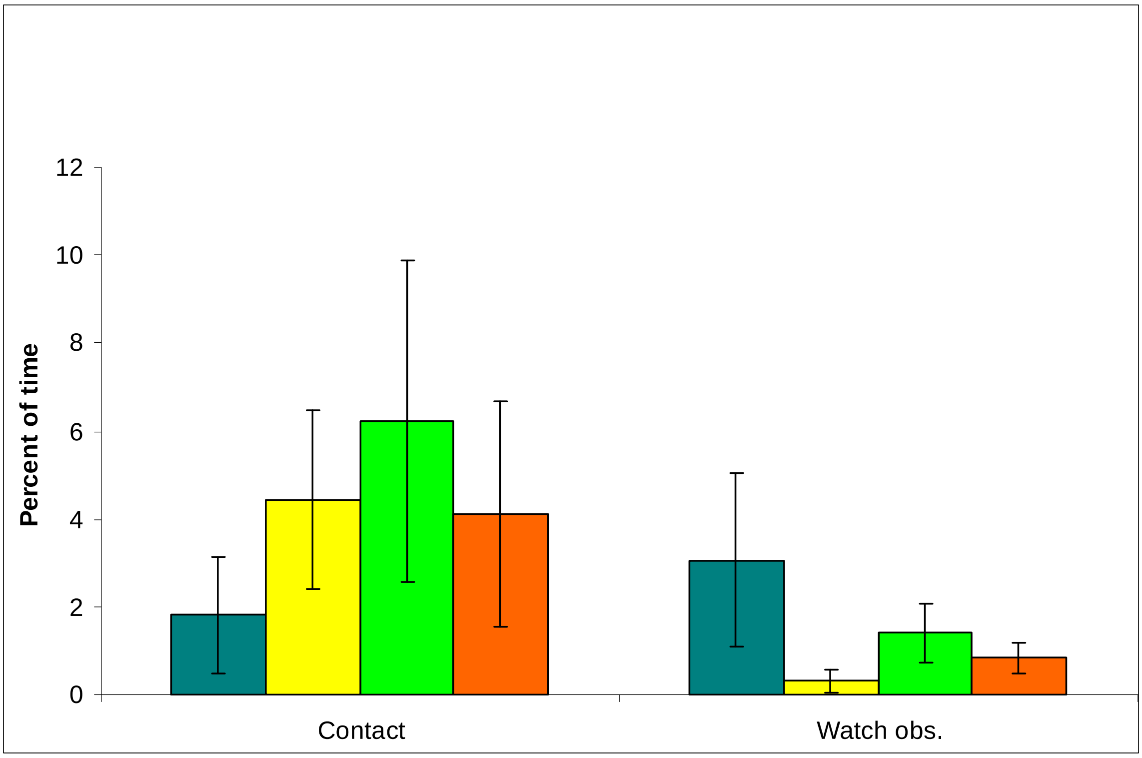
	Adults	**Adults**	**Young**	**Young**
	d.f.=3,27		d.f.=3,60	
	F	**P**	**F**	**P**
Agitated locomotion	4.24	0.014*	4.69	0.005**
Allogroom	6.68	0.002**	0.32	0.813
Calm locomotion	30.36	<0.001***	31.82	<0.001***
Contact	0.58	0.633	0.98	0.407
Explore	10.68	<0.001***	35.29	<0.001***
Autogroom	0.64	0.596	0.43	0.733
Inactive alert	65.34	<0.001***	46.76	<0.001***
Inactive rest	26.30	<0.001***	5.84	0.001**
Scent mark	3.22	0.038*	5.41	0.002**
Scratch	3.14	0.042*	0.43	0.729
Social play	1.00	0.408	0.51	0.678
Solitary play	no data	no data	1.74	0.168
Tree gouge	0.70	0.560	0.49	0.691
Watch observer	1.22	0.323	13.44	<0.001***

Figure 6.5: Mean percentage of time (±SE bars) spent in behaviours for adults in four study phases [two-way ANOVA with repeated measures (black marks) and Tukey post-hoc tests (red marks) *P<0.05; **P<0.01; ***P<0.001]

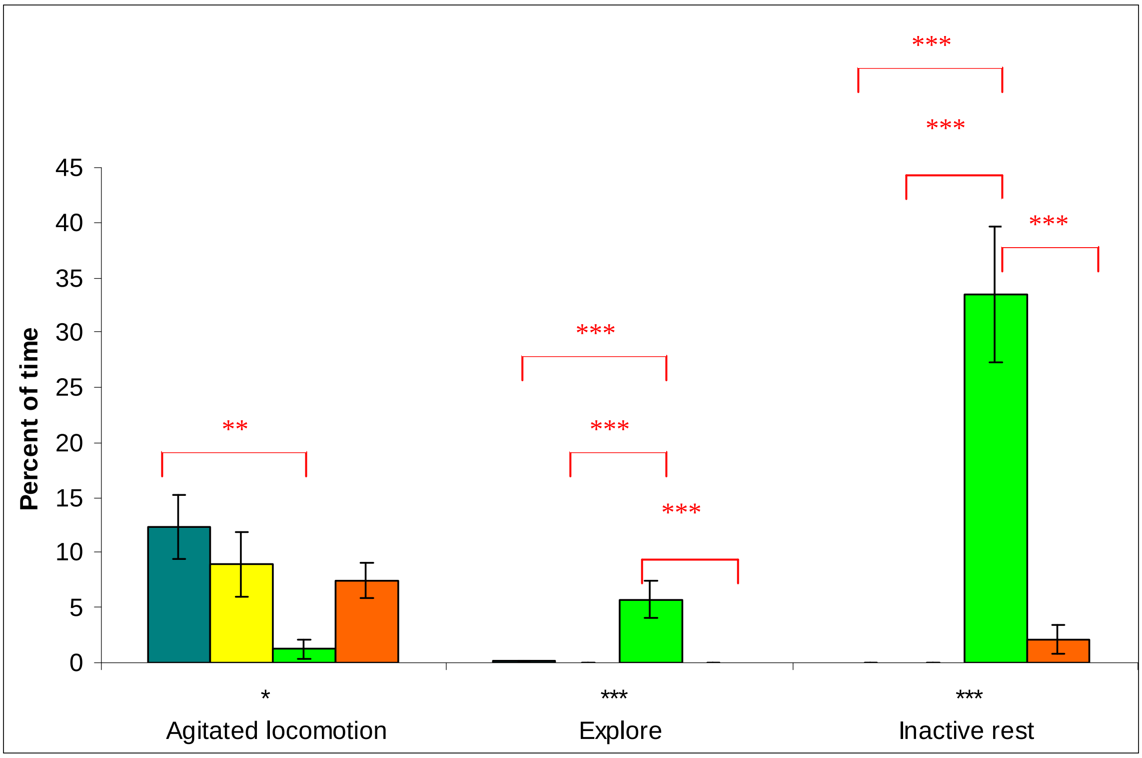
a.



b.



c.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***
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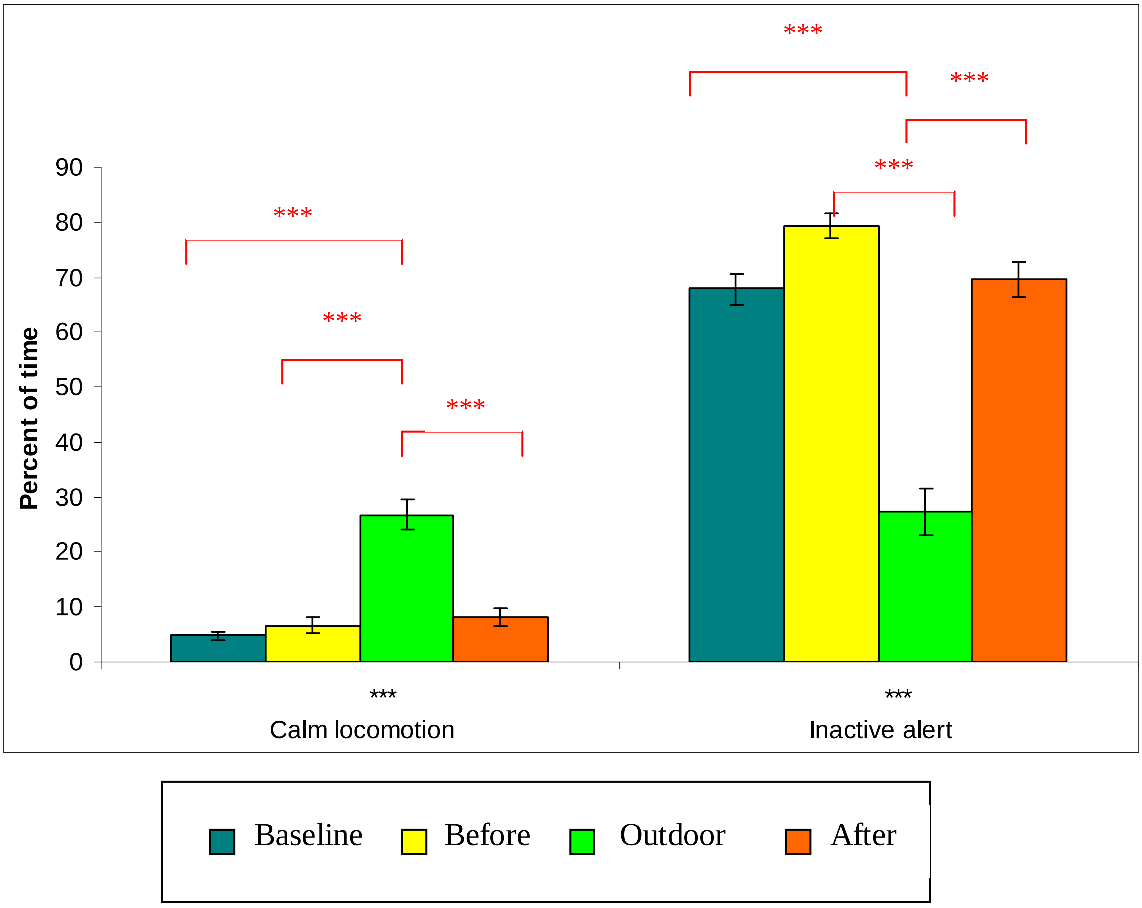
**
45
40
35
30
25
20
15
10
5
0
Percent of time
*
***
***
Agitated locomotion
Explore
Inactive rest

d.


***
***
***
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***
***
90
80
70
60
50
40
30
20
10
0
Percent of time
***
***
Calm locomotion
Inactive alert
Baseline
Before
Outdoor
After

Table 6.11: Results of Tukey post-hoc tests for effects of Outdoor phase on behaviour of adults (*P<0.05; **P<0.01; ***P<0.001)

		Baseline vs. Outdoor	**Before vs. Outdoor**	**After vs. Outdoor**
Agitated locomotion	t	-3.46	-2.40	-1.97
	P	0.007**	0.09	0.220
Allogroom	t	3.02	3.79	3.30
	P	0.023*	0.003**	0.011*
Calm locomotion	t	8.58	7.84	7.2*
	P	<0.001***	<0.001***	<0.001***
Explore	t	4.59	4.66	4.66
	P	<0.001***	<0.001***	<0.001***
Inactive alert	t	-8.97	-11.47	-9.33
	P	<0.001***	<0.001***	<0.001***
Inactive rest	t	4.47	7.47	7.00
	P	<0.001***	<0.001***	<0.001***
Scent mark	t	-2.66	-0.75	-1.38
	P	0.052*	0.876	0.518
Scratch	t	-2.95	-2.09	-2.23
	P	0.027*	0.176	0.135

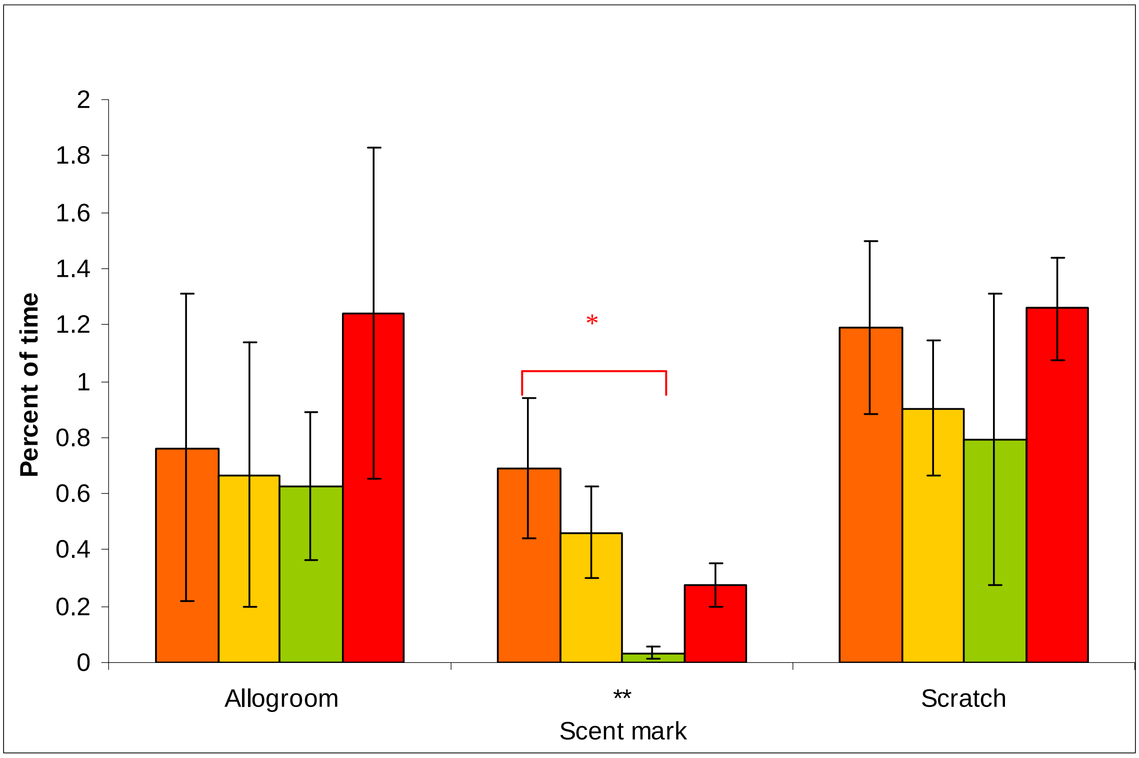
The behavioural variations between the different study phases shown by young animals were similar to those shown by adults. A significant main effect of study phase was found in scent marking, watching the observer, and exploratory behaviour. Further, a significant main effect was found in calm and agitated locomotion, as well as in inactive alert and inactive rest behaviours (see Table 6.10 and Figure 6.6 a, b, c and d). In common with adults, young spent significantly less time inactive alert, and showed significantly more calm locomotion, and exploratory behaviour during the Outdoor phase compared to all three indoor phases. Further, they scent marked significantly more during the Baseline phase compared to the Outdoor phase of the study. In addition, they rested significantly more during the Outdoor phase in comparison to the Before and After phases, and showed significantly more agitated locomotion during the After phase of the study compared to the Outdoor phase. However, they watched the observer significantly more during the Baseline and the Outdoor phases as compared to both Before and After phases of the study (see Table 6.12 and Figure 6.6 a, b, c and d).

Table 6.12: Results of Tukey post-hoc tests for effects of Outdoor phase on behaviour of young (*P<0.05; **P<0.01; ***P<0.001)

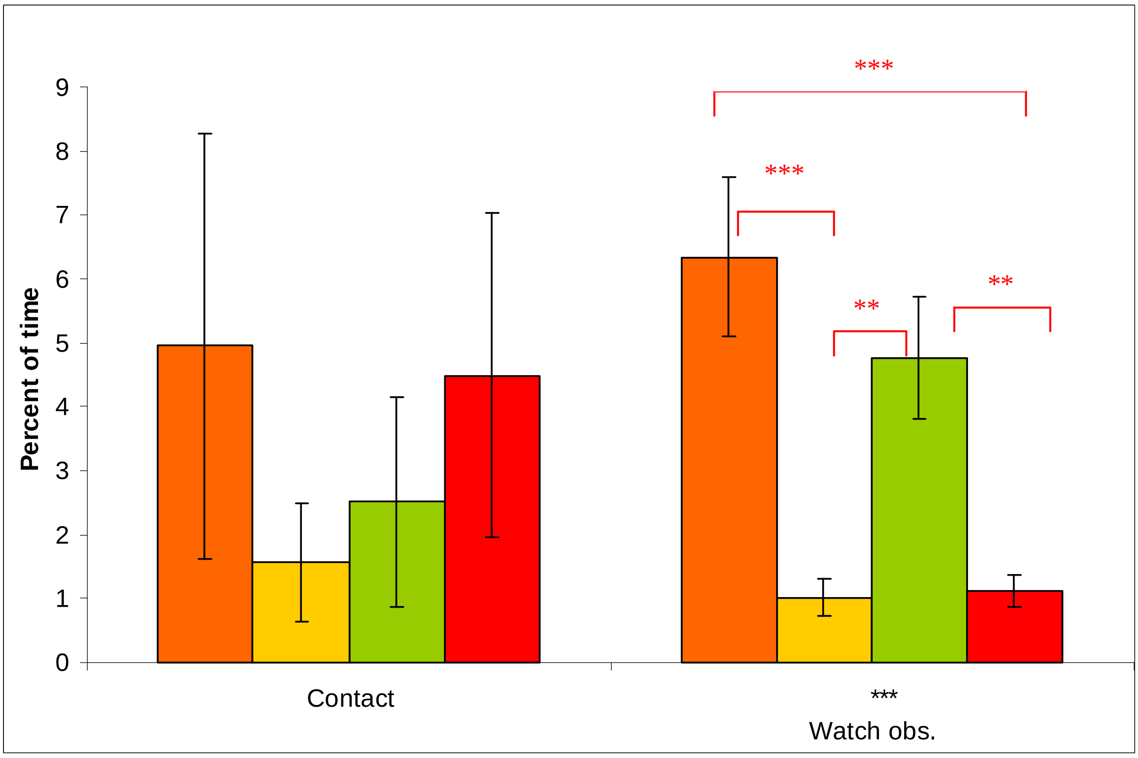
		Baseline vs. Outdoor	**Before vs. Outdoor**	**After vs. Outdoor**
Scent mark	t	-3.03	-1.98	-1.10
	P	0.017*	0.204	0.688
Agitated locomotion	t	-1.65	-1.71	-2.94
	P	0.357	0.325	0.022*
Watch observer	t	-1.04	3.29	3.20
	P	0.503	0.008**	0.010**
Explore	t	8.00	7.97	7.97
	P	<0.001***	<0.001***	<0.001***
Inactive rest	t	1.82	2.80	2.60
	P	0.272	0.032*	0.04*
Calm locomotion	t	7.19	6.45	6.73
	P	<0.001***	<0.001***	<0.001***
Inactive alert	t	-7.44	-9.30	-7.48
	P	<0.001***	<0.001***	<0.001***

Figure 6.6: Mean percentage of time (±SE bars) spent in behaviours for young in four study phases [two-way ANOVA with repeated measures (black marks) and Tukey post-hoc tests (red marks) *P<0.05; **P<0.01; ***P<0.001]

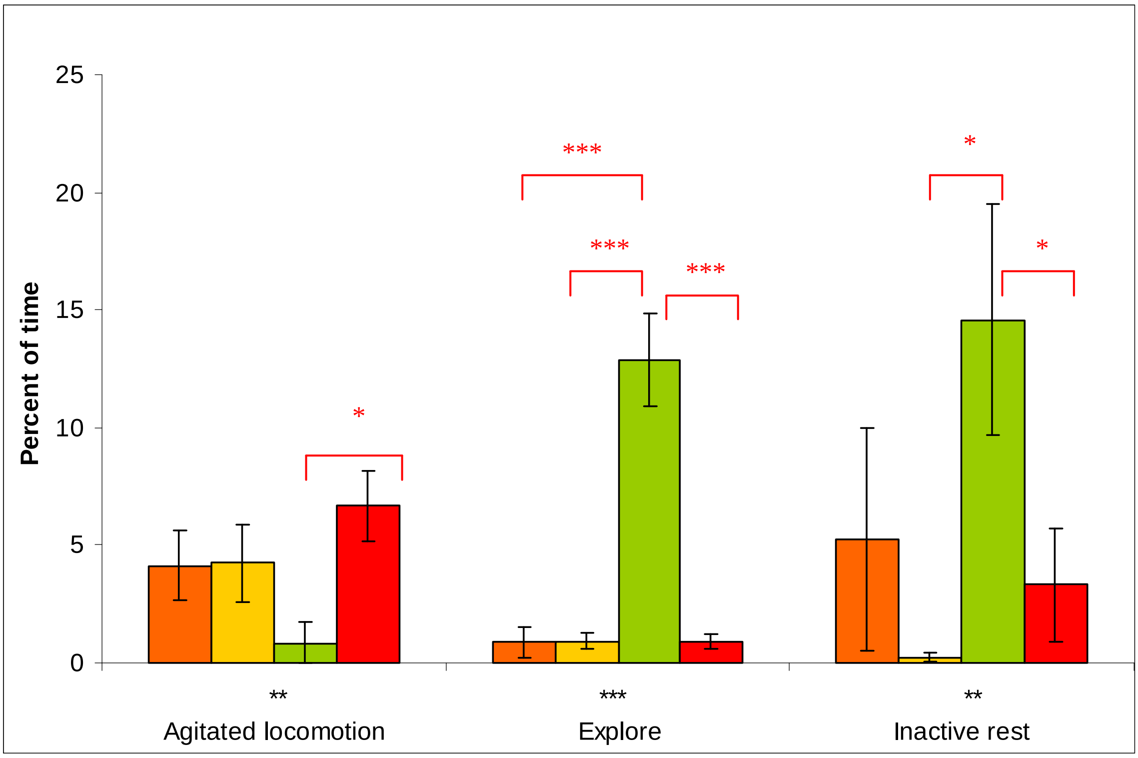
a.



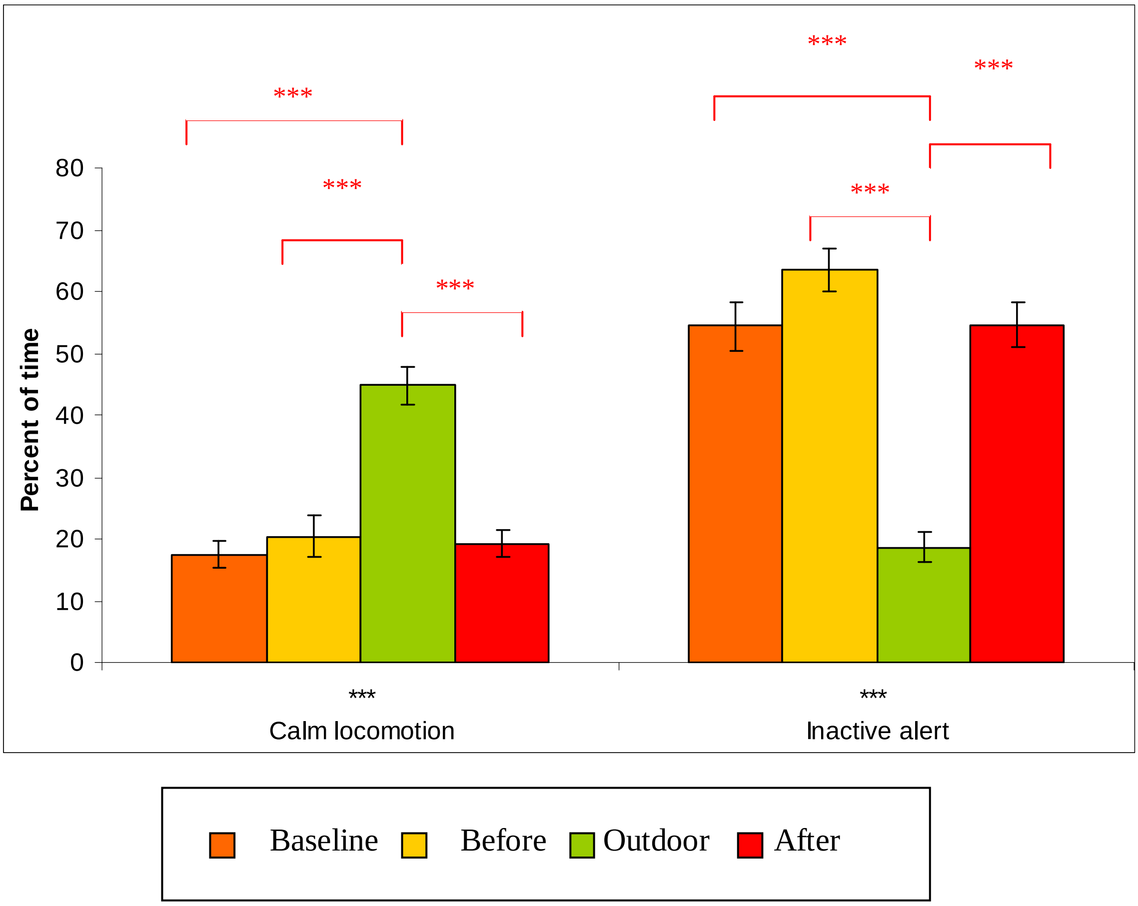
b.



c.


Percent of time
25
20
15
10
5
0
*
***
***
***
*
*
**
Agitated locomotion
***
Explore
**
Inactive rest

d.


Percent of time
80
70
60
50
40
30
20
10
0
***
***
***
***
***
***
***
Calm locomotion
***
Inactive alert
Baseline
Before
Outdoor
After

6.3.2.3 Effects of loss of complexity and choice

No significant behavioural differences between the Baseline phase and the After or Before phases were found for adults. Further, no significant differences between the Outdoor phase and the last two indoor phases, in the absence of significant differences between the Baseline and the Outdoor phases were found. Young showed significantly higher levels of agitated locomotion during the After phase compared to the Outdoor phase. In addition, they showed significantly less inactive rest behaviour during the Before and After phases compared to the Outdoor phase (see Table 6.12 and Figure 6.6 c). Further, the young marmosets watched the observer significantly more during the Baseline phase compared to the Before and After phases ($t=-4.69$, $P<0.001$; $t=-4.60$, $P<0.001$ respectively, see Figure 6.6 b), and during the Outdoor phase as compared to the Before and After phase of the study (see Table 6.12 and Figure 6.6 b). As few significant differences were found between the Baseline phase of the study and the other two indoor phases, no considerable impact of loss of choice was concluded.

6.4 DISCUSSION

In common with the findings of Chapters 4 and 5, the results of the present study show a positive (and greater, compared to previous chapters) impact of complexity and choice. Two differences between the present and the previous studies could be the cause of this larger influence of complexity and choice. First, in the present study the marmosets not only experienced the opportunity to make choices because the enriched environment was more complex, but they could also choose how to distribute their time between their home cages and the enhanced enclosure. Second, the enriched enclosure was not only more complex, but it was also located outdoors and thus afforded more stimulation. The first difference between the present and the previous studies emphasizes the significance of choice. The second difference demonstrates the importance of the location of the enriched enclosure and contradicts the argument of Wolfensohn and Honess (2005) that the quality of the accommodation matters more than its location.

Further, informal data from the present study contradict some other objections to the exposure of captive primates to outdoor enclosures. Several authors have warned of a potential risk of disease transmission from outside vectors (Novak & Suomi 1988; Honess & Marin 2006; Wolfensohn & Honess 2005). However, although one young female died several weeks after the end of Study II, the results of post mortem showed no connection between her death and the exposure to the outdoor environment. No injuries or diseases occurred as a direct result of the animals being outside. Another opposition to the provision of outdoor enclosures is the necessity of restricting food availability in them (Wolfensohn & Honess 2005). Here again, the present studies show that no restriction is necessary if the animals have free access to indoor cages, where food and water can be available at all times. Indeed one might argue that this situation more closely resembles the natural environment.

In contrast to the findings of Chapter 5, no effects of loss of complexity and choice were found in the present studies, either when access to the enriched cages was blocked after a long period of free access, or when exposure to the enriched cages was brief and rotational. This finding shows that occasional exposure to enriched enclosures can benefit the welfare of captive marmosets, and emphasizes the significance of the method that is used to transfer captive primates between different enclosures. In addition, the results show that the marmosets preferred to use the outdoor cages in warm and sunny weather, and avoided the wind and the rain. These preferences are similar to those of wild marmosets, which always try to shelter from heavy rain, and tend to show reduced activity levels on wet days (Stevenson & Rylands, 1988). Further, the location of the indoor home cage within the colony room also affected the usage of outdoor cages, as marmosets housed far from the room's door used the outdoor cages very infrequently.

6.4.1 Measures of the outdoor cages usage

Most of the marmosets in the present study were not familiar with the tubing system, and had been housed in indoor laboratory conditions for 11 generations. Nevertheless, the majority of the monkeys entered the tubing system, and used the outdoor cages almost immediately after the opportunity was given. The marmosets spent almost 25% of available time in the outdoor cages. When groups housed in cages number 4 (the furthest distance from the colony room's door) were taken out of the sample marmosets used the outdoor cages for almost 40% of the available time. Different factors affected the usage of outdoor cages.

Weather

The study took place during the summer, however, in Scotland, even during this season all types of weather, from warm and sunny, to cold, windy and wet, can be experienced. The marmosets were given access to the outdoor cages in all weather conditions. The marmosets showed a highly significant preference for sunny weather and tried to avoid windy and/or rainy weather. In partly cloudy weather, marmosets in both studies also spent relatively long periods outdoors, although their preference for these weather conditions was lower than for sunny weather. These findings are in line with the findings of Howell and colleagues (2002b) who reported that chimpanzees spent the majority of their time in a natural outdoor enclosure, except on cold or rainy days. Similarly, Bernstein (1980) studied stump-tail macaques in an outdoor enclosure (with an attached small indoor quarter). The author found that the monkeys' activity was suppressed on rainy days, and more animals were indoors during rainy weather than during any other time period. In contrast, Crowley and colleagues (1989) showed that Japanese macaques spent nearly all day outside even in snowy, windy, and cold weather. These differences are likely to result from differences in the natural habitat of the species.

Temperature

Marmosets showed a highly significant preference for higher temperatures. O'Neill-Wagner and Price (1995) studied rhesus monkeys in an outdoor enclosure, in which indoor heated accommodation was supplied. The monkeys showed the highest rates of indoor enclosure use when the temperature fell below 3.9ºC, or rose above 32ºC, and the lowest rates of indoor enclosure use when the outside temperatures were between 10ºC and 26.6ºC. Therefore, the rhesus monkeys still preferred the outdoor enclosure over the indoor accommodation when the temperature fell well below 18ºC. Here again, the difference between the present study and that of O'Neill-Wagner and Price may be a consequence of differences between the species. Further, the variations may be related to the different housing designs. In the present study, the indoor cages were the home cages of the marmosets and the outdoor cages were an additional enclosure that they could access (for limited periods of time in Study II). In contrast, in O'Neill-Wagner and Price's study, the outdoor and indoor enclosures formed a single unit, and the rhesus monkeys had lived there for several years before the study began.

Cage location inside the colony room

It was found that family groups which were housed closer to the colony room's door spent significantly more time in the outdoor cages. There are two possible explanations for this finding. First, the distance of the outdoor cage from the home cage might affect the reaction of the marmosets to the novel enclosure; it is possible that when the home cage is located farther from the colony room's door, the distance that the marmosets have to cover before reaching the outdoor cage is too long for them. Informal observations show that marmosets from all study groups used the tubes (youngsters used them for exercise and play). Therefore, the long tube could satisfy the marmosets as additional space, so they are not eager to search for even more. This explanation is in line with the findings of McGrew and McLuckie (1986) that showed that family groups of cotton-top tamarins were less exploratory if they had to travel a long distance through tubes and along an unfamiliar route in order to reach new enclosures.

Another explanation could be a basic difference in the behaviour of the marmosets in respect to the location of their home cage inside the colony room. Preliminary results show that the location of the home cage, in respect to the room's door (and hence to the main corridor) affected the behaviour of the marmosets, and mainly the behaviour of young. Adults watched the observer significantly more when housed close to the door. Young animals spent more time playing, foraging (a behaviour that occurs on the cage's floor), and less time in agitated locomotion when housed far from the door. Further, they showed more inactive alert behaviour and less calm locomotion when housed close to the room's door, however, these differences were only close to significance. This preliminary study on the effects of cage location on behaviour was not a planned study; and therefore the sample was small. However, these preliminary findings showed significant effects of cage location on the behaviour of captive marmosets, and further study is needed. The finding that marmosets (mainly young) that are housed farther from the colony room's door appear to be more relaxed might explain their minimal usage of the outdoor cages, as their well-being in their home cages is better than those of marmosets that are housed closer to the door, and so their motivation to use additional enclosures is less.

6.4.2 Effects of complexity, choice and exposure to outdoor cages on behaviour

The opportunity to choose between two different enclosures, together with exposure to complex outdoor cages, had considerable effects on the welfare of the marmosets. This was shown by the large number of significant behavioural differences between the outdoor phases and all indoor phases of both studies.

Locomotion and inactivity

Elevations in levels of calm locomotion and inactive rest, together with reductions in levels of agitated locomotion and inactive alert in Outdoor phase compared to indoor phases were found for both adult and young animals. All these changes in locomotion and inactivity patterns were considered to be desirable (see Chapter 3) and indicated, together with other behavioural changes, positive influences of complexity, choice and exposure to an outdoor environment. In common with the results of the present study, Chamove and Rohrhuber (1989) found differences in the activity patterns of common marmosets in indoor and outdoor enclosures, as the marmosets showed less vigorous activity patterns in the outdoor enclosure. In contrast, Pines and co-workers (2002, 2003) found no effects of cage location on general activity levels, when common marmosets were studied in similar indoor and outdoor cages. However, they did not discriminate between different types of locomotion and this may explain this result. Alternatively, it is possible that the combination of a more complex enclosure, increased choice, and the exposure to outdoor conditions was the cause for the great differences that were found in the present study.

Exploratory behaviour

The finding that all individuals (adults and young) explored the outdoor environment significantly more than they explored their indoor home cages was expected. Both complexity and novelty are some of the most important stimuli that elicit exploratory behaviour (Hughes, 1997). These two stimuli were integral characteristics of the outdoor enclosures. The importance of exploratory behaviour was discussed in Chapter 3; however, it is essential to emphasize the value of exploratory behaviour for captive primates who spend most of their time inactive when their environment is simple and/or familiar.

Scent marking

Both adults and young animals scent marked significantly less during the Outdoor phase compared to the indoor phases of the studies. These results, together with changes in the levels of other behaviours may indicate better welfare conditions in the outdoor cages than in the indoor cages (see Chapters 3). Similarly, Schoenfeld (1989) found that common marmosets showed increased rates of scent marking in an indoor and less complex enclosure. It is also possible that marmosets scent marked more indoors due to close proximity to other groups. The possible effects of contact with other groups are discussed in the General Discussion.

Scratching

Adults scratched themselves less in the Outdoor phase as compared to the Baseline phase of these two studies. This decrease in scratching behaviour is also thought to be desirable for captive primates.

Allogrooming

Adults showed significantly higher levels of allogrooming in the outdoor cages compared with levels in their indoor home cages. In common with the present findings, previous research has found that common marmosets show increased levels of allogrooming in larger and/or more complex cages (Kitchen & Martin, 1996; Schoenfeld, 1989; Ventura & Buchanan-Smith, 2003). Although the function of allogrooming in marmosets is not fully understood (see Chapter 3), increased levels in the enriched cage indicate a wider range of natural behaviour, as allogrooming is observed infrequently in marmosets housed in standard laboratory cages.

Watch the observer

In line with the findings of Chapter 4, the marmosets in the present study watched the observer less after the Baseline phase. As mentioned in Chapters 3 and 4, several explanations may be offered for this behavioural tendency and they are presented in the General Discussion.

To sum up, the many desirable behavioural changes shown in the present study clearly indicate a positive impact of the enriched cages on the welfare of the marmosets. However, it is impossible to separate the effects of complexity, choice, and the exposure to outdoor environment. The greater influence of the enriched enclosure in the present studies compared to the impact of the enhanced enclosures in Chapters 4 and 5 on the behaviour of the marmosets suggests that the effects of the ability to choose between two different enclosures and/or the exposure to outdoor conditions have a considerable value. Previous studies have also suggested a great importance of choice.

Rumbaugh and co-workers (1989) argued that when captive chimpanzees were moved to a larger and more complex environment, they benefited more from the ability to change location at will (and to choose their companions) than from the increased cage size. Similarly, Owen and co-workers (2005) allowed giant pandas to choose between indoor and outdoor enclosures, and suggested that the ability to choose had positive effects on the welfare of the animals (but see section 2.4.1). In the present study the impact of choice *per se* was not studied, as only one observer recorded the monkeys' behaviour. In order to isolate the effects of the ability to choose between two different enclosures from the effects of the characteristics of these enclosures, observations would also have to be taken indoors, during the Outdoor phase.

6.4.3 Effects of loss of complexity and choice on behaviour

No negative effects of loss of complexity and choice on the behaviour of adults were found. Young marmosets watched the observer significantly less during the After and Before phases compared to the Baseline phase. However, they rested significantly less during the After and Before phases compared to the Outdoor phase, when no significant differences were found between the Outdoor and the Baseline phases. In addition, they showed significantly more agitated locomotion in the After phase compared to the Outdoor phase. Nevertheless, no significant differences were found between the Outdoor and the Before phases, which may indicate that even if the young animals were agitated as a reaction to the loss of complexity and choice, this influence lasted less than nine days. However, as the differences between the Outdoor phase and the After and Before phases in the different behaviours of young are not consistent, no negative effects of loss of complexity and choice can be concluded.

The results of the present study, which show no negative effects of loss of complexity and choice, contradict those of Chapter 5 in which a strong negative influence of loss of complexity and choice was found. Two reasons may explain this variation. First, in contrast to the previous study, in the present study the marmosets were not transferred between the two enclosures. Instead, they were given free access between the two enclosures. It is possible that the method that was used to transmit the monkeys between the enclosures in the previous study had in itself detrimental effects on their welfare. Second, because the marmosets in the present study were given free access between the two enclosures, and as food was supplied only indoors, they kept using the indoor cage as their home cage (they always slept indoors). Therefore the loss of the choice between the enclosures, and the loss of the enhanced enclosure had no significant effects on their behaviour.

6.4.4 Effects of rotational and occasional access to outdoor cages on behaviour

In contrast to Study I, in which the marmosets were allowed free access to the enhanced cages for eight consecutive weeks, in Study II the marmosets were given free access to the enriched enclosure for only three consecutive days every second week. Thus, they could taste the “good life” but it was taken from them shortly after. This short exposure to better housing conditions might have had negative effects on the welfare of the marmosets in their standard home cages. However, as was discussed above, no significant effects of loss of choice and access to the enhanced enclosure were found in any of the studies. Therefore, no significant impact of the occasional exposure to these enhanced conditions on the behaviour of the marmosets in Study II was concluded. These results are in line with Kessel and Brent (1995a, 1995b) who found no adverse effects of occasional access to exercise cages on the behaviour of baboons in their home cages. In conclusion, if animals are to be housed for long periods of time in small and simple cages, occasional exposure to enhanced enclosures is beneficial for their welfare. However, it is important to consider the method that is used to transfer the animals between the enclosures as some methods by themselves may have detrimental effects on welfare.

6.5 CONCLUSIONS

The effects of complexity and choice, together with the effects of outdoor conditions, and the effects of occasional access to these conditions on the behaviour of family housed marmosets were studied. The main results are presented in Table 6.13.

The recommendations made from this study are:

1) Outdoor cages are a very useful method of improving welfare. This is particularly true if the climate is good and temperatures are high.
2) Care should be taken in choice of groups for access as location in colony room may affect usage.
3) If continuous access cannot be given, rotational access is also beneficial and there are no adverse effects of loss of access.

Table 6.13: Summary of the main results of Chapter 6

	Adult	**marmosets**	**Young**	**marmosets**
	Elevated levels	**Reduced levels**	**Elevated levels**	**Reduced levels**
Effects of complexity, choice, and outdoor enclosure	Calm locomotion Explore	Contact Inactive alert	Calm locomotion Explore Watch observer	Agitated locomotion Inactive alert Scent mark Scratch
Effects of loss of complexity and choice in Study I				Agitated locomotion Watch observer
Effects of occasional exposure to complexity, choice, and outdoor enclosure	Allogroom Calm locomotion Explore Inactive rest	Agitated locomotion Inactive alert Scent mark Scratch	Calm locomotion Explore	Inactive alert Scent mark
Effects of loss of complexity and choice in Study II			Agitated-locomotion	Inactive rest Watch observer

In this, and the previous chapters, the effects of complexity and choice have been studied. In the next chapter, the effects of the other “C”, control, are investigated.

Chapter 7

Does Control Over Light Improve the Welfare of Captive Common Marmosets Housed in Small Family Groups?

7.1 INTRODUCTION

The positive impact of complexity and choice on the welfare of pair and family housed marmosets has been described in previous chapters. In the present study, family groups of marmosets were given control over additional illumination in their home cage, and the impact of light intensity, control over light and loss of control was studied. There have been many recommendations relating to the positive effects that control over the environment may have on the welfare of primates in captivity. However, there is little quantitative evidence behind these recommendations (see Chapter 2). The effects of control in general were discussed in Chapter 2 and the significance of light intensity in Chapter 4. These factors are combined below, and studies on the effects of control over illumination are discussed.

7.1.1 Effects of control over illumination

Few studies have looked at the effects of control over light on primates. In an early study, immature rhesus monkeys were able to control light intensity inside a box in which they were placed individually. In two separate conditions, monkeys could increase or decrease light intensity by pressing a lever. In two additional conditions, monkeys stayed in continuous high or low light intensities, and pressing a lever had no consequences. The results of this study indicate that the effective factor was the change itself rather than the direction of it, as the frequency of lever-pressing increased significantly when the action was accompanied by a change in the level of environmental illumination, with no significance of the change's direction (Moon & Lodahl, 1956). Tokura and Aschoff (1979) studied adult squirrel monkeys (*Saimiri sciureus*) under three different conditions: permanent dim illumination (dim LL), identical illumination but with an additional self-controlled source of light, which turned off automatically 30 minutes after being turned on by the animal (bright LL), and a full self-controlled dark-light cycle in which the additional light stayed on as long as the monkey handled a ring, and stayed off while the monkey rested (LD). They found that the mean circadian period and the activity time were longer in bright light than in continuous dim light. Further, there was a positive correlation between illumination intensity and amount of activity in the bright LL condition. The longest mean circadian period and the highest amount of activity were achieved in the LD condition, in which the monkeys usually handled the ring repeatedly for several hours immediately after being given an access to it, following by a couple of hours' rest. These results suggest that monkeys would work to get brighter light intensity.

The effects of control over light have also been studied in other species. Kavanau (1963; 1964) allowed deer mice (*Peromyscus maniculatus*) to control light levels in their cage. These mice repeatedly manipulated the device (by pressing levers) to achieve the opposite outcome to the experimenter's operation, that is to say, they always turned the light off in reaction to the experimenter turning it on and vice versa. When the mice were given the opportunity to turn the light in either direction (on or off) they repeatedly ran from one lever to the other in order to control the situation and to change the outcome. When the mice could set the light level (by pressing the same lever to increase illumination level in increments, and pressing another lever to reduce light level again in increments), only after weeks of outcome opposition (running between levers to change the light in the opposite direction) did they adapt to the regime and adjust the intensity to the preferred low intensity. Kavanau and colleagues repeated this study with different species (six carnivore species: Kavavau et al., 1973; nocturnal mammals: Kavanau & Havenhill, 1976; *Peromyscus eremicus*: Kavanau, 1978). However, in these studies the main focus on was the light level that the animals chose to set and not on the impact of having control.

Joffe and co-workers (1973) allowed rats to control food and water delivery as well as lighting conditions. They found that rats that were housed in cages allowing such control defecated significantly less (the authors did not offer any interpretation for this finding, although there was no significant difference in body weight between the two groups) and their mean activity score was significantly higher than yoked rats. Further, when tested in an open field as adults, rats which experienced some control over the environment as infants showed less “emotionality” compared to those that did not experience direct control over their early environment. In another study, laying hens (*Gallus gallus domesticus*) were given the opportunity to control food and light (in addition to their restricted regime). Although the birds were more motivated to gain access to additional food than they were to increase light intensity, they still worked to increase the light intensity for an average of 30 minutes per day. Animals with control showed lower levels of peering and resting (suggesting lower levels of stress and passivity) compared to birds without control. However, as they showed more interest in increasing their food supply, the effects of control over illumination are not clear (Taylor et al., 2001).

The obvious conclusion from the above studies is that the control itself may be of greater significance than the environmental light intensity. However, more research is needed, since in most of the research the outcomes regarding controllability are not isolated from effects of the controllable factors, therefore, the impact of control *per se* is not clear.

7.1.2 Aims of the present study

The aim of the present study was to test the effects of controllability of additional light on the welfare of captive common marmosets. The decision to use white light as the controllable stimulus was based on previous research that has shown a significant positive impact of light intensity on animals' behaviour and well-being.

The following questions were asked:

1) How does light intensity affect the welfare of captive common marmosets?
2) How does the opportunity to control light intensity in the cage affect the welfare of the marmosets?
3) How is control distributed among the members of the group?
4) How do the environmental changes affect members in the group that have no control relative to other members?
5) How does loss of control affect the welfare of the monkeys?

It was expected that the increase in illumination intensity would improve the marmosets' welfare in itself. Additionally, it was hypothesized that control over additional cage light would improve the welfare of captive marmosets more than mere changes in the cage’s illumination. It was further expected that the welfare of ALL members of the controlling group would improve, even individuals in the Master group that did not actually controlled the device, since by watching the controlling member they would be able to foresee the coming changes, and therefore have better predictability than members of groups without any control.

7.2 METHODS

7.2.1 Study animals and housing

The study animals were 43 common marmosets divided into 12 small family groups, housed in double cages. Each group contained three to five individuals, which included one or two adults (mother, father or both) and one to three youngsters. Six groups served as Master groups while the other six were Unaffected groups. There were no significant differences between Master and Unaffected groups in terms of the total number of animals per group (t=0.349; P=0.734), number of adults (t=0.542; P=0.599) or number of youngsters (t=0.000; P=1.000). Group details and individuals’ ages and sexes are presented in Table 7.1. There were no significant differences in the mean age of adults or youngsters between Master and Unaffected groups. Mean age of adults in Master groups was 1630 days (±S.E. 261.9 days; n=10) on the first day of the study, and 1606.11 days (±S.E. 204.8 days; n=9) for adults in Unaffected groups (t=0.071; P=0.944). Mean age of youngsters was 160.58 days (±S.E. 20.0 days; n=12) for Master groups and 203.75 days (±S.E. 22.0 days; n=12) for Unaffected groups (t=-1.450; P=0.161).

7.2.2 Experimental design

The twelve study groups were housed in two separate colony rooms. Each room housed six groups- three Master groups and three Unaffected groups. The two colony rooms were identical and group and individual details for each are presented in Table 7.1.

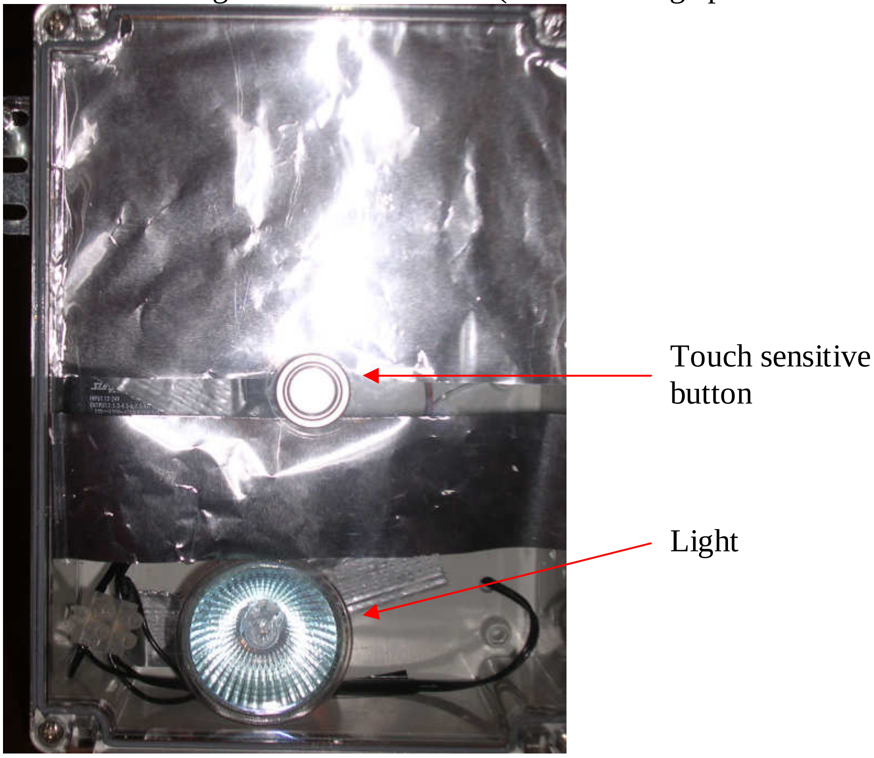
The study included two conditions: an Unaffected group was defined as a group in which no manipulation was applied in any study phase. A Master group was defined as a group in which a manipulation was applied during the Test phase of the study. During the morning of the fifth day of the study a light box was hung on the lower part of each Master group's cage. The waterproof light box contained a halogen dichroic, realite 12V 20W bulb, a touch sensitive button, an electronic counter to measure the frequency of button touches (switching the light on/off) and a quartz alarm clock which measured the duration of time used (see Plates 3.5 and 7.1).

Table 7.1: Group and individual details (sex, date of birth (D.O.B) and age on first day of the study)

Group type	Group identifier	Individual	D.O.B.	Age (days)
Master	1-2Ra	12W (adult ♀)	11/01/2000	1466
		5BB (adult ♂)	15/01/2000	1462
		♂	24/07/2003	176
		♀♀	26/12/2003	21
	1-3Ra	743R (adult ♀)	16/08/1995	3075
		962BK (adult ♂)	27/06/2001	933
		♀	30/08/2003	139
	1-3Rb	15W (adult ♀)	02/02/2000	1444
		861BK (adult ♂)	08/04/1999	1744
		♀♂	17/07/2003	183
	4-1Ra	70BL (adult ♀)	26/06/1995	3143
		♀♂	23/06/2003	224
	4-2Ra	55Y (adult ♀)	02/01/2001	1126
		943BK (adult ♂)	05/02/2001	1092
		♀♂	12/08/2003	174
	4-2Rb	981BK (adult ♂)	09/11/2001	815
		♀♂	13/07/2003	204
Unaffected	1-2Lb	850R (adult ♀)	10/10/1997	2289
		♀♂	08/09/2003	130
	1-1Ra	782R (adult ♀)	22/08/1996	2703
		950BK (adult ♂)	17/04/2001	1004
		♀♂	04/08/2003	165
	1-1Rb	85Y (adult ♀)	10/07/2001	920
		♂♂	25/06/2003	205
	4-1Rb	21W (adult ♀)	28/11/2000	1161
		866BK (adult ♂)	23/04/1999	1746
		♂	01/06/2003	246
	4-4Rb	842BK (adult ♂)	10/09/1998	1971
		♀♀	16/04/2003	292
	4-4Ra	37Y (adult ♀)	02/09/2000	1248
		901BK (adult ♂)	21/03/2000	1413
		♂	27/04/2003	281
		♂ (847R's)	01/05/2003	277
		♀	07/12/2003	57

The light box was connected to the main power supply through a timer, thus it was powered for only ten hours a day, 0700 to 1700 (on with normal room illumination). While the light box was powered, a red light circle around the touch sensitive button was on, to signal to the animals that they could switch the light on or off. When the red light circle was off, the halogen light was also off, and it was not possible to turn it on. The light box supplied additional light to the main room lighting and illuminated mainly the lower part of the cage.

Plate 7.1: The light box from its front (the inside-cage point of view)



The light box was removed from the cage on the morning of the 23rd day of the study (see Table 7.2). The monkeys were not trained to use the light box, since a preliminary test showed that they touched the touch sensitive button immediately after being given access to it. Illumination measures were taken using a Jessop light-meter and showed that the light intensity inside the cage with the additional light was almost 2.5 times higher than normal (see Table 7.3 and Plate 7.2). The light also produced heat and increased the temperature within its very near environment (up to 15cm from the light) from around 23°C to around 34°C. However, this thermal change did not affect the whole cage as the source of the heat was very small.

Table 7.2: Study protocol

	Days	**1-4**	**Days**	**5-22**	**Days**	**23-27**
	Baseline	**phase**	**Test**	**phase**	**Post-test**	**phase**
	light	**observations**	**light**	**observations**	**light**	**observations**
Master groups	no	3 focal obs. per individual	yes	10 focal obs. per individual	no	3 focal obs. per individual
Unaffected groups	no	3 focal obs. per individual	no	10 focal obs. per individual	no	3 focal obs. per individual

Plate 7.2: Two double cages, one with additional illumination

Table 7.3: Light measures (in EV- exposure value) in two different locations in the lower part of the Master groups' cages

Additional light	Centre of the cage	Back of the cage
on	10	9
off	4.5	4

7.2.3 Data collection

Each animal was observed for three separate four-minute sessions during the Baseline phase of the study (total observation time of 4 hours and 24 minutes for Master groups and 4 hours and 12 minutes for Unaffected groups), for ten sessions during the Test phase (total of 14 hours and 36 minutes for Master groups and 14 hours for Unaffected groups) and for three sessions during the Post-test phase (total observation time of 4 hours and 24 minutes for Master groups and 4 hours and 12 minutes for Unaffected groups). Each observation session took place on a separate day. The first observation session for the Test phase was carried out on day 5 of the study, two hours after the installation of the light boxes. The first observation session for the Post-test phase took place on day 23, two hours after the light boxes were removed from the cages. Behaviours recorded were as discussed in Chapter 3.

The light's condition (whether on or off) was recorded at all times, and when possible the identification of the individual who turned it on or off was recorded, even when it was not the focal animal for that observation. Further, any other behaviour related to the device (manipulate the device, and sit close to the light box) was recorded for the focal animal. The frequency of button touches and percentage time that the light was used were also recorded. These data were collected at approximately the same time once a day between days 5 and 23 of the study.

7.2.4 Statistical analysis

Different statistical analyses were carried out to examine the effects of light intensity and control on the behaviour of adult and young marmosets (see Table 7.4).

Table 7.4: Statistical analyses used in the present study

Research question	Statistical test	Factors	Levels	Analysis
Habituation to device (percent of time on)	One-way ANOVA	Period	4 first days/ middle/ 4 last days	Within subjects
Habituation to device (frequency of button touches)	One-way ANOVA	Period	4 first days/ middle/ 4 last days	Within subjects
Effects of light condition on adults	Paired samples t-test	Light condition	On/off	Within subjects
Effects of light condition on youngsters	Paired samples t-test	Light condition	On/off	Within subjects
Effects of control on adults	Two-way ANOVA with mixed design	Study phase	Base/Test/Post	Within subjects
		Study condition	Master/Unaffected	Between subjects
Effects of control on youngsters	Two-way ANOVA with mixed design	Study phase	Base/Test/Post	Within subjects
		Study condition	Master/Unaffected	Between subjects

In order to measure the percentage time and frequency of light usage, means were calculated for each Master group. In addition, measurements of device usage were calculated for three periods (first 4, middle 10 and last 4 days) of the Test phase in order to examine habituation. For the analysis of the effects of light intensity on behaviour, only five Master groups were included. For group 4-2Rb, no data were available for the condition ‘light off’, as the light in the cage of this group was on during all observation sessions in the Test phase.

7.3 RESULTS

The results of the present study are discussed in relation to three factors:

1) Usage of light
2) Effects of light on the animals’ welfare
3) Effects of control on the animals’ welfare

7.3.1 Measure of light usage

Only two out of six groups in this study kept the cage lit for relatively large percentages of time (see Table 7.5). As can be seen in Figure 7.1, these two groups (1-3Rb and 4-2Rb) showed similar rates of light use throughout the whole Test phase of the study. Group 1-3Ra showed a medium rate and the last three groups (1-2Ra, 4-2Ra and 4-1Ra) showed low rates of light usage. However, the last four groups showed no consistency in the rates of light usage. The frequency of button touches was low for all Master groups (see Table 7.6). The mean frequency during the first four days of the Test phase was higher than that for the last 14 days, for five out of six Master groups, however, no significant differences between the three periods of the Test phase were found for any measure of light usage.

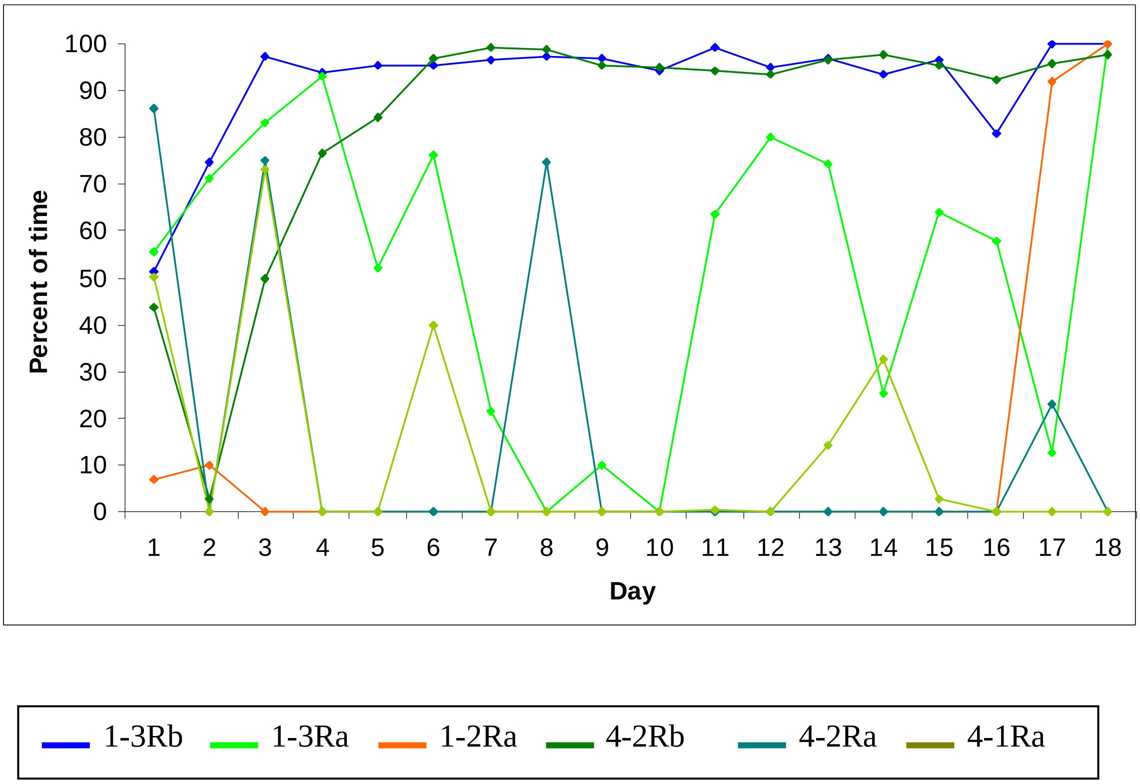
Table 7.5: Mean (±S.E.) percentage time per day of device usage in six Master groups, during the Test phase

	1-3Rb	1-3Ra	1-2Ra	4-2Rb	4-2Ra	4-1Ra
All Test phase	91.98±2.8	52.28±7.7	11.62±7.3	83.63±6.1	14.4±7.1	11.83±5.2
First 4 days	79.3±10.6	77.36±8.9	5.36±3.3	41.39±15.2	41.99±24.3	32.59±19.7
Middle period	95.92±0.6	40.07±10.2	0	94.85±1.3	7.26±7.6	8.36±4.9
Last 4 days	93.85±4.8	60.56±17.5	49.83±28.8	95.01±1.4	6.44±6.4	0.63±0.6

Table 7.6: Mean (±S.E.) frequency per day of device usage in six Master groups, during the Test phase

	1-3Rb	1-3Ra	1-2Ra	4-2Rb	4-2Ra	4-1Ra
All Test phase	2.53±0.8	3.79±1	0.58±0.4	4.26±1.6	0.58±0.2	2.11±1.6
First 4 days	6.25±3.3	7.25±2.6	0.75±0.5	12.75±6.3	0.75±0.3	0.75±0.5
Middle period	1.82±0.3	3.18±1.3	0.64±0.6	2±0.3	0.36±0.2	3.27±2.8
Last 4 days	0.75±0.3	2±1.22	0.25±0.2	2±0.7	1±1	0.25±0.2

Figure 7.1: Percentage time of light usage for Master groups during the Test phase



7.3.2 Distribution of control among group members

In order to obtain data regarding the way control over illumination was distributed among group members, details of the controller were recorded each time the light was switched on or off (no matter whom the focal animal was). In only 17 out of 210 records was information about the controller available. Whenever the information was available, it was a youngster, either male or female. As these are the only existing data relating to control distribution among group members, no further analysis was carried out.

7.3.3 Effects of light intensity on behaviour

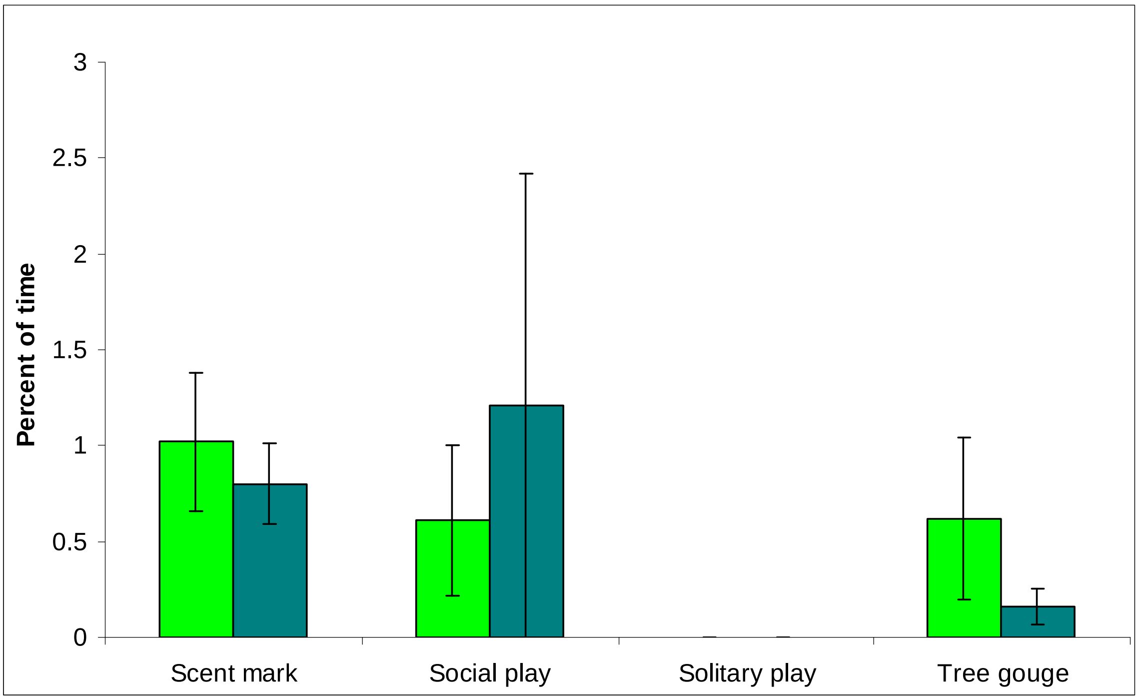
Although only three out of the six Master groups had high durations of light usage, all groups (apart from 4-2Rb, see 7.2.4 for explanation) were taken into account when analysis with reference to light effect on animals' welfare was carried out. Adults showed few significant differences in behaviour in relation to light condition. Only two behaviours were significantly affected by light intensity; adults spent more time sitting close to the device when the light was on, and they watched the observer significantly more when the light was off (see Table 7.7 and Figure 7.2 a, b, c and d). Young animals were more affected by illumination. They showed significantly more calm locomotion and social play behaviour, and less inactive rest and contact behaviours when the light was on (see Table 7.7 and Figure 7.3 a, b, c and d).

Table 7.7: Results of ANOVAs for effects of light on behaviour and cage locations for adults and youngsters (*P<0.05)

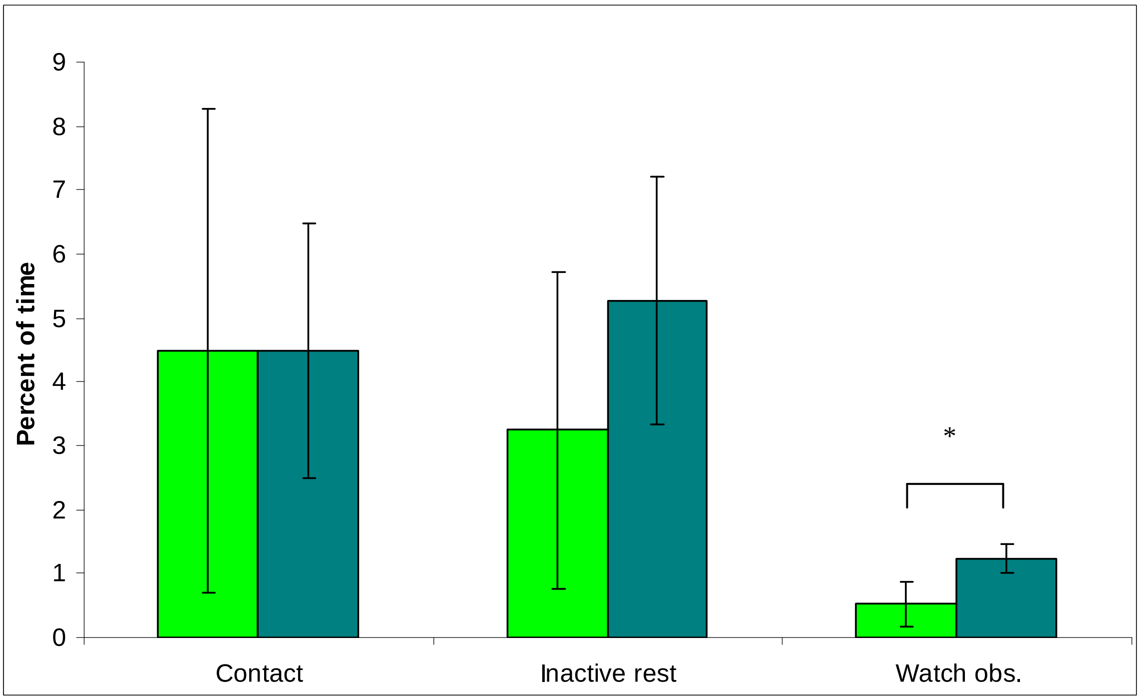
	Adults	**Adults**	**Youngsters**	**Youngsters**
	t	**P**	**t**	**P**
Agitated locomotion	-2.39	0.075	-2.14	0.099
Allogroom	1.53	0.200	1.42	0.227
Autogroom	-0.13	0.905	-0.64	0.560
Calm locomotion	0.102	0.924	3.71	0.021*
Contact	-0.001	0.999	-4.15	0.014*
Explore	-0.25	0.813	0.71	0.515
Inactive alert	-0.05	0.959	-2.359	0.078
Inactive rest	-0.86	0.438	-3.31	0.030*
Scent mark	0.83	0.453	-0.65	0.554
Scratch	-0.50	0.643	-0.68	0.530
Social play	-0.67	0.540	2.86	0.046*
Solitary play	no data	no data	-0.49	0.653
Tree gouge	1.26	0.275	0.23	0.828
Watch observer	-3.24	0.032*	-1.30	0.264
Lower	1.66	0.172	0.71	0.517
Upper	-1.65	0.174	-0.78	0.482
Close to device	4.39	0.012*	1.07	0.344
Manipulate device	0.85	0.443	0.03	0.980

Figure 7.2: Mean percentage time (±SE bars) spent in behaviours and in cage locations for adults in Master groups during two light conditions (*P<0.05)

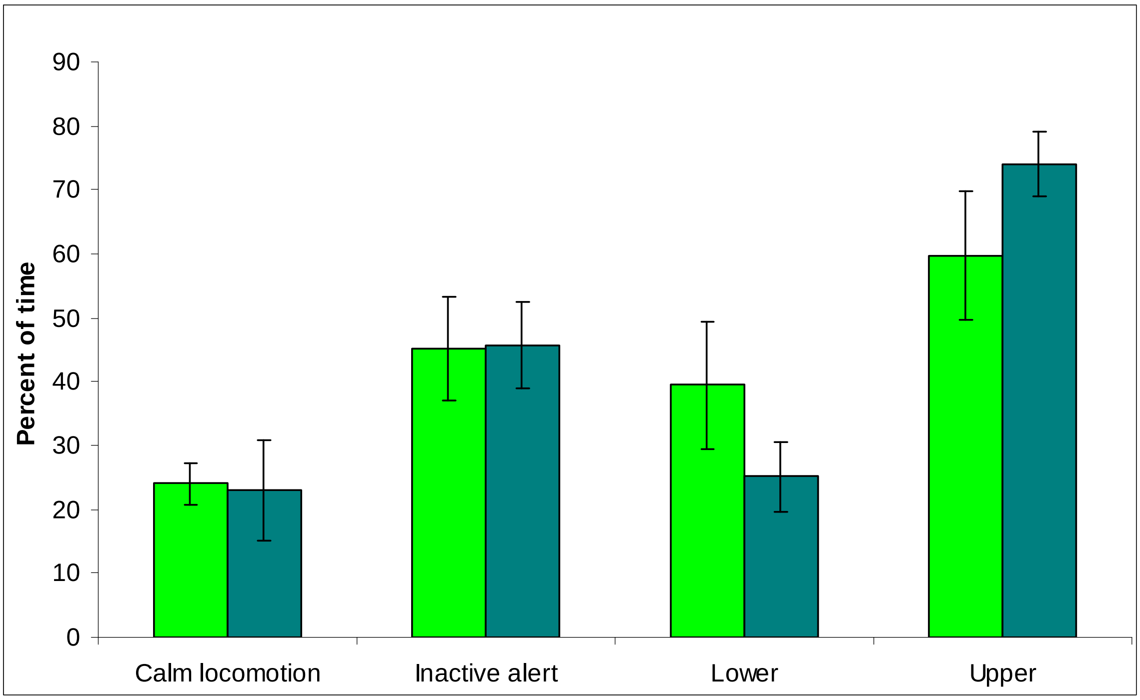
a.



b.



c.


Percent of time
90
80
70
60
50
40
30
20
10
0
Calm locomotion
Inactive alert
Lower
Upper

d.

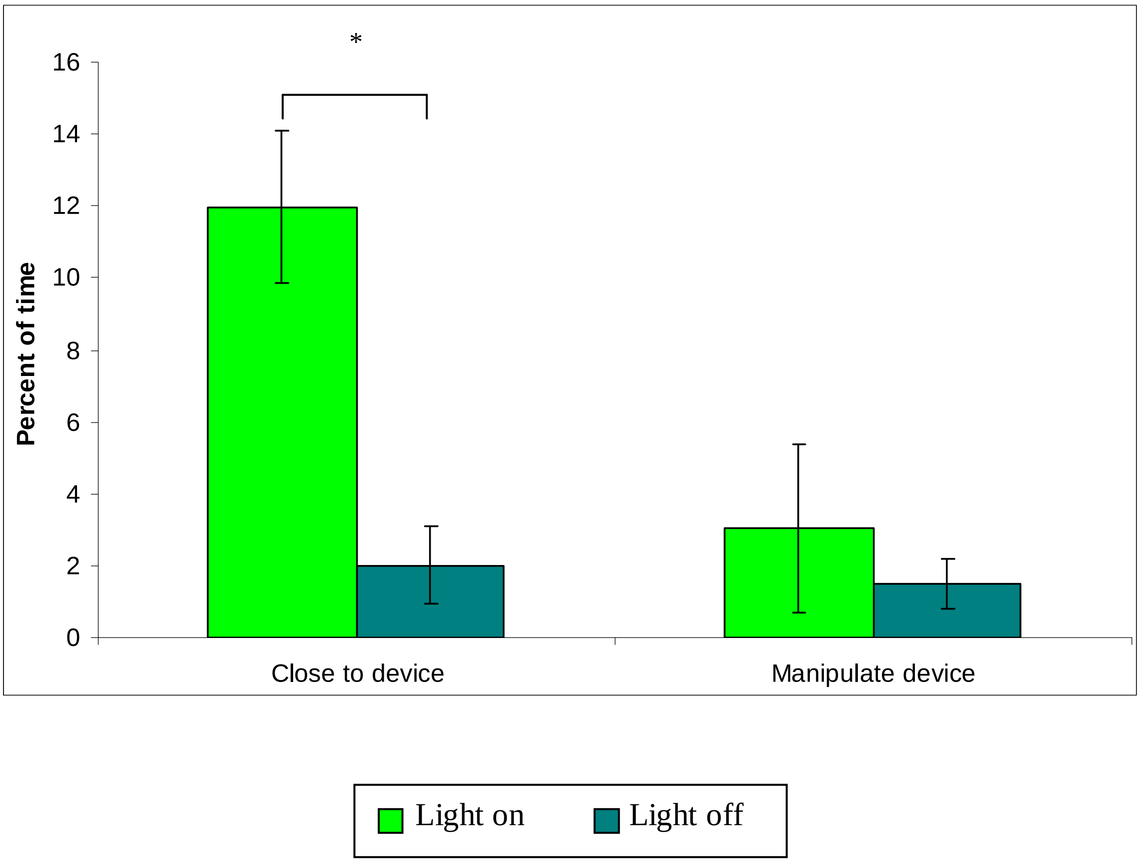
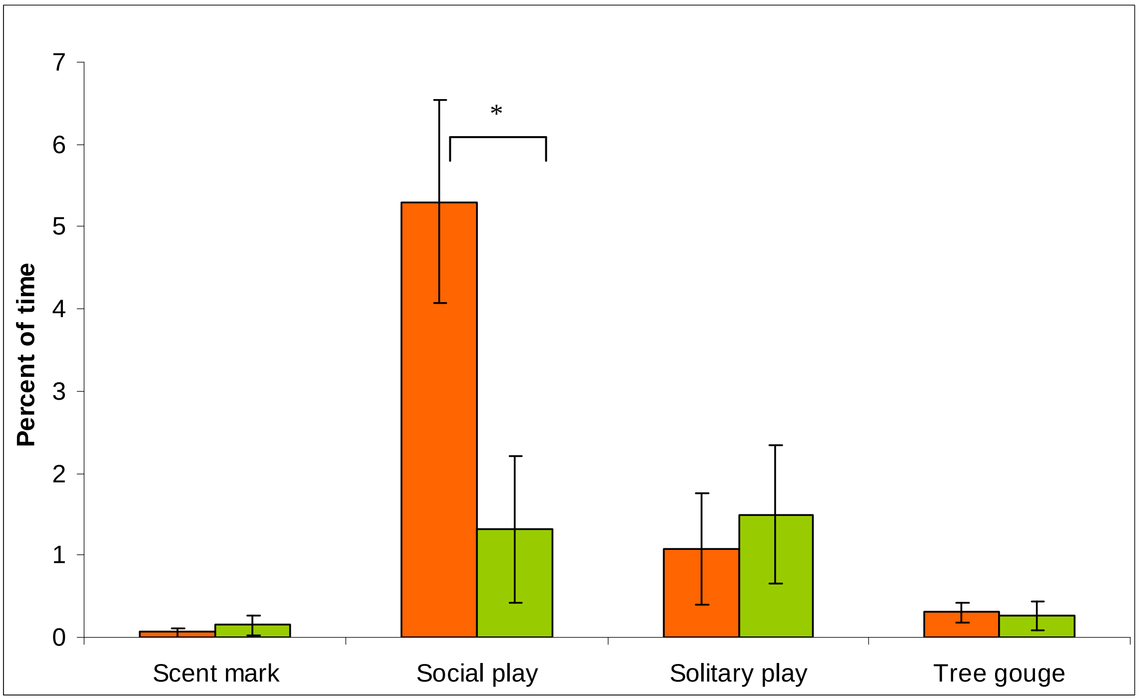
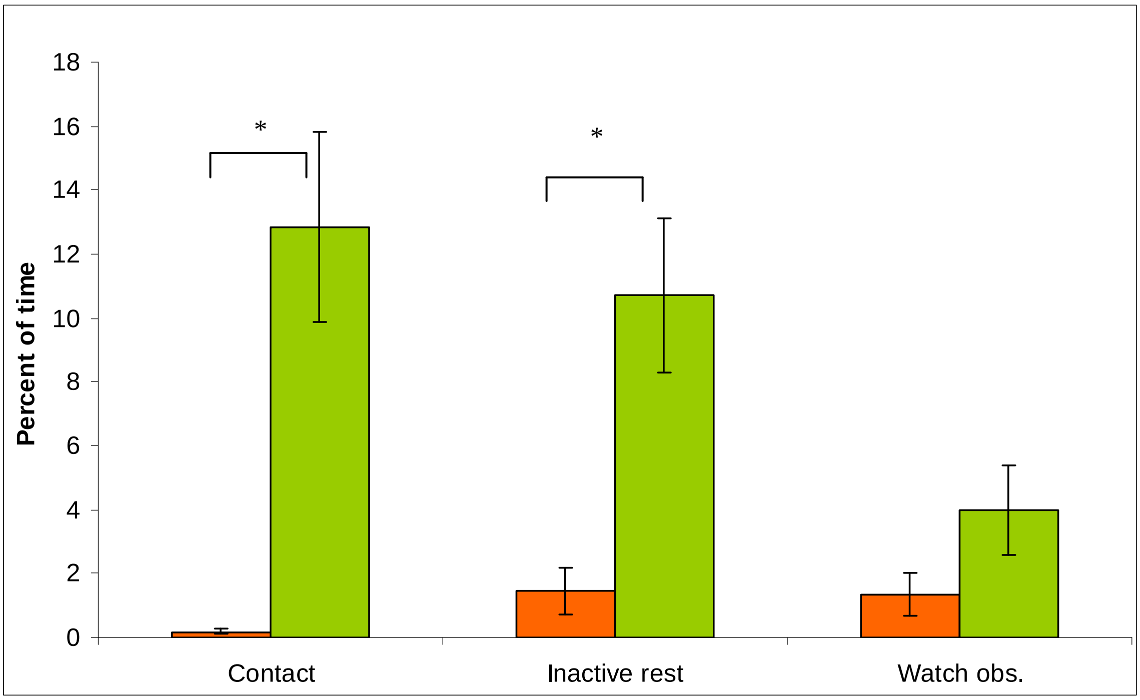

Percent of time
16
14
12
10
8
6
4
2
0
*
Close to device
Manipulate device
🟩 Light on
🟩 Light off

Figure 7.3: Mean percentage time (±SE bars) spent in behaviours and in cage locations for youngsters in Master groups during two light conditions (*P<0.05)

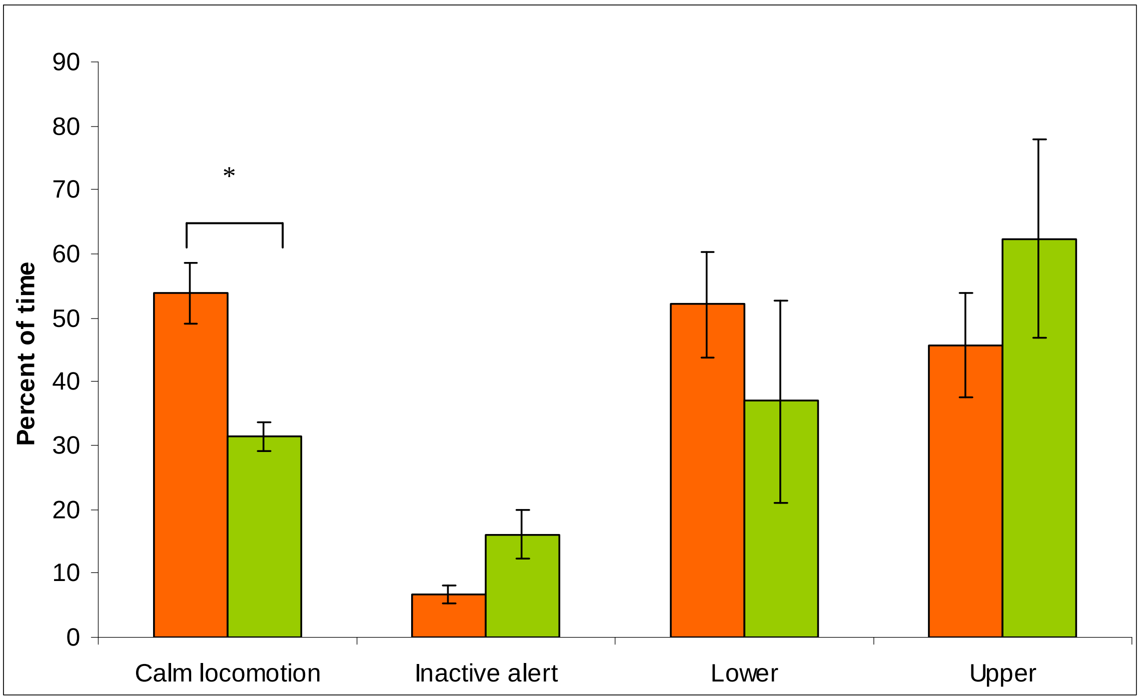
a.



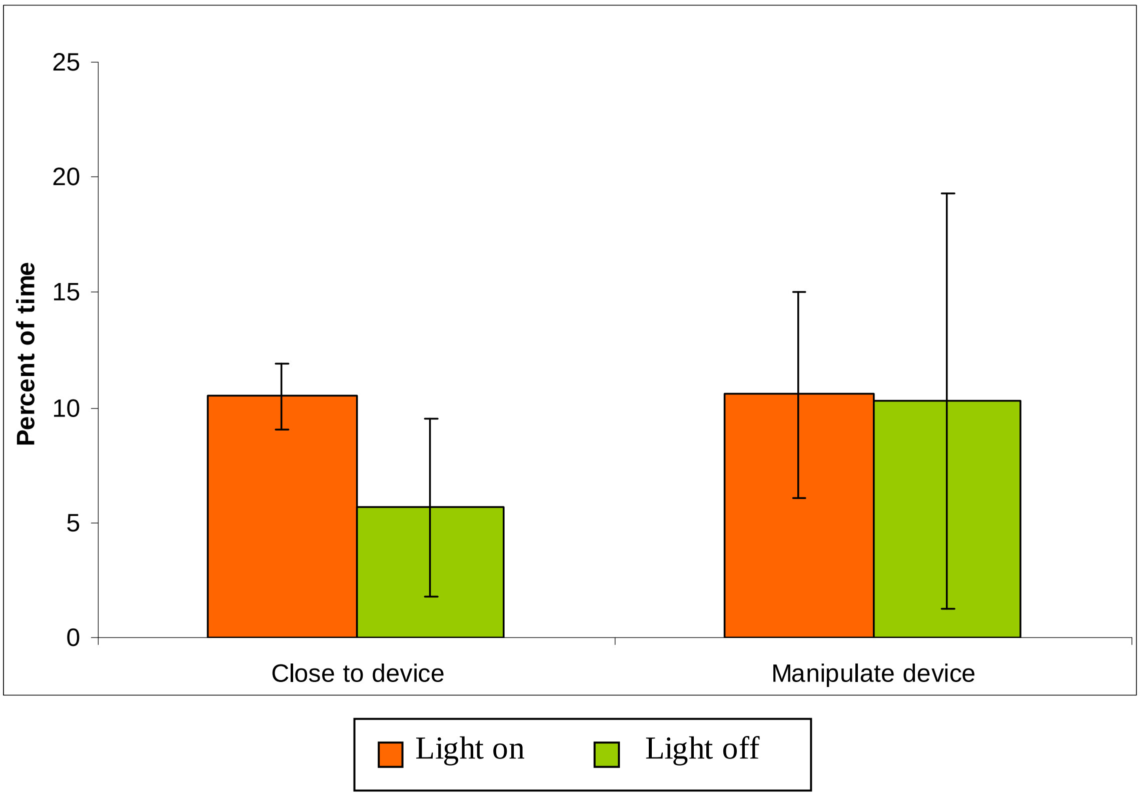
b.



c.


Percent of time
0
10
20
30
40
50
60
70
80
90
*
Calm locomotion
Inactive alert
Lower
Upper

d.


Percent of time
0
5
10
15
20
25
Close to device
Manipulate device
Light on
Light off

7.3.4 Effects of control over light on behaviour

Two-way ANOVAs with mixed design were carried out to investigate effects of control over light. Whenever a significant difference was found between study groups or study phases, or for the interaction between them, Tukey post-hoc tests were applied. Three different occurrences could indicate an impact of control over light on the behaviour of the marmosets:

1) Differences between monkeys in Master and Unaffected groups during the Test phase.
2) Differences in the behaviour of marmosets in Master groups between the Test phase and the other two phases of the study.
3) Interactions between study phases and study conditions.

These three indicators are described separately.

7.3.4.1 Differences between Master and Unaffected groups during the Test phase

Although only two groups were compared, Tukey post-hoc tests were applied when ANOVAs showed a significant difference to examine whether these differences between Master and Unaffected groups stemmed from differences during the Test phase (only results of post-hoc tests are presented in figures). With regard to variation between study groups, adults showed fewer significant differences than youngsters did. Adult members of Master groups displayed significantly more calm locomotion activity compared to adults in Unaffected groups (t=-4.62, P=0.002; see Table 7.8 and Figure 7.4 a, b, and c).

Results of ANOVAs showed that youngsters in Master groups spent significantly more time in calm locomotion and solitary play behaviour. Further, they showed significantly less inactive alert and scent marking and watched the observer less than youngsters in Unaffected groups during the Test phase. Results of post-hoc tests (that were carried out due to an interaction between study groups and study phases) showed that youngsters in Master groups spent significantly less time in the upper part of the cage compared to youngsters in Unaffected groups (see Tables 7.8 and 7.9 and Figure 7.5 a, b and c).

Table 7.8: Results of ANOVAs for effects of study condition on behaviours and cage locations for adults and youngsters (*P<0.05; ***P<0.001)

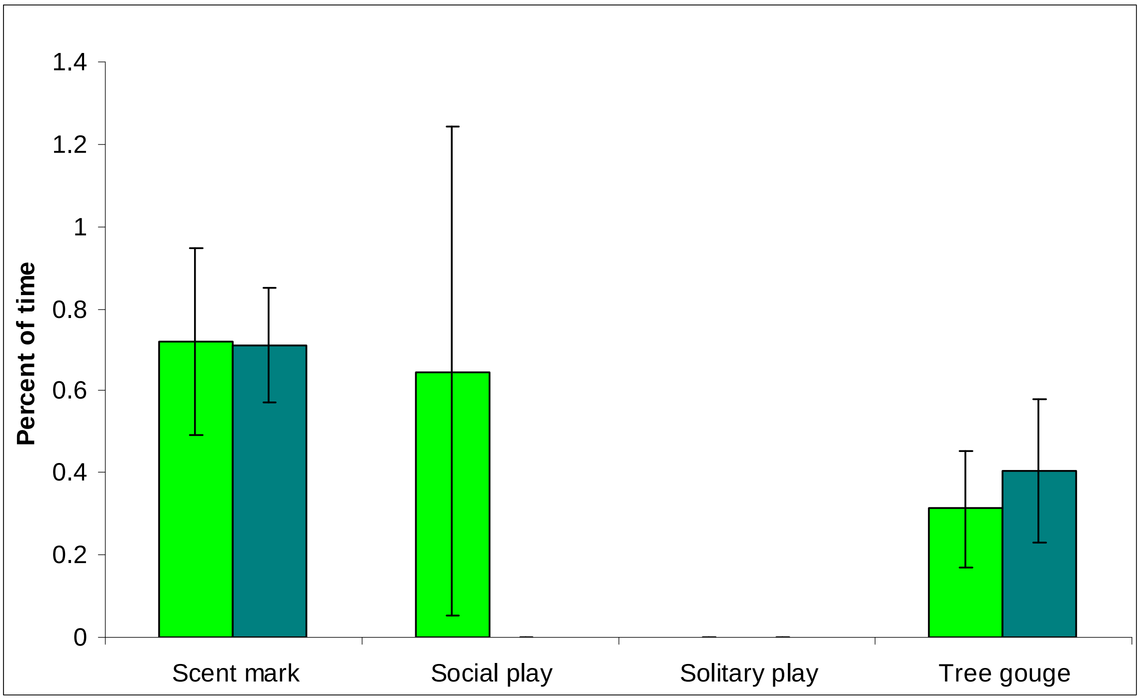
	Adults d.f.=1,10	**Adults**	**Youngsters** d.f.=1,10	**Youngsters**
	F	**P**	**F**	**P**
Agitated locomotion	0.28	0.608	0.96	0.350
Allogroom	0.33	0.578	3.54	0.089
Autogroom	0.00	0.95	0.10	0.762
Calm locomotion	4.99	0.05*	5.23	0.045*
Contact	0.05	0.833	0.22	0.651
Explore	0.85	0.378	3.59	0.087
Inactive alert	1.83	0.206	7.07	0.024*
Inactive rest	0.00	0.971	0.13	0.725
Scent mark	0.03	0.865	6.50	0.029*
Scratch	0.39	0.546	1.72	0.219
Social play	2.51	0.145	2.37	0.155
Solitary play	no data	no data	5.13	0.047*
Tree gouge	0.39	0.544	0.06	0.819
Watch observer	0.73	0.411	21.25	0.001***
Lower	1.06	0.326	0.64	0.442
Upper	1.00	0.342	0.30	0.596

Table 7.9: Results of Tukey post-hoc tests for effects of condition on behaviours for youngsters during the Test phase of the study (*P<0.05; **P<0.01)

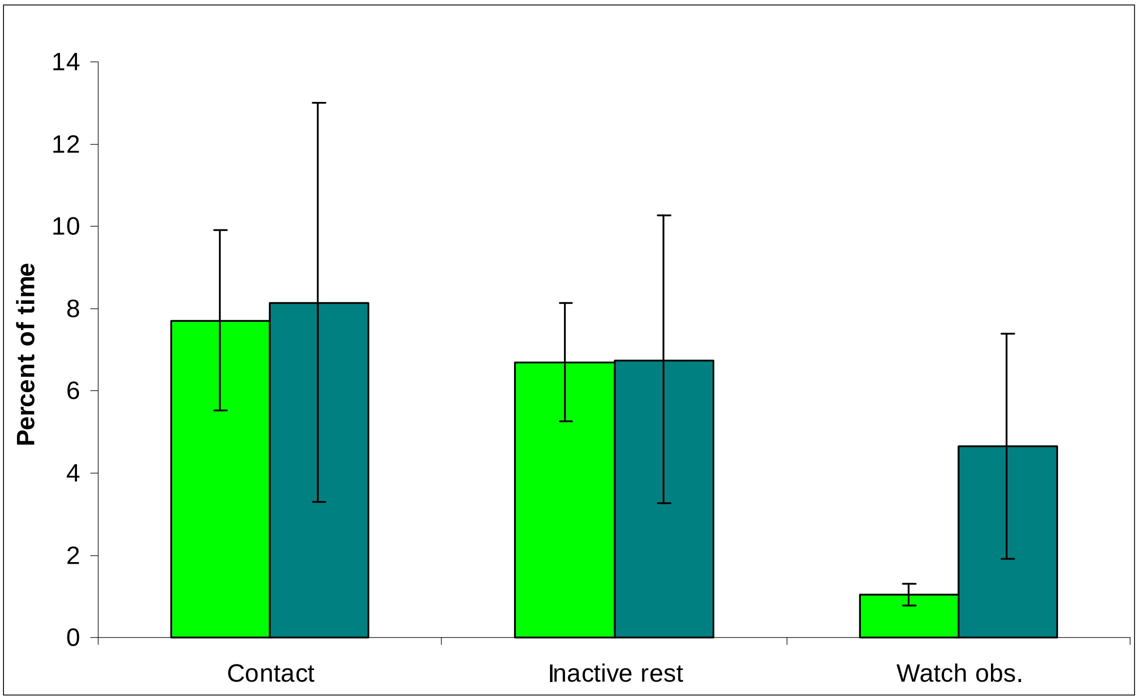
	t	P		t	P
Calm locomotion	-4.39	0.003**	**Solitary play**	-4.24	0.005**
Inactive alert	3.44	0.027*	**Watch observer**	2.9	0.082
Scent mark	3.16	0.049*	**Upper**	3.34	0.033*

Figure 7.4: Mean percentage time (±SE bars) spent in behaviours and cage locations for adults in Master and Unaffected groups during the Test phase of the study (*P<0.05)

a.



b.


Percent of time
14
12
10
8
6
4
2
0
Contact
Inactive rest
Watch obs.

c.

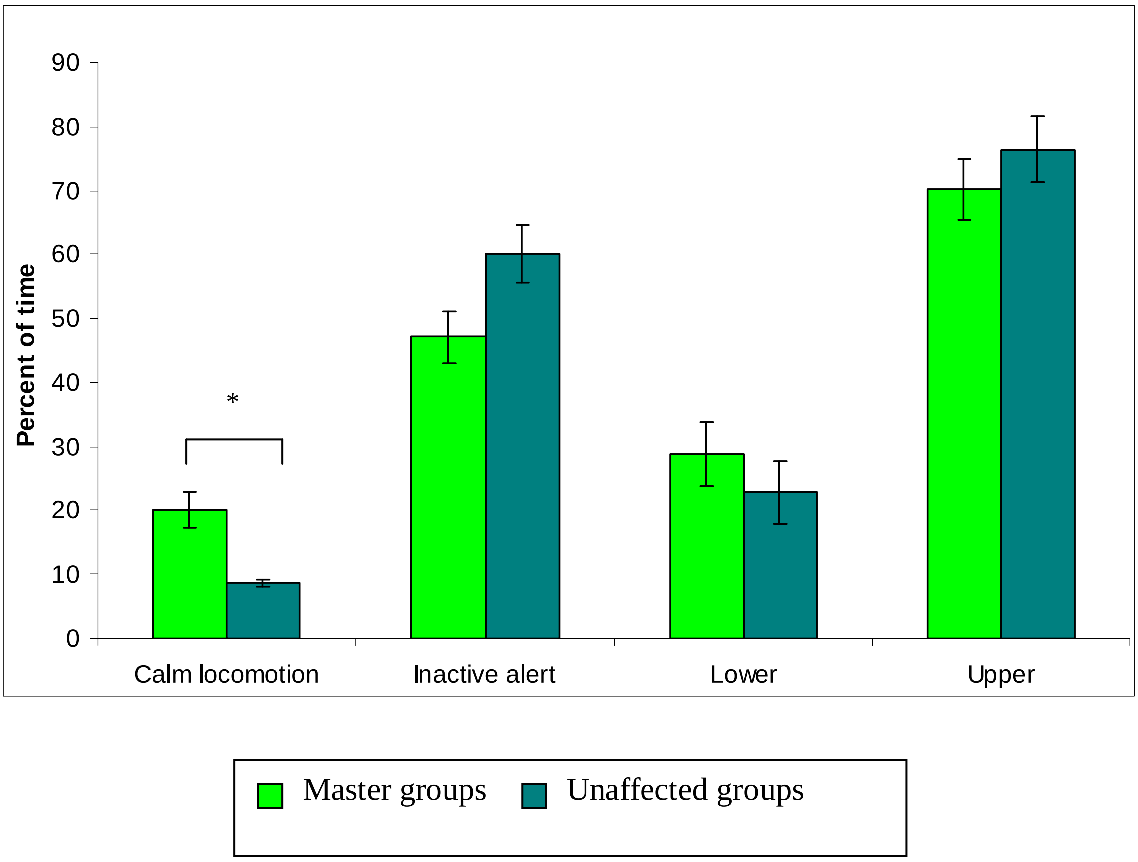
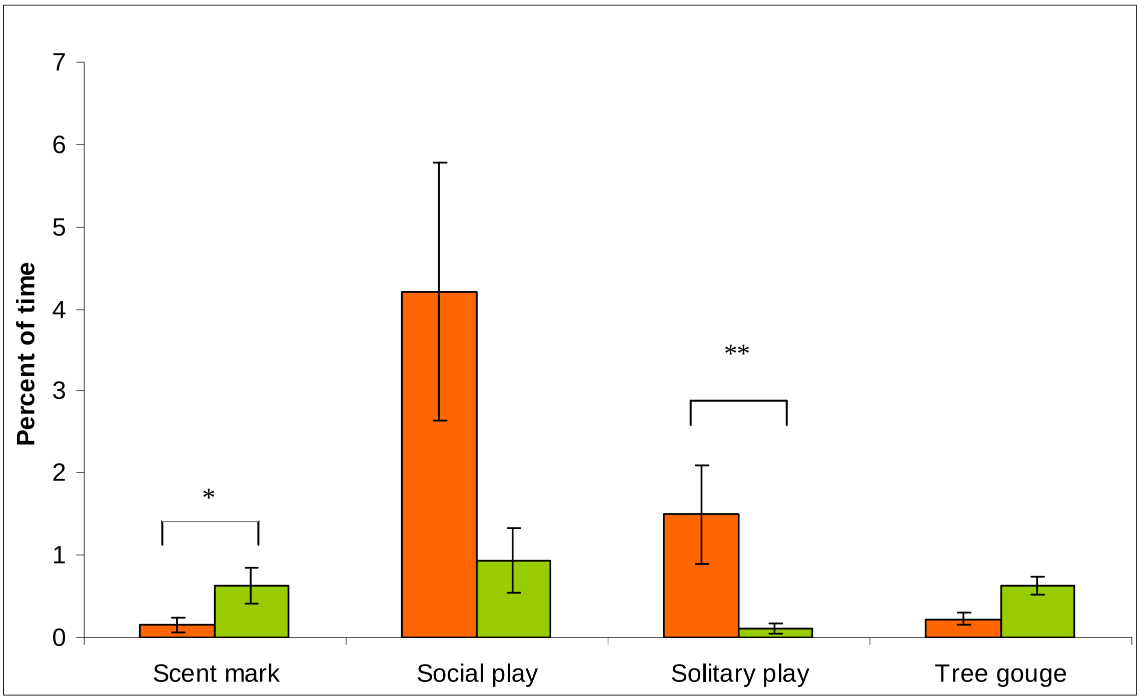
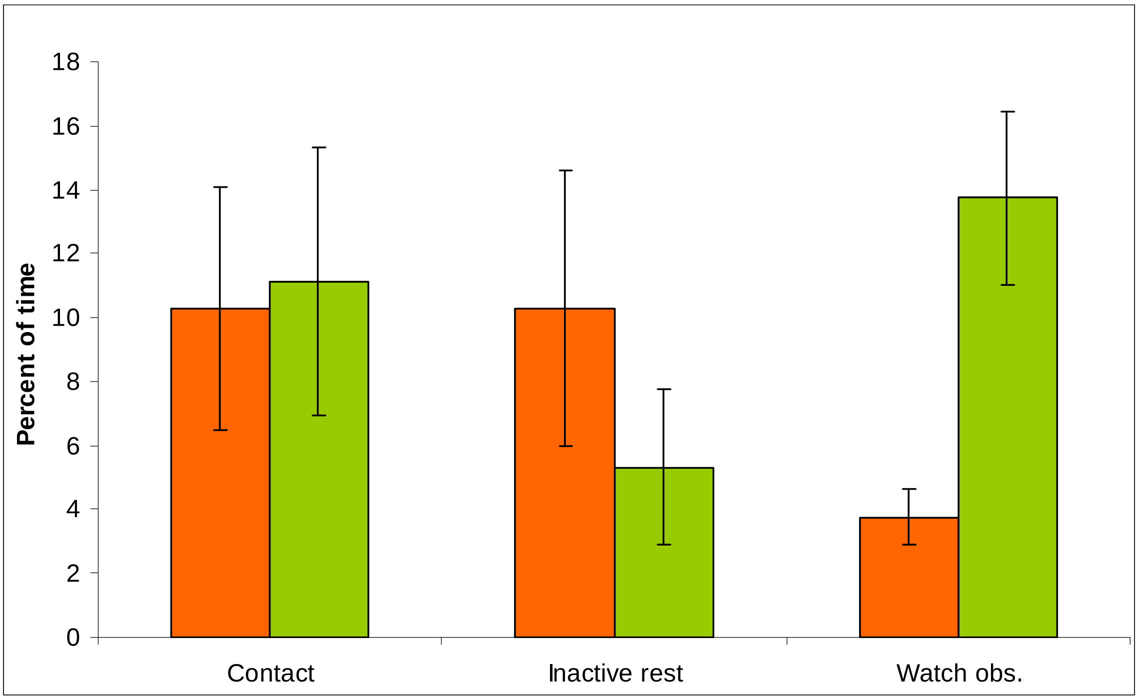

Percent of time
90
80
70
60
50
40
30
20
10
0
*
Calm locomotion
Inactive alert
Lower
Upper
🟩 Master groups
🟦 Unaffected groups

Figure 7.5: Mean percentage time (±SE bars) spent in behaviours and cage locations for youngsters in Master and Unaffected groups during Test phase of the study (*P<0.05; **P<0.01)

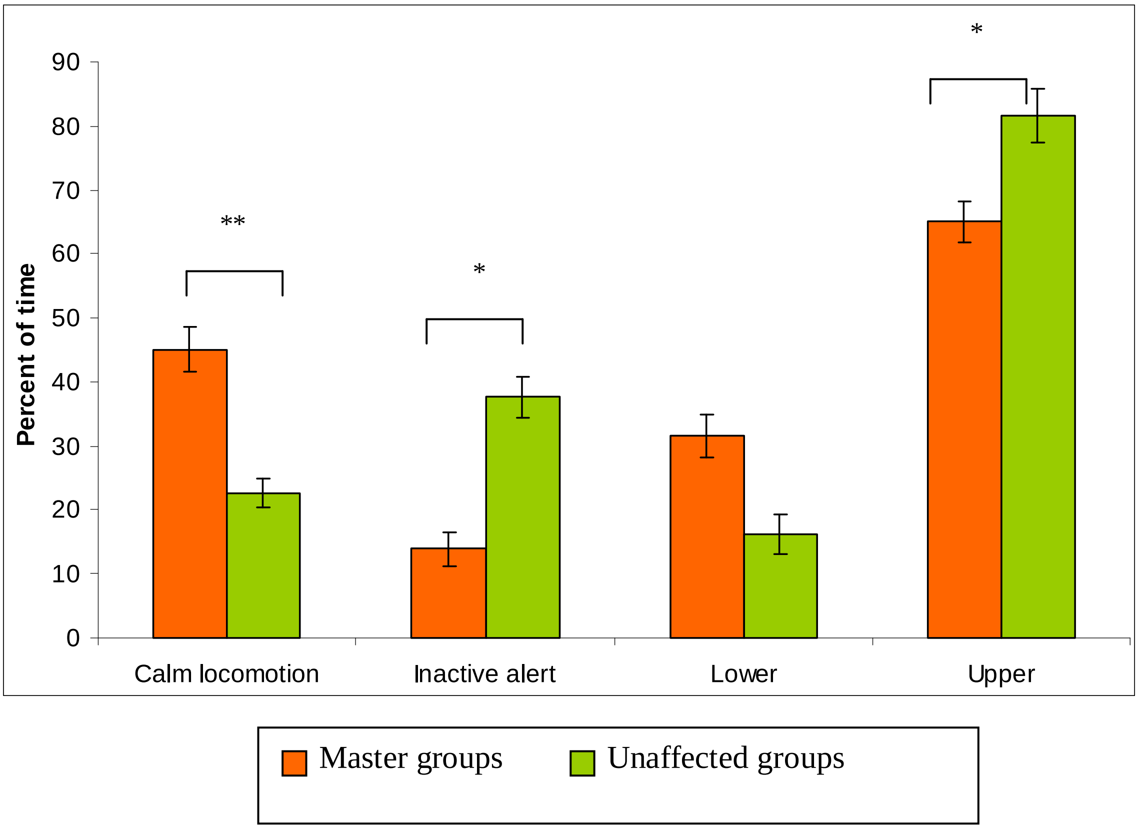
a.



b.



c.



7.3.4.2 Effects of study phases on behaviour in Master groups

Another way to look for the effects of control on the animals' welfare is to compare the behaviour of Master groups during the three phases of the study. Tukey post-hoc tests were applied in order to find exactly where these differences lay. Adults showed a significant main effect of study phase in calm locomotion. Tukey post-hoc tests showed that adults in Master groups spent significantly more time in calm locomotion during the Test phase compared to both Baseline and Post-test phases (see Tables 7.10 and 7.11 and Figure 7.6 a, b and c).

Table 7.10: Results of ANOVAs for effects of study phase on behaviours and cage locations for adults and youngsters in Master groups (*P<0.05; **P<0.01)

	Adults	**Adults**	**Young**	**Young**
	d.f.=2,20		d.f.=2,20	
	F	**P**	**F**	**P**
Agitated locomotion	0.96	0.399	2.19	0.138
Allogroom	0.28	0.756	0.56	0.582
Autogroom	2.10	0.148	0.89	0.425
Calm locomotion	6.82	0.006**	3.65	0.045*
Contact	0.75	0.485	1.85	0.183
Explore	1.27	0.304	1.25	0.307
Inactive alert	0.25	0.783	8.60	0.002**
Inactive rest	1.15	0.337	4.03	0.034*
Scent mark	0.10	0.907	0.09	0.914
Scratch	0.23	0.800	1.40	0.269
Social play	2.04	0.156	3.60	0.046*
Solitary play	no data	no data	2.15	0.143
Tree gouge	0.98	0.393	8.46	0.002**
Watch observer	2.06	0.154	3.93	0.036*
Lower	0.08	0.923	3.47	0.051*
Upper	0.03	0.973	3.07	0.069

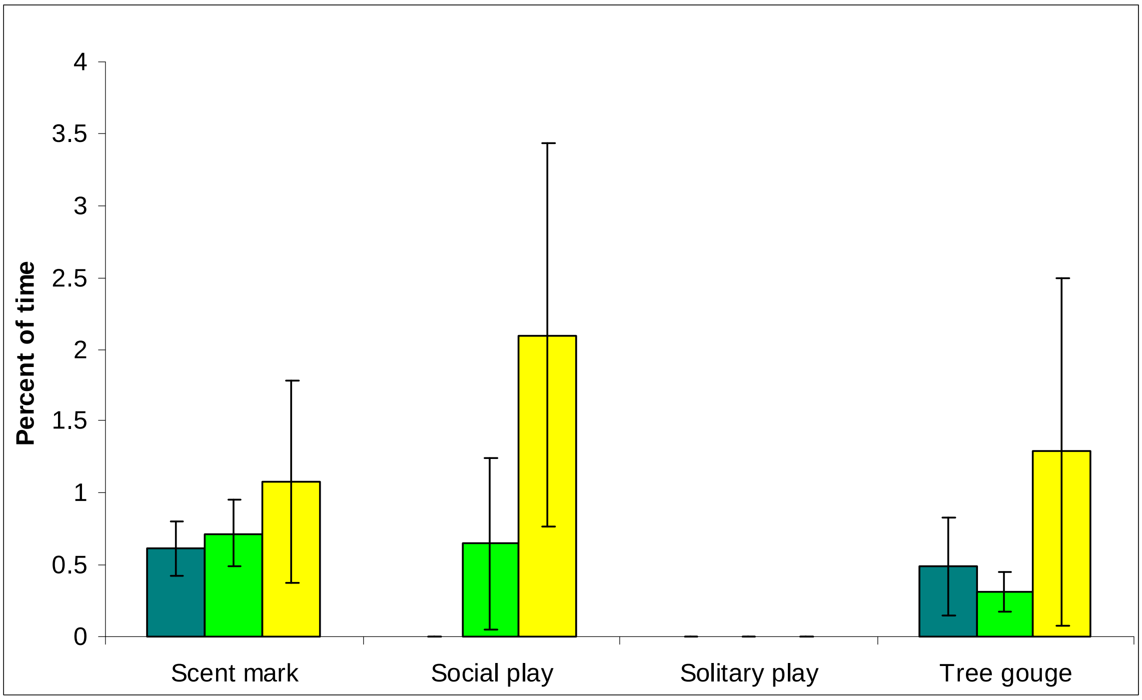
For youngsters, significant main effects were found in calm locomotion, inactive alert, inactive rest, social play, tree gouging and watching the observer behaviours, and also for time spent in lower part of the cage. The results of Tukey post-hoc tests show that youngsters spent significantly more time in calm locomotion and in the lower part of the cage, and also less time in the upper part of the cage during the Test phase compared to the Baseline phase. In addition, youngsters showed significantly more inactive alert and tree gouging behaviours during the Post-test phase compared to both Test and Baseline phases (see Tables 7.10 and 7.11 and Figure 7.7 a, b and c).

Table 7.11: Results of Tukey post-hoc tests for effects of study phase on behaviour and cage locations for adults and youngsters in Master groups (*P<0.05; **P<0.01)

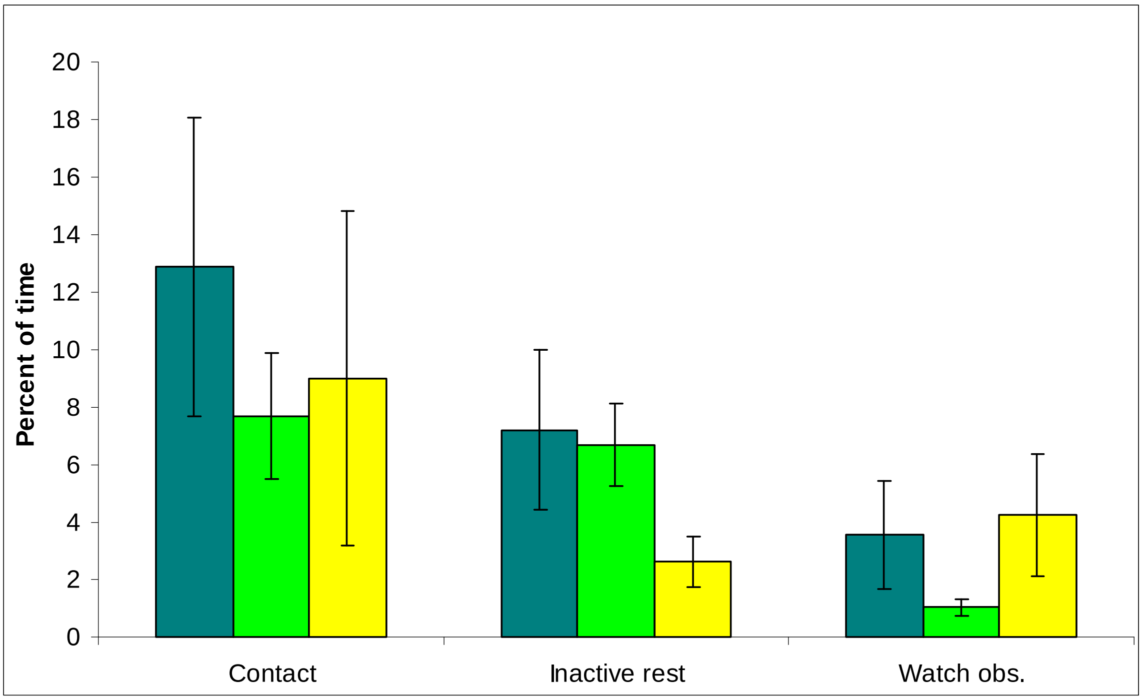
	Baseline vs. Test		Test vs. Post-test		Baseline vs. Post-test	
	t	**P**	**t**	**P**	**t**	**P**
ADULTS						
Calm locomotion	4.56	0.002**	-3.89	0.010**	0.67	0.983
YOUNGSTERS						
Calm locomotion	4.04	0.007**	-2.95	0.073	1.09	0.879
Inactive alert	0.10	1.00	3.58	0.020*	3.68	0.016*
Inactive rest	-1.06	0.89	-0.92	0.93	-1.98	0.388
Social play	3.10	0.055	-2.19	0.286	0.91	0.939
Tree gouge	0.09	1.00	3.67	0.016*	3.76	0.013*
Watch observer	-1.85	0.458	0.57	0.992	-1.28	0.790
Lower	3.57	0.020*	-2.29	0.245	1.28	0.791
Upper	-3.59	0.019*	2.57	0.152	-1.02	0.905

Figure 7.6: Mean percentage time (±SE bars) spent in behaviours and cage locations for adults in three study phases [one-way ANOVA with repeated measures (black marks) and Tukey post-hoc tests (red marks) **P<0.01]

a.



b.


Percent of time
20
18
16
14
12
10
8
6
4
2
0
Contact
Inactive rest
Watch obs.

c.

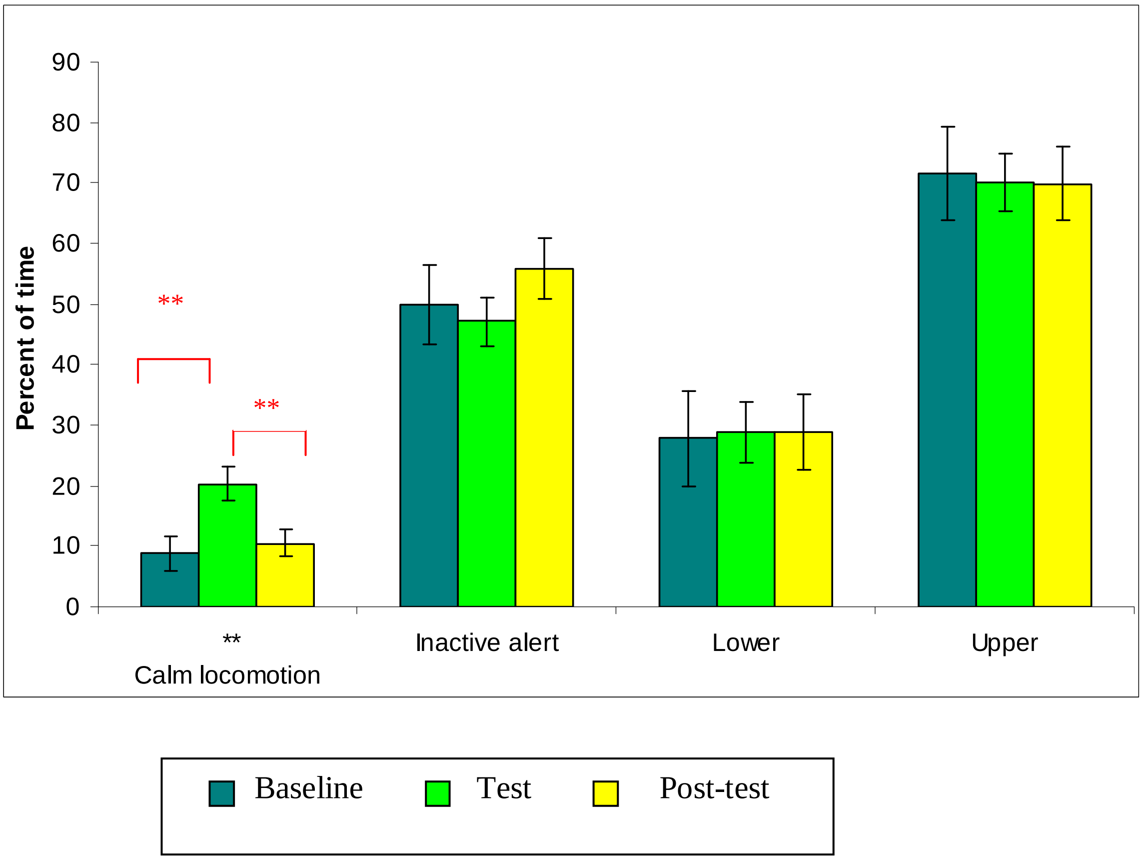
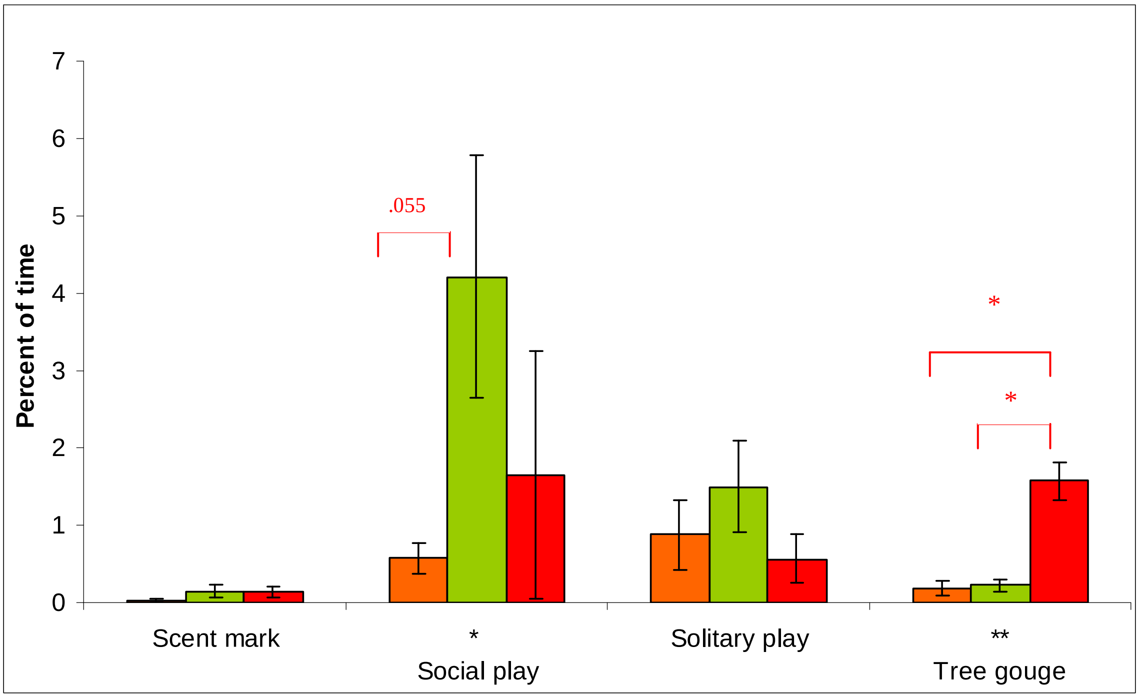
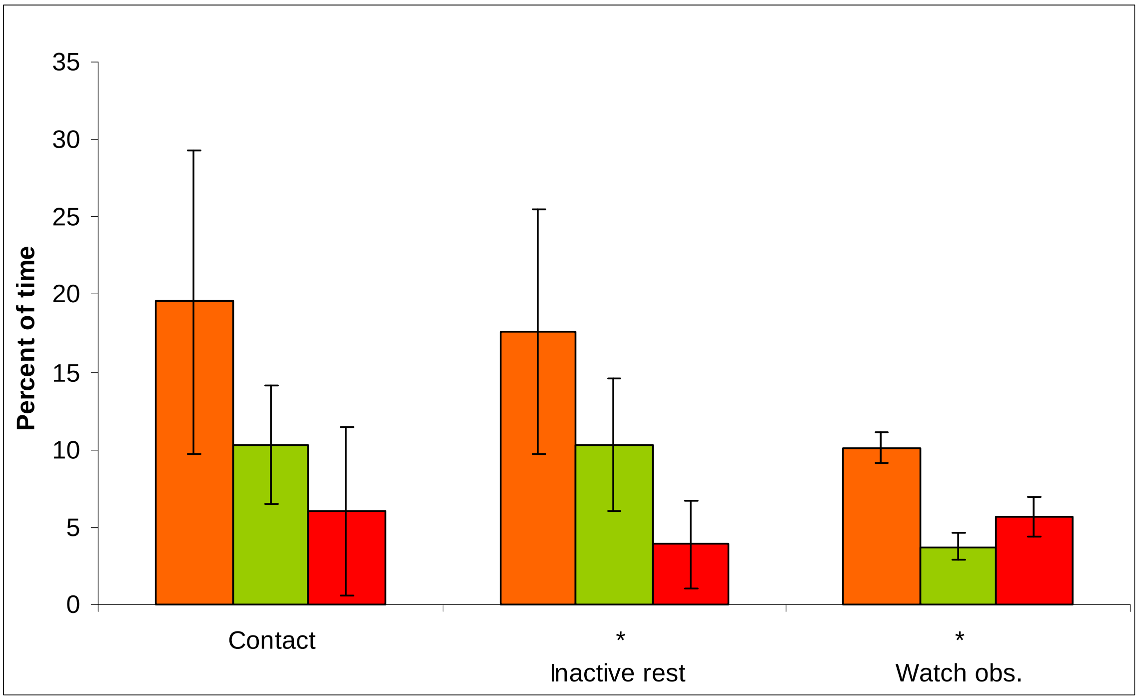

Percent of time
90
80
70
60
50
40
30
20
10
0
**
**
**
Calm locomotion
Inactive alert
Lower
Upper
Baseline
Test
Post-test

Figure 7.7: Mean percentage time (±SE bars) spent in behaviours and cage locations for youngsters in three study phases [one-way ANOVA with repeated measures (black marks) and Tukey post-hoc tests (red marks) *P<0.05; **P<0.01]

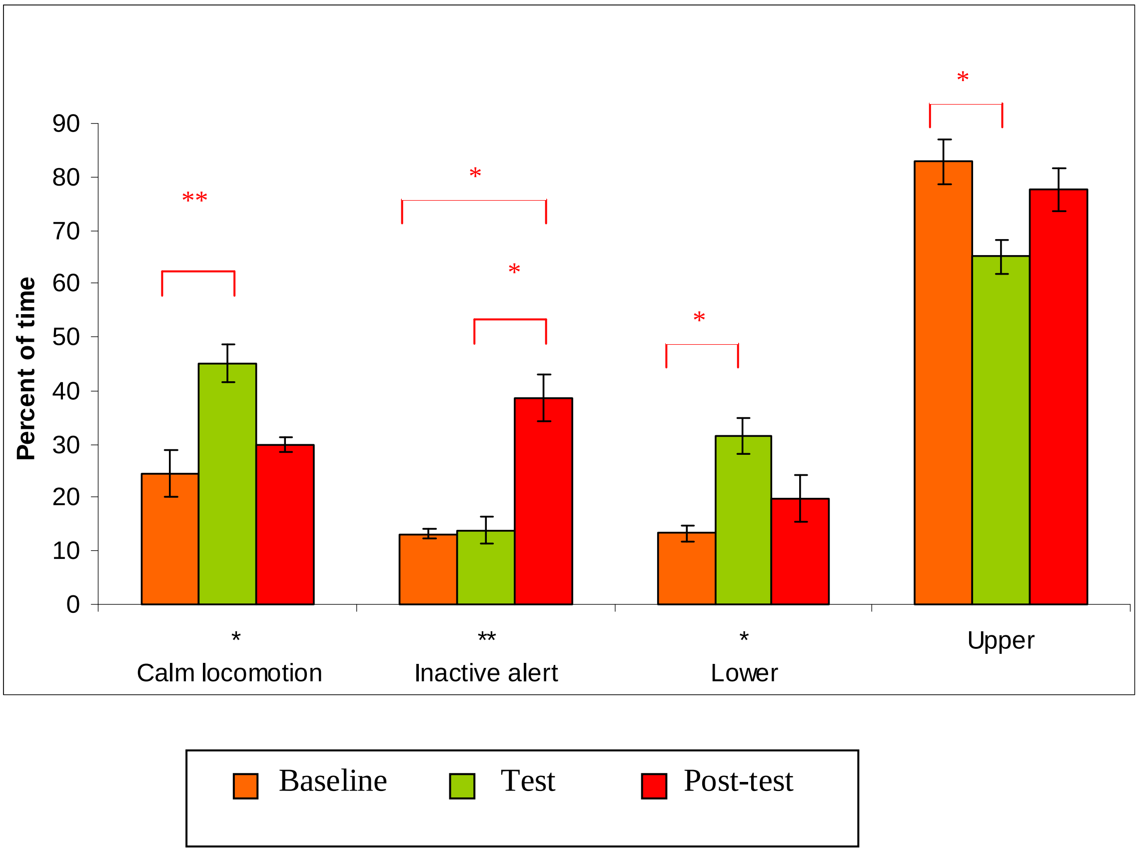
a.



b.



c.



7.3.4.3 Interactions between study groups and study phases

The ANOVAs revealed several significant interactions between study groups and study phases. For adults there was a significant interaction in calm locomotion. Master groups showed a strong increase in calm locomotion in the Test phase followed by a strong decrease in the Post-test phase, while Unaffected groups showed a moderate decrease along the whole study period (see Table 7.12 and Figure 7.8).

For youngsters significant interactions were shown in calm locomotion and in time spent in lower and upper parts of the cage. Members of Master groups showed significantly increased levels of calm locomotion in the Test phase of the study, followed by decreased (although not to baseline) levels in the Post-test phase. Conversely, Unaffected groups displayed similar levels throughout the whole study period. With regard to location inside the cage, Unaffected groups continued to use each part of the cage for similar percentages of the time throughout the whole study. In contrast, Master groups showed a steep increase in time spent in the lower part of the cage and a sharp reduction in time spent in the upper part of the cage during the Test phase, followed by return to baseline levels in the Post-test phase (see Table 7.12 and Figure 7.9 a, b and c). Time spent in the lower and upper parts of the cage were not reciprocal. Marmosets spent some time inside the nest box and in verandas (whenever these were available), although data relating to the amount of time spent in these two locations are not discussed as they were low and no significant differences between study groups or study phases were found.

Table 7.12: Results of ANOVAs for interactions between study groups and study phases
($*P<0.05$; $**P<0.01$)

	$F_{2,20}$	**P**
ADULTS		
Calm locomotion	6.09	0.009**
YOUNGSTERS		
Calm locomotion	6.13	0.008**
Lower	4.21	0.030*
Upper	6.28	0.008**

Figure 7.8: Interaction between study group and study phase for adults

a. Calm locomotion

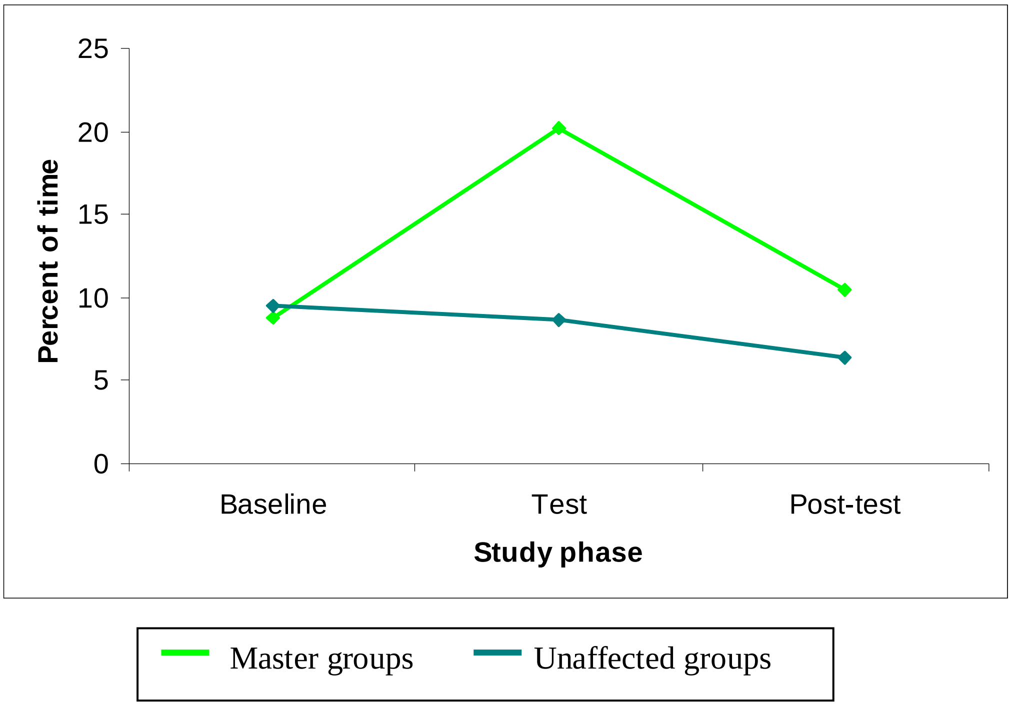
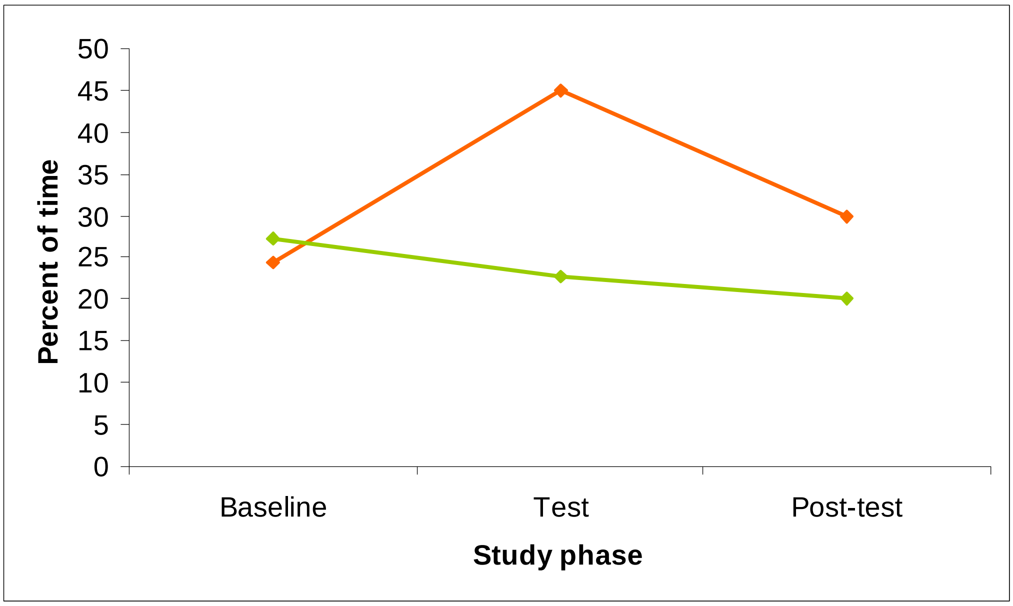
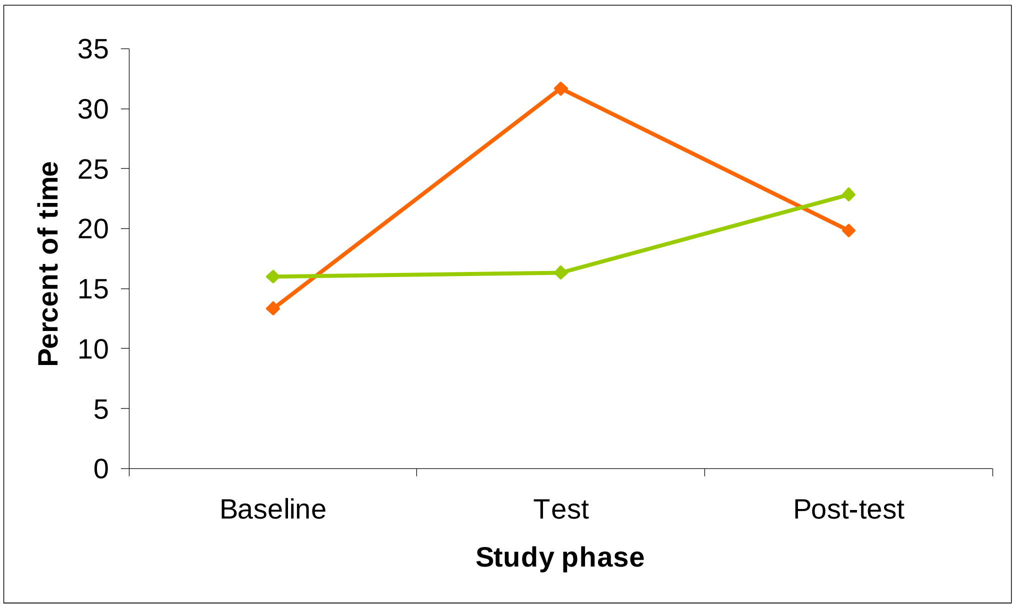


Figure 7.9: Interaction between study group and study phase for youngsters

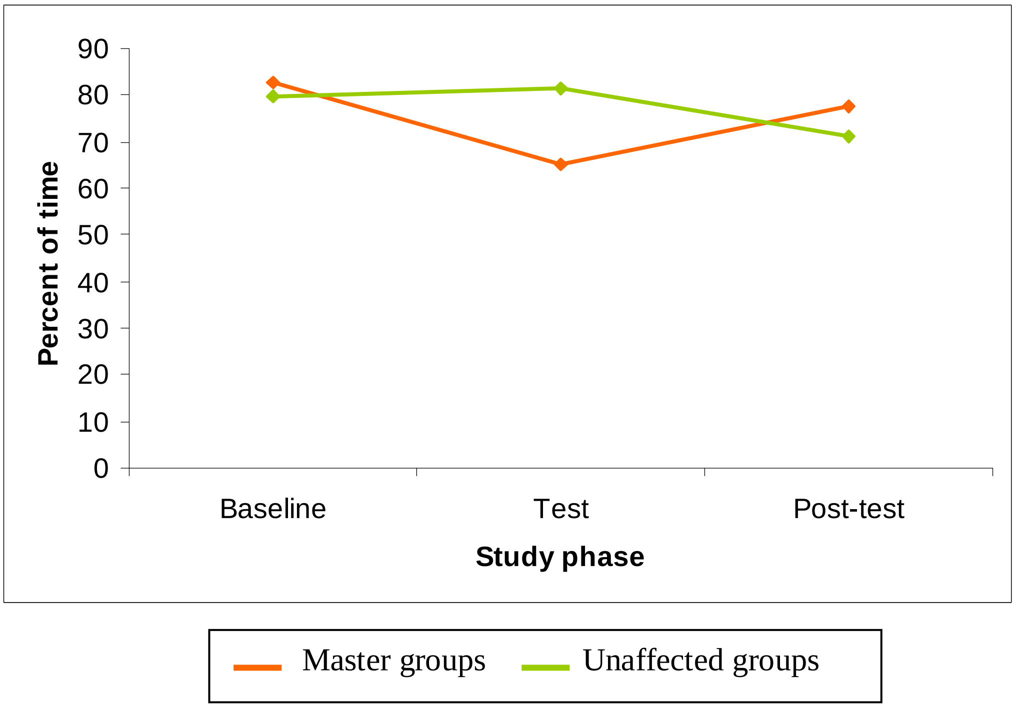
a. Calm locomotion



b. Percentage time spent in the lower part of the cage



c. Percentage time spent in the upper part of the cage



7.3.5 Effects of loss of control (or light/heat) on behaviour

Behavioural changes were considered to be a consequence of loss of control when significant differences were found between the Post-test phase and the other two phases of the study. Youngsters in Master groups showed significantly higher levels of inactive alert and tree gouging behaviours during the Post-test phase compared to levels in the Baseline and the Test phases (see Table 7.11 and Figure 7.7). These behavioural differences may indicate an impact of loss of control and are discussed below.

7.4 DISCUSSION

The results of this study show that both illumination intensity and the opportunity to control it positively affected the welfare of captive common marmosets. The positive effects of control over light intensity were shown even when marmosets did not utilize their ability to control the light and, hence, increased the light intensity of their cage infrequently. Furthermore, youngsters were more affected by increased light levels, as well as from the option to control them than were adults.

7.4.1 Measures of light usage

Three out of six Master groups in this study used the light for an average of over 50% of the time during the whole Test phase of the study. Two of these groups left the light on for more than 80% of the available time. However, the frequencies of button usage were very low. Although mean frequency of button touches decreased after the first four days of the Test phase, this decrease was not significant and therefore evidence of habituation was not found.

Line and co-workers (Line et al., 1990a, 1991a) allowed singly housed adult female rhesus monkeys control over a music-feeder box. Hence, monkeys could operate a radio set by touching two different levers (one turned the radio on while the other turned it off). Additionally they could get banana-flavoured food pellets by touching a third lever. In the first study (Line et al., 1990a), each of five animals earned a total average number of 24 to 66,000 pellets over the 20 weeks of the study. The total number of music lever presses ranged from 5 to 600 per monkey during the experimental period. In the second study (Line et al., 1991a), ten animals were studied; the average number of touches to the feeder control lever was 8221 per day (over 12 weeks), and the average playing time of the radio was 76 minutes per day (touch frequency was not reported). The results of these studies suggested that animals became obsessive with the enrichment device, which is an undesirable outcome. Kavanau (1963, 1964) described a similar tendency when deer mice were given control over illumination. This phenomenon did not occur in the present study, as the durations of light usage were relatively high, while the frequencies of button touches were relatively low.

In two other studies, animals showed no obsession with operating the devices. However, the situations in these two studies were different from that in the present one. In the first study, growing pigs were allowed to control their thermal environment using a photo electric beam to turn on an infra-red heater for five minutes. The pigs responded at a mean rate of 1.78 times per hour, obtaining an overall mean of 44.5±10 heat reinforcements per day across the 14 experimental days. However, in this study pigs were not able to switch the heaters off; further, each response turned the heaters on for five minutes only, so they had to react every five minutes in order to maintain the high temperature for longer periods (Jones & Nicol, 1998). A similar situation was implemented by Taylor and colleagues (2001), when domestic hens were given control over food and light. In this study any peck delivered to the operant feeder-key caused the feeder lid to open for 30 seconds, and any peck delivered to the light-key caused a bulb above the key to turn on for two minutes. Animals used the keys to open the feeder for an average of 92 minutes per day and to turn on the light for an average of 46 minutes per day. A simple calculation shows that hens pecked the feeder-key 184 times a day and the light-key 23 times a day, indicating that they vastly preferred the food over the light. Animals in this study used the keys much more than animals in the present study used the button, however, they did so in order to control additional food and light. Perhaps the study design of Jones and Nicol (1998) and Taylor and co-workers (2001) gives the researchers a better view of the animal's willingness to achieve some control over their environment, or a better evaluation of the efforts they are willing to invest in changing some aspects of their environment. However, it forces the animals to work almost continuously in order to keep their environment in a preferable state. In the present study, the animals could turn on the light once a day in order to raise the light intensity in the cage. One could say that they might touch the button accidentally, yet, since some groups turned the light on almost every morning during the whole Test phase of the study, it may be concluded that they turned the light on purposely rather than simply at random and that they preferred the higher illumination intensity. Informal observations showed that on some occasions when the device was disconnected for few minutes (for room cleaning) the marmosets turned the light on immediately after the device was reconnected.

7.4.2 Effects of light intensity on behaviour

The results of the present study show that youngsters were affected by the intensity of the light inside their cage much more than adults; these effects were expressed in several behaviours. Two significant differences were found in adults' behaviour between the two conditions, light on and light off. Adults watched the observer significantly more when the light was off. Possible explanations for this difference will be given in the General Discussion. Further, adults spent significantly more time sitting in front of the light when it was on. There are three potential explanations for this difference. First, it is possible they preferred to be close to the device so they could control it better than other members of their group (this is the weakest explanation, since on all the observed occasions only youngsters turned the light on or off). The second possible reason is that they liked the high illumination intensity, so they tried to stay as close as possible to it. However, this explanation is also not very likely as the light intensity increased within the whole cage. The third and the most reasonable explanation is that they liked the warmth that the light created and had to sit close to the light as the temperature further from the device was not affected by it.

Youngsters spent significantly more time in calm locomotion when the light was on. It was noted by Hampton and colleagues (1966) that marmosets are sensitive to illumination levels. They reported markedly reduced activity when the light was dimmed; however, they described a standard situation in which the light dimmed in the end of the day before a complete darkness approached, when all activity stopped altogether. Isaac and DeVito (1958) and Draper (1965) also found increased activity levels when illumination intensity was increased, in rhesus macaques. These results are compatible with those of the current study. However, in this study the light intensity affected only the youngsters, while in the two earlier studies all animals were adults; hence there is no information about differences between adults and youngsters. Further, in both previous studies, the monkeys were placed alone inside a test cage. In the present study, the animals stayed inside their home cages with their family groups, and were able to control the light intensity in their own familiar environment. The home environment is likely to be less stressful; it is possible that the environmental change has to be extreme in order to affect the adults.

Other significant differences in youngsters' behaviour were shown in contact and inactive rest behaviours; they spent more time resting and in contact with other group members when the light was off. This variation may stem from the lower proportions of time spent in calm locomotion when the light was off. However, there is no clear explanation for these behavioural changes, as in previous studies in the present thesis the marmosets showed higher levels of inactive rest behaviour when housing conditions improved, and elevated levels of this behaviour were considered to be desirable based on previous research (see Chapter 3). In addition, the interpretation of rates of contact with other group members in relation to welfare is not clear and will be discussed in Chapter 10. Youngsters also spent significantly more time involved in social play when the light was on. There are no previous reports of this in the literature, yet social play behaviour is considered to be a desirable behaviour for captive primates.

7.4.3 Effects of control over light on behaviour

The effects of control over illumination were analysed using two different methods; one was a comparison between Master and Unaffected groups during the Test phase of the study, while the other was a comparison of animals from Master groups only, throughout all study phases. The effects of control were tested on all study groups with no connection to the measures of device usage, since even when marmosets did not use the option of lighting their environment they still remained in control of it. The influence of control affected several behaviours, and again was more obvious in youngsters.

Locomotion and Inactivity

Increased levels of calm locomotion as well as decreased levels of inactive alert behaviour are considered to be desirable (see Chapter 3). In the present study both adults and youngsters showed significantly more calm locomotion behaviour when they had control over illumination. This was shown both when Master and Unaffected groups were compared and when the three phases of the study were compared for marmosets from the Master groups only. Further, significant interactions between study group and study phase were found for both adults and young. These interactions resulted from the significant differences between study phases that were found for Master groups, while levels of calm locomotion were similar throughout the study phases for Unaffected groups. Youngsters also spent significantly less time inactive alert while they had control. They also showed a gradual decrease in time spent in inactive rest; however, post-hoc tests revealed no significant differences between the study phases, although a main significant effect was found in the ANOVA. These results may indicate a better welfare state, at least for youngsters, although no significant differences between the study phases were found for agitated locomotion. Similarly, Taylor and colleagues (2001) found that laying hens that had control over food and light spent less time inactive, compare to non-controlling animals. Line and co-workers (1991a) reported that adult rhesus monkeys spent significantly less time sitting and more time standing when they were allowed to control a music-feeder device. Conversely, pigs were significantly less active when given control over their thermal environment, compared to non-controlling animals. However, the researchers tended to ascribe this outcome to the heating conditions in the cages, since the uncontrollable cages were warmer than the controllable ones (Jones & Nicol, 1998).

Social and solitary play

Play behaviour is considered to be an extremely desirable behaviour for captive primates (see Chapter 3). In the present study, youngsters from Master groups showed significantly more solitary play behaviour compared to youngsters from Unaffected groups. Further, they performed more social play during the Test phase of the study compared to other phases (although a significant main effect of study phase was found only in ANOVA and not in post-hoc tests). In contrast to the present results, pigs displayed less play behaviour when they had control over heating conditions in their cages, compared to pigs that had no control but whose cages were constantly warm. Nevertheless, it appears that in this study thermal conditions affected the animals more than the opportunity to control this environmental aspect; it is possible that the need to turn the heating back on every five minutes was too demanding for the animals, which consequently suffered from an inappropriate temperature in their environment. Conversely, in the present study, the marmosets could turn the light on or off at any time for an unlimited period, hence, they had full control over the additional light.

Scent mark

Although scent marking is a well known natural behaviour of marmosets in captivity and in the wild, high frequencies of this behaviour are considered to be stress related. In the present study, youngsters from Unaffected groups showed significantly higher rates of scent marking compared to youngsters from Master groups. This result suggests better welfare conditions for Master group youngsters, although no significant differences were found in scratching behaviour which is another stress related indicator.

Tree gouge

Youngsters in Master groups showed higher levels of tree gouging during the Post-test phase compared to the Test phase. Although tree gouging is a natural behaviour for marmosets, the interpretation of changes in levels of performance of this behaviour in captivity is not clear. The relation between levels of tree gouging and welfare will be discussed in Chapter 10.

Watch the observer

Youngsters in Master groups watched the observer less than youngsters in Unaffected groups. In addition, a significant main effect of study phase was found for youngsters in Master groups. As mentioned earlier, this will be addressed in the General Discussion.

Location inside the cage

Although marmosets are arboreal, an increase in usage of the lower part of the cage is desirable as it indicates a better utilization of the cage space. Significant interactions between study group and study phase were found for the time youngsters spent in lower and upper parts of the cage. Post-hoc tests show that youngsters in Master groups spent less time in the upper part of the cage compared to youngsters in Unaffected groups during the Test phase. Further, youngsters in Master groups spent more time in the lower part and less time in the upper part of the cage during the Test phase compared with the Baseline phase. These results suggest that the better lighting conditions in the lower part of the cage encouraged the marmosets to spend more time there. Alternatively, it is possible that youngsters preferred to stay closer to the light box, so they could manipulate it. The result that this behavioural tendency was seen only in youngsters is reasonable, as adults were not observed manipulating the light.

7.4.4 Effects of loss of control (or light/heat) on behaviour

Negative consequences of loss of control were discussed in Chapter 2. However, in the present study the effects of loss of control over illumination are not obvious. Youngsters in Master groups showed increased levels of inactive alert and tree gouging behaviours during the Post-test phase compared to both Baseline and Test phases. Although an increase in levels of inactive alert behaviour is undesirable, the interpretation of increased levels of tree gouging behaviour is, as yet unclear. Hence, no clear conclusions may be drawn regarding the effects of loss of control. In addition, although the light was not on constantly throughout the whole Test phase, it is possible that the loss of better lighting conditions or the loss of heat (when sitting in front of the light box) was the cause of the observed behavioural changes during the

Post-test phase. However, in the present study, the effects of control, light and heat are confounded. The confound between control and light and heat is removed in the experiment reported in Chapter 9.

7.5 CONCLUSIONS

Effects of lighting conditions, control over these conditions, and the loss of that control were studied. Results are presented in Table 7.14.

The conclusions made from these results are:

1) An increase in illumination intensity has positive effects on the welfare of captive marmosets.
2) The ability to control light has positive effects on welfare.
3) The increase in light intensity and the control over it, have a greater impact on young marmosets than on adults.
4) Loss of control over cage illumination, and/or loss of increased light intensity, does not affect the welfare of marmosets.

Table 7.14: Summary of the main behavioural results of Chapter 7

	Adult marmosets		**Young marmosets**	
	Elevated levels	**Reduced levels**	**Elevated levels**	**Reduced levels**
Effects of increased light intensity	Close to device	Watch observer	Calm locomotion Social play	Contact Inactive rest
Effects of control over light intensity (study group comparison)	Calm locomotion		Calm locomotion Solitary play	Inactive alert Scent mark Watch observer Usage of upper part of cage
Effects of control over light intensity (study phase comparison)	Calm locomotion		Calm locomotion Social play Usage of lower part of cage	Inactive alert Inactive rest Tree gouge Watch observer Usage of upper part of cage
Effects of loss of control over additional light			Inactive alert Tree gouge	

In the next chapter the effects of coloured light on the behaviour of family housed marmosets are studied.

Chapter 8

Effects of Control over Coloured Lights on the Welfare of Family Housed Common Marmosets

8.1 INTRODUCTION

The effects of control over additional light inside the home cage on the behaviour of family groups of marmosets were reported in Chapter 7. This study showed that increased light intensity, together with the opportunity to control it, enhanced the welfare of the marmosets. It is now interesting to investigate whether the ability to control another environmental stimulus will reveal similar effects on the monkeys' behaviour. In the previous study, marmosets could control white light intensity. Although it is unnatural for nonhuman primates to manipulate light, white light and illumination changes are natural components of every wild and captive environment. In the present study marmosets were allowed to control coloured 'disco lights'. These lights are clearly unnatural and unfamiliar to the monkeys, but were chosen to help clarify further the impact of control of a visual stimulus. The effects of complexity of the environment have been previously studied in this thesis (see Chapters 4, 5 and 6). The projection of coloured 'moving' lights into the enclosure of the marmosets increases the visual complexity of this environment. Therefore, the response of the marmosets to this stimulus may also contribute to the study of the effects of complexity.

Fritz and co-workers (1997) studied the effects of coloured lights on the behaviour of captive chimpanzees. They found differences in the reactions of the apes to lights of different colours. However, in the present study it was impossible to investigate the marmosets' reaction to different light colours, as there are potential sex differences in the ability of callitrichids to see colour. All males and some females are dichromatic (similar to colloquially 'colour blind' humans), whilst other females are trichromatic (e.g. Surridge et al., 2003). Dichromatic individuals may confuse reds and greens that can be discriminated by their trichromatic counterparts (Smith et al., 2003). Therefore, the disco light sequencer with six different coloured lights was used, which served as a visual stimulus with no importance of the exact colours that each individual could perceive.

8.1.1 Effects of sensory enrichment on the behaviour of captive primates

Only one previous study has examined the effects of sensory enrichment on callitrichids. Pook (1978) studied the reactions of common marmosets and saddleback tamarins to several types of pictorial stimuli. Monkeys of both species responded to most of the pictures with an approach and close visual scrutiny. They were also able to discriminate between different images. However, no effects of the exposure to visual stimuli on other behaviours were reported. The effects of several types of sensory enrichment on the behaviour of other captive nonhuman primates have been studied. Most of these sensory enrichments have been auditory or visual stimuli, and the different studies have revealed contradictory findings (see Table 8.1). When reactions to music have been studied, results have shown positive behavioural (Howell et al., 2002a) and physiological (Brent & Weaver, 1996) effects. Similarly, when a playback of conspecifics' song was played to lar gibbons, the impact on behaviour was positive

(Shepherdson et al., 1989). Several types of stimuli have been used to study the effects of visual stimulation (videotapes, television sets, computer tasks and projected moving lights). In only one study were the effects of a visual stimulus (moving lights) clearly positive (Kissinger & Bouwens, 2006). In some studies no effects of these stimuli on behaviour were found (Brent et al., 1989; Schapiro & Bloomsmith, 1995; Schapiro et al., 1995; Bloomsmith & Lambeth, 2000), while in others the interpretation of the behavioural changes was not clear (Platt & Novak, 1997). Rumbaugh and colleagues (Rumbaugh et al., 1989; Washburn & Rumbaugh, 1992) found that rhesus macaques showed reduced levels of certain behaviours (e.g. inactivity, stereotypy, foraging, autogrooming) when a video task was available to them. However, it is possible that these behavioural changes occurred simply because they were mutually exclusive with the time that the monkeys spent manipulating the task.

Table 8.1: Effects of sensory stimuli on the behaviour of captive primates. (+)= positive effects of stimulus; (-)= negative effects of stimulus; (none) no effects on behaviour; (?)= effects of stimulus were unclear; (blank)= behavioural effects were not mentioned; (§)= information not reported. See key below the Table.

Author	**Species**	**Housing (sample size)[a]**	**Stimulus**	**Time exposed**	**Time used/ watched**	**Effects on behaviour (in brackets) and comments**
Pook, 1978	*Callithrix jacchus,* *Saguinus fuscicollis*	Social (1 pair, 1 trio) (3 pairs)	Photographs (conspecifics/ favourite foods/ snakes)	§	§	Responded to photos in relation to the item on them
Brent et al., 1989	*Pan troglodytes*	Single (14)	Videotapes (local TV channel)	6 hours daily	§	(none)
Rumbaugh et al., 1989	*Macaca mulatta*	Single (2)	Computer tasks	Several months	Over 80% of time	(?)[6,8,11,13,19]

Continuation of Table 8.1

Author	**Species**	**Housing (sample size)**	**Stimulus**	**Time exposed**	**Time used/ watched**	**Effects on behaviour (in brackets) and comments**
Shepherdson et al., 1989	*Hylobates lar*	Social (1 pair)	Gibbons' song playback	Twice daily	§	(+)[1,10] Gibbons responded with a duet, and spent more time on top of the cage
Bloomsmith et al., 1990	*P. troglodytes*	Single/ separated from social group (10)	Videotapes (chimpanzees/ humans/ other animals)	Two weeks	Mean of 42% per session	Singly-housed watched more than socially-housed which were removed from group
Washburn & Rumbaugh, 1992	*M. mulatta*	Single (10)	Computer tasks	30 days	40% of a 24-hour day	(?)[6,8,13]
Schapiro & Bloomsmith, 1995;	*M. mulatta*	Single (98)	Videotapes (primates)	4 months	§	(none) Not as effective as physical and feeding enrichment
Schapiro et al., 1995	*M. mulatta*	(64)	Videotapes (primates)	4 months	§	
Brent & Stone, 1996	*P. troglodytes*	Single/ socially (20)	Videotapes (commercial programme)	6 hours daily for 24.75 months	1.5% of total time	Data are for eight last weeks of the two years
Brent & Weaver, 1996	*Papio hamadryas anubis*	Single (4)	Music	§	§	No effect on blood pressure, mean heart rate reduced with music
Platt & Novak, 1997	*M. mulatta*	Single/ separated from group (9)	Videotapes (monkeys/ humans, familiar/ unfamiliar)	4 hours per day for 20 days	Mean of 25% per session	(?)[1,17] Males habituated to the stimulus
			Computer tasks	13 days	8%	(?)[1,5,17,19]

Continuation of Table 8.1

Author	**Species**	**Housing (sample size)**	**Stimulus**	**Time exposed**	**Time used/ watched**	**Effects on behaviour (in brackets) and comments**
Bloomsmith & Lambeth, 2000	*P. troglodytes*	Single/ Social (10)	Videotapes (chimpanzees/ humans/ other animals)	20 minutes per day	9.8-57.8% of total time	(none) Apes habituated to the stimulus
Howell et al., 2002a	*P. troglodytes*	Social (57)	Music	§	§	$(+)^{2,3,5,18}$
Kissinger & Bouwens, 2006	*Gorilla gorilla*	Social (8)	Moving lights	5x6 minutes	§	$(+)^{1,13}$ Apes preferred to stay in a room with lights

a) Number of individuals unless otherwise noted

Key to specific behavioural changes (arrows describe changes in rates when sensory stimuli were available):

1) locomotion ↑
2) aggressive behaviour ↓
3) affiliative behaviour ↑
4) play ↑
5) resting ↑
6) inactivity ↓
7) abnormal behaviour ↓
8) stereotypy ↓
9) cage manipulation ↓
10) vocalization ↑
11) foraging ↓
12) display ↑
13) autogrooming ↓
14) scratching ↓
15) aggressive behaviour ↑
16) scratching ↑
17) affiliative behaviour ↓
18) exploration ↓
19) gaze outside the cage ↓

The amount of interaction with visual stimuli is affected by different factors such as age (Brent & Stone, 1996), social setting (Bloomsmith et al., 1990; Bloomsmith & Lambeth, 2000), type of stimulus and sex (Platt & Novak, 1997). Primates did not watch video stimulation for long periods of time (Brent & Stone, 1996; Bloomsmith et al., 1990; Bloomsmith & Lambeth, 2000). However, they still used them more than they used balls and mirrors after they had had them for almost two years (Brent & Stone, 1996).

8.1.2 Effects of control over sensory stimuli on the behaviour of captive primates

In common with effects of sensory stimuli, when the effects of control over sensory stimuli have been studied, studies have revealed contradictory findings. In some experiments animals chose to manipulate devices and their behaviour was positively affected, whereas in others they hardly utilized the opportunity to operate sensory stimuli (see Table 8.2). In some cases it was difficult to separate studies in which primates were just exposed to visual stimuli from those in which they could control those stimuli. Therefore, only studies in which primates were able to operate the device and/or choose between different stimuli (in the case of computer tasks) are described below.

When primates were given control over music, the impact on their behaviour was always positive (Novak & Drewsen, 1989; Markowitz & Line, 1989; Line et al., 1990a, 1991a). However, in Line and colleagues' studies the monkeys were allowed to control music and the supply of banana-flavored pellets simultaneously, hence, it is impossible to distinguish between the effects of the two stimuli. The impact of control over visual stimuli on behaviour has not been recorded in all studies, however when the effects on behaviour have been reported the results have been ambiguous (see Table 8.2). In several studies monkeys were allowed to choose between a food reward and videotape reward (or a combination of both). In most studies the food reward was more effective than the videotapes (Washburn et al., 1997; Brannon et al., 2004).

Table 8.2: Effects of control over sensory stimuli on the behaviour of captive primates. (+)= positive effects of stimulus; (-)= negative effects of stimulus; (none) no effects on behaviour; (?)= effects of stimulus were unclear; (blank)= behavioural effects were not mentioned; (§)= information not reported. See key below the Table 8.1.

Author	**Species**	**Housing (sample size)**[a]	**Stimulus**	**Time exposed**	**Time used/ watched**	**Effects on behaviour (in brackets) and comments**
Swartz & Rosenblum, 1980	*Macaca. radiata*	Social (6)	Videotape of a conspecific	1 hour x 3-5 days	20.1-80.6% per session	Preferred conspecific over non conspecific
Novak & Drewsen, 1989	*M. mulatta*	Social (not given)	Music	2 hours daily x 4 days x 9 weeks	37-50% per day, reduced with time	(+)[3]
Line et al., 1990a	*M.mulatta*	Single (5)	Music/ (food)	20 weeks	0-168 hours per week	(+)[1,8,9,13] Cortisol levels reduced, heart rate increased
Line et al., 1991a	*M.mulatta*	Single (10)	Music/ (food)	12 weeks	A mean of 76 minutes per day	(+)[1,6,7,9,13]
Lincoln III et al., 1994	*M. nemestrina*	Social (8)	Video task	24 hours access to device	~954 trials per day (each of about 8sec) when only one unit was available	When more units were available usage increased
Washburn et al., 1997	*M. mulatta*	Single (4)	Computer task	20x6 hours	§	Preferred food reward with blank screen over food + videotapes
Harris et al., 1999	*M. mulatta*	Single (8)	Videotapes (primates/ humans)	1 hour daily x 5 days x 6 weeks	3.5-11.2 minutes per session	Only 4 monkeys showed interest

Continuation of Table 8.2

Author	**Species**	**Housing (sample size)[a]**	**Stimulus**	**Time exposed**	**Time used/ watched**	**Effects on behaviour (in brackets) and comments**
Bloomsmith et al., 2000a	*Pan troglodytes*	Social (62 in 6 groups)	Videotapes	180 hours	§	(+)[4,14]
Bloomsmith et al., 2000b	*P. troglodytes*	Social (12 in four groups)	Computer task	§	§	(?)
Baker et al., 2001	*P. troglodytes*	Social (20)	Computer task	§	§	(?) No immediate effects, under mild stress showed less scratching
Lambeth et al., 2001	*P. troglodytes*	Social (20)	Videotapes	§	§	(+)[3,4,14] In reaction to mild stress (+)[7,12,13,14]
Andrews & Rosenblum, 2001, 2002	*M. radiata*	Single (3)	Computer task	75 weeks	Rates of usage reduced when the same videotape was used	Preferred videotapes over food reward when videos included new stimuli
Brannon et al., 2004	*M. radiata*	Social (7)	Computer task	10 hours daily x 8 weeks	§	Preferred food reward, but preferred videotapes over no reward
Tarou et al., 2004	*Pongo pygmaeus*	Social (4 pairs)	Computer task	120 hours	An average of 25.9% of observed time	(?)[3,4,15,16] Females dominated devices, no habituation

a) Number of individuals unless otherwise noted

However, the content of the videotape was also important. Monkeys preferred videotapes of themselves to those of other conspecifics (Washburn et al., 1997) or vice versa (Brannon et al., 2004). In other studies, singly-housed monkeys preferred videotapes over a food reward, but it was important to vary the social content of the videotapes to maintain its incentive value at high levels for long periods (Andrews & Rosenblum, 2001, 2002). In contrast, young monkeys maintained consistently high levels of response to obtain visual access to videotapes of conspecifics, even when the stimulus was repetitive (Swartz & Rosenblum, 1980). Therefore it is possible that the age of the monkeys and/or their housing conditions may affect their reactions to sensory stimuli.

When primates are housed socially, competition over the device may negatively affect welfare (e.g. Tarou et al., 2004), and such consequences should be taken into account in the design of further studies. However, in other studies no influence of device presence on aggression levels has been found (Lincoln III et al., 1994). Rates of usage have also varied between studies. In some studies monkeys showed higher rates of device usage (Swartz & Rosenblum, 1980; Lincoln III et al., 1994; Swartz & Rosenblum, 1980) than in others (Harris et al., 1999). However, in most studies, rates of device usage reduced over time (e.g. Novak & Drewsen, 1989; Andrews & Rosenblum, 2001, 2002), and usually when high rates of usage were reported, monkeys were exposed to the stimuli for shorter durations.

In summary, findings from previous research regarding the effects of sensory stimuli and the opportunity to control them, on the behaviour of captive primates are varied. Therefore, more research is needed on the effects of sensory stimuli in general and on the ability to control sensory stimuli in particular.

8.1.3 Aims of the present study

Findings from the previous chapter showed positive effects of control over white light on the behaviour of family housed marmosets. The aim of this study was to investigate the effects of control over a different stimulus on the behaviour of family groups of common marmosets. The stimulus in the present study was a coloured light sequencer, which served as a sensory stimulus for the monkeys. A sensory stimulus was chosen as findings from previous research regarding the effects of sensory stimuli in general, and the effects of control over them in particular, on the behaviour of captive primates are contradictory. From among all types of sensory stimuli, the visual stimulus was chosen as its impact could remain localised. That is to say, in a colony room that contains several separate groups of monkeys, auditory or olfactory stimuli could affect other individuals, which have no control over them. The light sequencer was chosen as a visual stimulus, as it affected the whole cage (or at least the lower part of it). In previous research where monkeys or apes could control television sets (e.g. Washburn et al., 1997; Andrews & Rosenblum, 2002; Bloomsmith et al., 2000a), or computers (e.g. Washburn et al., 1991; Bloomsmith et al., 2000b; Tarou et al., 2004), the controllable devices were located out of the animals' cage and did not affect the immediate home environment. In the present experiment, the coloured lights were reflected inside the cage, and hence affected the home environment of the monkeys.

The following questions were asked:

1) How does the exposure to visual stimulus affect the welfare of captive common marmosets?
2) How does the opportunity to control coloured lights affect the welfare of the marmosets?
3) How does loss of control affect the welfare of the monkeys?

8.2 METHODS

8.2.1 Study animals and housing

The study animals were 44 common marmosets housed in twelve small family groups in double cages. Each group contained three to five marmosets, which included one or two adults (mother, father, or both), and one to three youngsters. Six groups served as Master groups, while the other six groups served as Unaffected groups. No significant differences were found between Master and Unaffected groups in terms of total number of individuals per group (t=0.725; P=0.485), number of adults per group (t=-0.542; P=0.599), or number of youngsters per group (t=1.464; P= 0.174). There were no significant differences between Master and Unaffected groups in mean age of adults or youngsters. Mean age of adults in Master groups was 1466 days (±SE 172 days; n=8), and 1794 days (±SE 317 days; n=10) for adults in Unaffected groups (t= 2.18; P= 0.16). Mean age of youngsters in Master groups was 223 days (±SE 23 days; n=15), and 198 (±SE 23 days; n=11) for youngsters in Unaffected groups (t= 0.04 P= 0.84). Further details regarding study groups and animals are presented in Table 8.3.

8.2.2 Experimental design

The twelve groups in this study were housed in three colony rooms. Each room housed two Master groups and two Unaffected groups. The study protocol was the same as in Chapter 7 (see Table 7.2). The study was divided into three phases: Baseline (days 1-4), Test phase (days 5-22), and Post-test phase (days 23-27). The study groups were divided to two conditions: Master and Unaffected. For Unaffected groups no manipulation was applied in any phase of the study, while a controllable coloured light sequencer was hung on the cages of Master groups on the morning of the fifth day of the study (first day of Test phase). The same device as in Chapter 7 was used; the only difference between the previous and the current devices was that the white light bulb was replaced by a coloured light sequencer, which contained lights in six different colours (see Plates 8.1 and 8.2). When the sequencer was activated, two different lights were on simultaneously and every five seconds the two lights were changed automatically, giving the sensation of moving lights. The device was removed on the morning of the 23rd day of the study, when the Post-test phase began.

8.2.3 Data collection

During the Baseline phase of the study, each monkey was observed three times for four minutes (total observation time of 4 hours and 36 minutes for Master groups and 4 hours and 12 minutes for Unaffected groups). Each focal animal was observed ten times during the Test phase (total observation time of 15 hours and 18 minutes for Master groups and 14 hours for Unaffected groups), and three times during the Post-test phase (total observation time of 4 hours and 36 minutes for Master groups and 4 hours and 12 minutes for Unaffected groups). All other details of data collection were the same as in Chapter 7.

Table 8.3: Group and individual details (sex, date of birth (D.O.B), age on first day of the study)

Group type	**Group identifier**	**Individual**	**D.O.B.**	**Age (in days)**
Master	3-1Ra	14W (adult ♀)	02/02/2000	1545
		♀♂	20/07/2003	281
		♀	27/11/2003	151
	3-1Rb	21W (adult ♀)	28/11/2000	1245
		867BK (adult ♂)	29/04/1999	1824
		♂♂	10/07/2003	291
		♂	20/2/2004	66
	4-3Rb	982BK (adult ♂)	09/11/2001	872
		♀♂	13/7/2003	213
	4-4Ra	37Y (adult ♀)	02/09/2000	1305
		901BK (adult ♂)	21/03/2000	1470
		♂	27/06/2003	277
		♂	25/06/2003	279
		♀	07/11/2003	144
	1-1Ra	850R (adult ♀)	10/10/1997	2418
		♀♂	08/09/2003	259
	1-1Rb	85Y (adult ♀)	10/07/2001	1049
		♂♂	15/08/2003	283
Unaffected	3-4Ra	685R (adult ♀)	15/06/1993	3968
		♀♂	22/01/2004	95
	3-3Lb	868BK (adult ♂)	29/04/1999	1824
		94Y (adult ♀)	13/09/2001	956
		♀	19/08/2003	251
		♂	20/08/2003	250
	4-1Ra	70BL (adult ♀)	26/06/1995	3200
		♀♂	23/06/2003	281
	4-2Ra	55Y (adult ♀)	02/01/2001	1183
		943BK (adult ♂)	05/02/2001	1149
		♀♂	20/11/2003	131
	1-2Ra	12W (adult ♀)	11/01/2000	1595
		5BB (adult ♂)	15/01/2000	1591
		♀♀	26/12/2003	150
	1-4Ra	1Y (adult ♀)	28/02/2000	1547
		979BK (adult ♂)	07/11/2001	929
		♀	02/08/2003	296

Plate 8.1: Coloured lights sequencer

Plate 8.2: Two double cages with an activated coloured light sequencer

8.2.4 Statistical analysis

Different statistical analyses were carried out to examine the effects of coloured lights and control on the behaviour of adult and young marmosets (see Table 8.4). In order to measure the percentage time and frequency of light usage, means were calculated for each Master group. In addition, measurements of device usage were calculated for three periods (first 4, middle 10 and last 4 days) during the Test phase in order to examine habituation.

Table 8.4: Statistical analyses used in the present study

Research question	Statistical test	Factors	Levels	Analysis
Habituation to device (percentage time on)	One-way ANOVA	Period	first 4 days/ middle/ last 4 days	Within subjects
Habituation to device (frequency of button touches)	One-way ANOVA	Period	first 4 days/ middle/ last 4 days	Within subjects
Effects of light condition on adults	Paired samples t-test	Light condition	On/off	Within subjects
Effects of light condition on youngsters	Paired samples t-test	Light condition	On/off	Within subjects
Effects of control on adults	Two-way ANOVA with mixed design	Study phase	Base/Test/Post	Within subjects
		Study condition	Master/Unaffected	Between subjects
Effects of control on youngsters	Two-way ANOVA with mixed design	Study phase	Base/Test/Post	Within subjects
		Study condition	Master/Unaffected	Between subjects

8.3 RESULTS

The results of the present study include several factors:

1) Amount of device usage
2) Effects of visual stimuli on the behaviour of captive common marmosets
3) Effects of control over visual stimuli on behaviour
4) Effects of loss of control

8.3.1 Measures of coloured lights usage

All Master groups used the device, however, not constantly and only for relatively low percentages of total time (see Tables 8.4 and 8.5). Further, there was no consistency in the usage pattern for any group (see Figure 8.1). Marmosets used the device throughout the whole Test phase and showed no habituation to it. No significant differences were found in percentage time the light was on between the three periods of the Test phase; however, a significant main effect of study period was found for frequencies of device usage ($F_{2,10}$=9.04, P=0.006). Results of post-hoc tests show that frequencies of device usage were significantly higher during the first four days of the study compared to the middle period of the Test phase (t=-3.93, P=0.007) and the last four days of the phase (t=-3.37, P=0.02). No significant difference was found between the middle and the last periods of the Test phase.

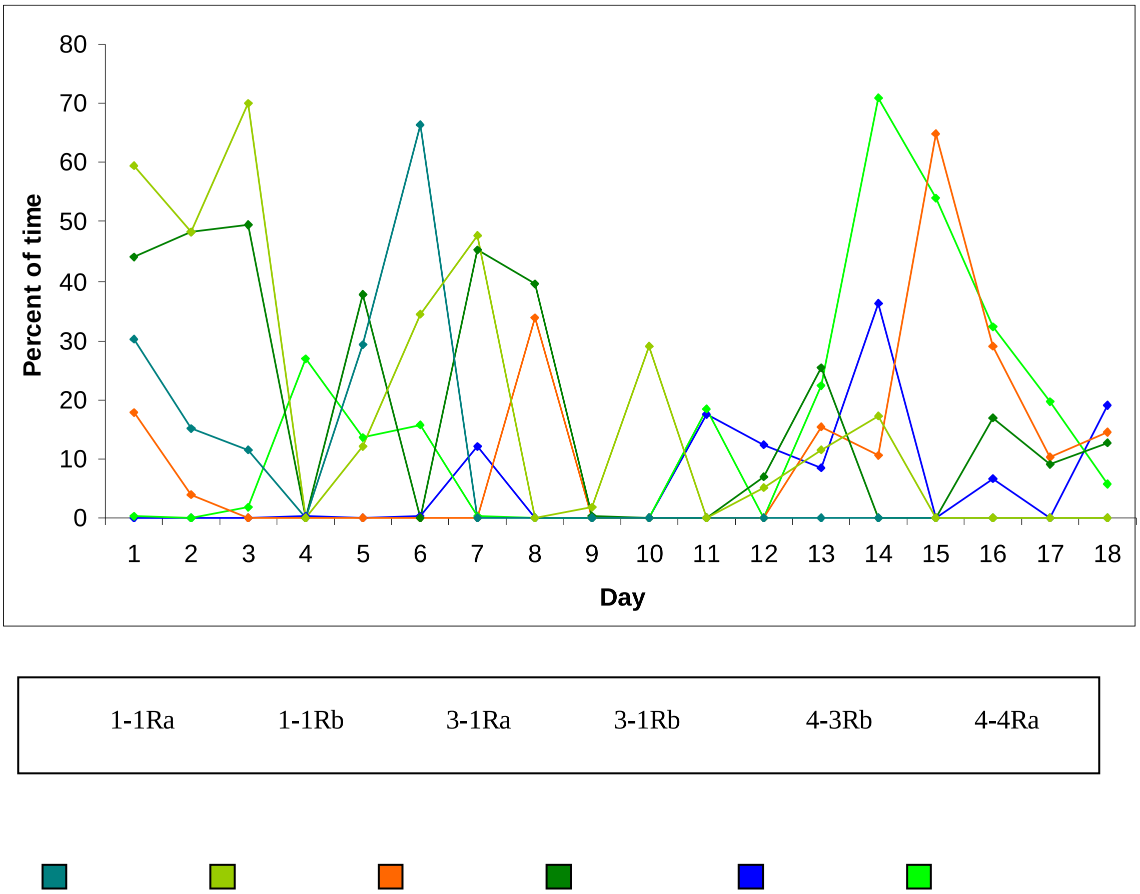
Table 8.4: Mean (±S.E.) percentage time per day of device usage in six Master groups, during the Test phase

	1-1Ra	1-1Rb	3-1Ra	3-1Rb	4-3Rb	4-4Ra
All Test phase	8.5±4.2	18.7±5.6	11.1±4	18.7±4.7	6.3±2.4	15.7±4.8
First 4 days	0.04±0.04	7.2±6.6	5.4±4.2	35.5±11.9	14.2±6.3	44.5±15.5
Middle period	8.7±3.7	14.1±6.9	6±3.6	15.5±6.1	9.6±6.9	15.9±5.2
Last 4 days	6.4±4.5	27.9±10.3	29.6±12.4	9.7±3.6	0	0

Table 8.5: Mean (±S.E.) frequency per day of device usage in six Master groups, during the Test phase

	1-1Ra	1-1Rb	3-1Ra	3-1Rb	4-3Rb	4-4Ra
All Test phase	0.44±0.2	0.78±0.2	1.06±0.3	1.11±0.4	0.94±0.6	0.83±0.3
First 4 days	3±2.3	1.5±0.6	1.8±1.4	2.3±1.6	1.5±0.6	1.3±0.5
Middle period	0.3±0.2	0.2±0.1	0.7±0.2	0.8±0.2	0.2±0.1	0.9±0.2
Last 4 days	0.5±0.3	1.8±0.5	1.3±0.3	0.8±0.3	0	0

Figure 8.1: Percentage time light usage for six Master groups during the Test phase of the study



8.3.2 Effects of coloured lights on behaviour

Although marmosets did not activate the coloured light sequencer for high percentages of the time that it was available, they were affected by it when it was on. Only five out of the six Master groups were used for the analysis of the effects of the visual stimulus on behaviour, since the device was off during all the observation sessions of group 1-1Ra (although data show that marmosets in this group activated the device during non observation periods).

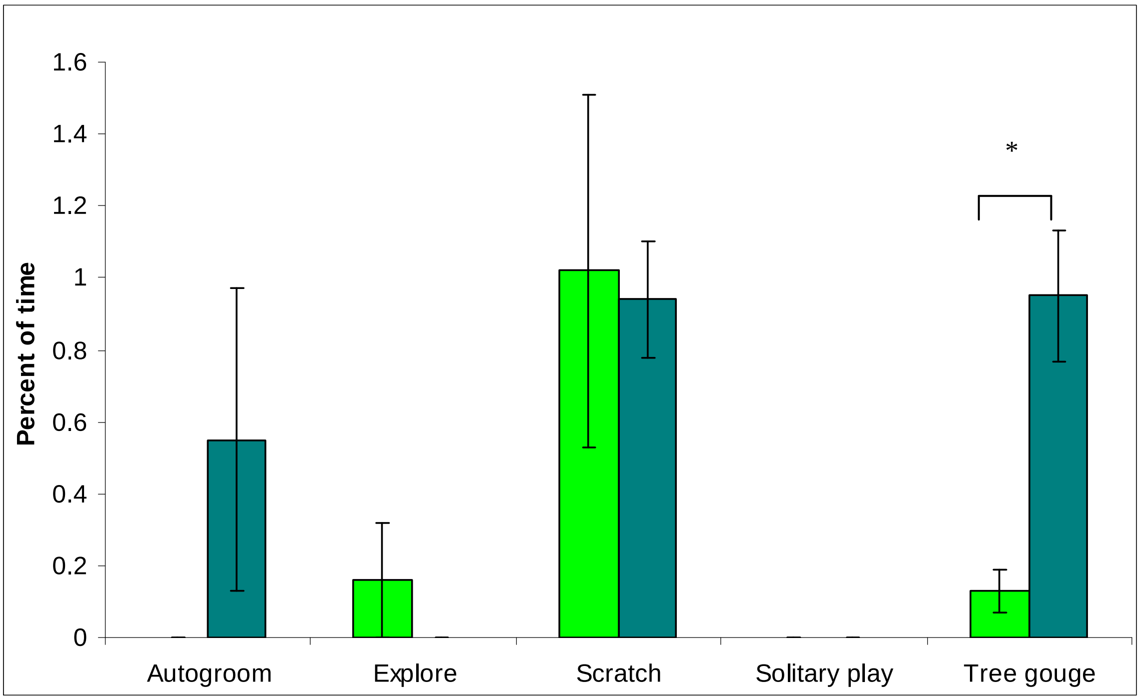
The impact of the visual stimulus on youngsters was greater than its impact on adults. Adults spent significantly more time in the upper part of the cage when the device was off. Further, they engaged in tree gouging behaviour significantly more when the device was off (see Table 8.6 and Figure 8.2 a, b, c and d). Youngsters spent significantly less time in the upper part of the cage and more time in the lower part of the cage when the device was on. Further, they spent significantly more time scratching themselves, watching the observer and inactive alert and less time in calm locomotion when the lights were off. Youngsters also spent more time manipulating the device and looking at it (or at the reflected lights) when the device was on (see Table 8.6 and Figure 8.3 a, b, c and d).

Table 8.6: Results of ANOVAs for effects of coloured lights on behaviour and cage locations of adults and youngsters (*P<0.05)

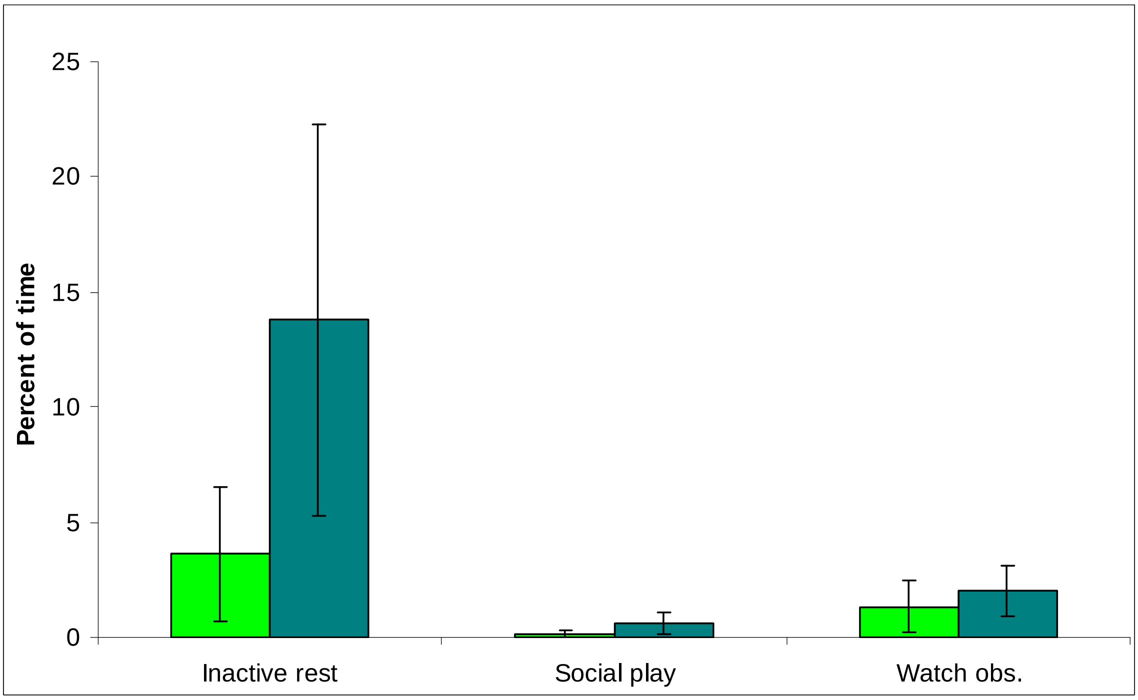
	Adults	**Adults**	**Youngsters**	**Youngsters**
	t	**P**	**t**	**P**
Agitated locomotion	-1.85	0.139	-1.75	0.155
Allogroom	-1.14	0.318	0.99	0.377
Autogroom	-1.31	0.260	0.64	0.559
Calm locomotion	2.63	0.058	2.96	0.042*
Contact	-1.20	0.295	-1.60	0.185
Explore	1	0.374	1.54	0.199
Inactive alert	-.034	0.748	-3.02	0.039*
Inactive rest	-1.03	0.359	-2.36	0.078
Scent mark	0.68	0.532	-0.59	0.585
Scratch	0.21	0.844	-3.90	0.018*
Social play	-0.95	0.394	-0.33	0.760
Solitary play	no data	no data	0.29	0.787
Tree gouge	-4.38	0.012*	-0.69	0.528
Watch observer	-0.40	0.707	-3.91	0.042*
Lower	2.31	0.082	3.25	0.031*
Upper	-5.53	0.005**	-3.98	0.016*
Close to device	1.19	0.299	1.69	0.167
Look at the device	1.33	0.256	3.82	0.019*
Manipulate device	1	0.374	3.35	0.029*

Figure 8.2: Mean percentage time (±SE bars) spent in behaviours and cage locations for adults in Master groups when the lights were on and off (*P<0.05; **P<0.01)

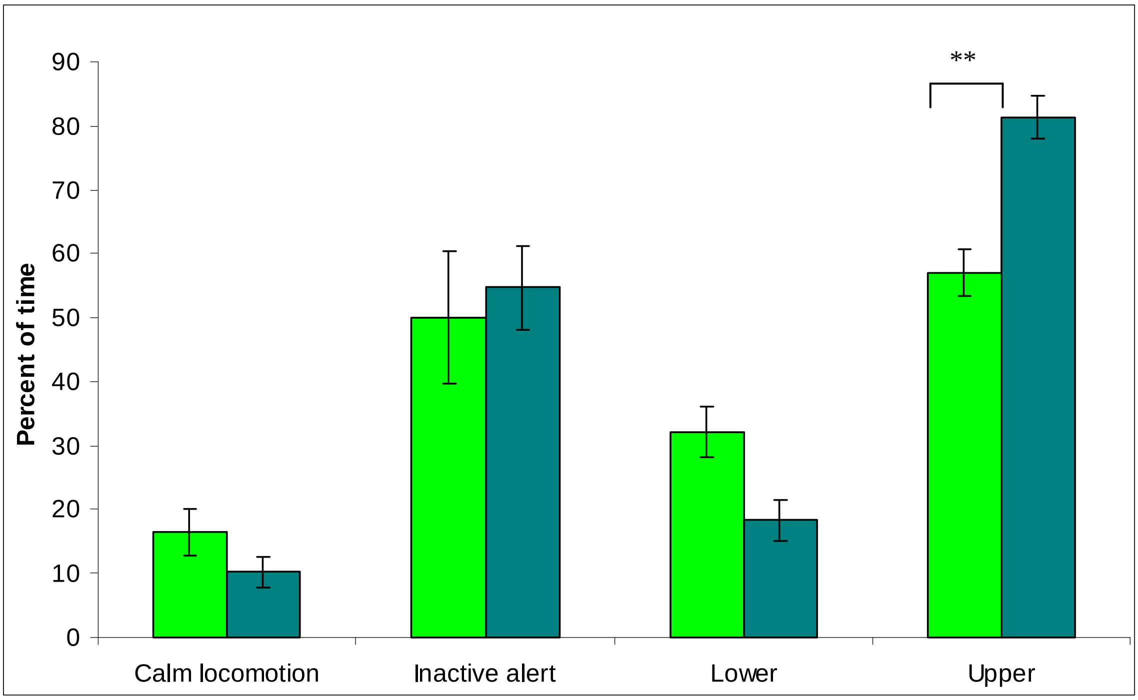
a.



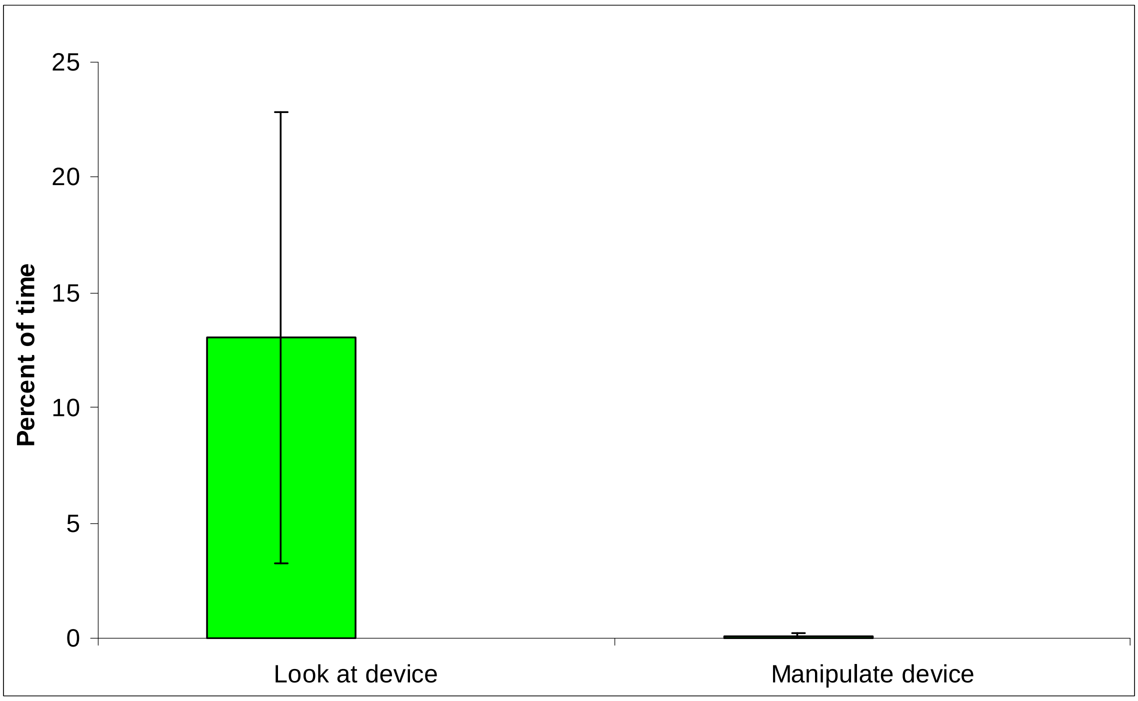
b.



c.



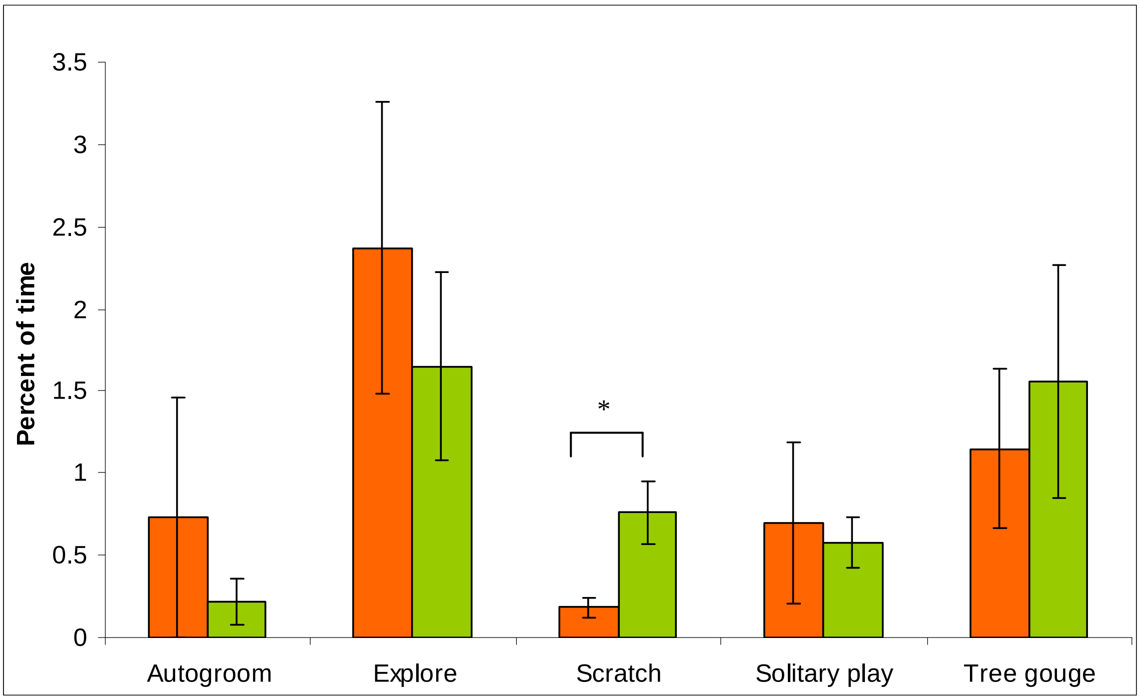
d.



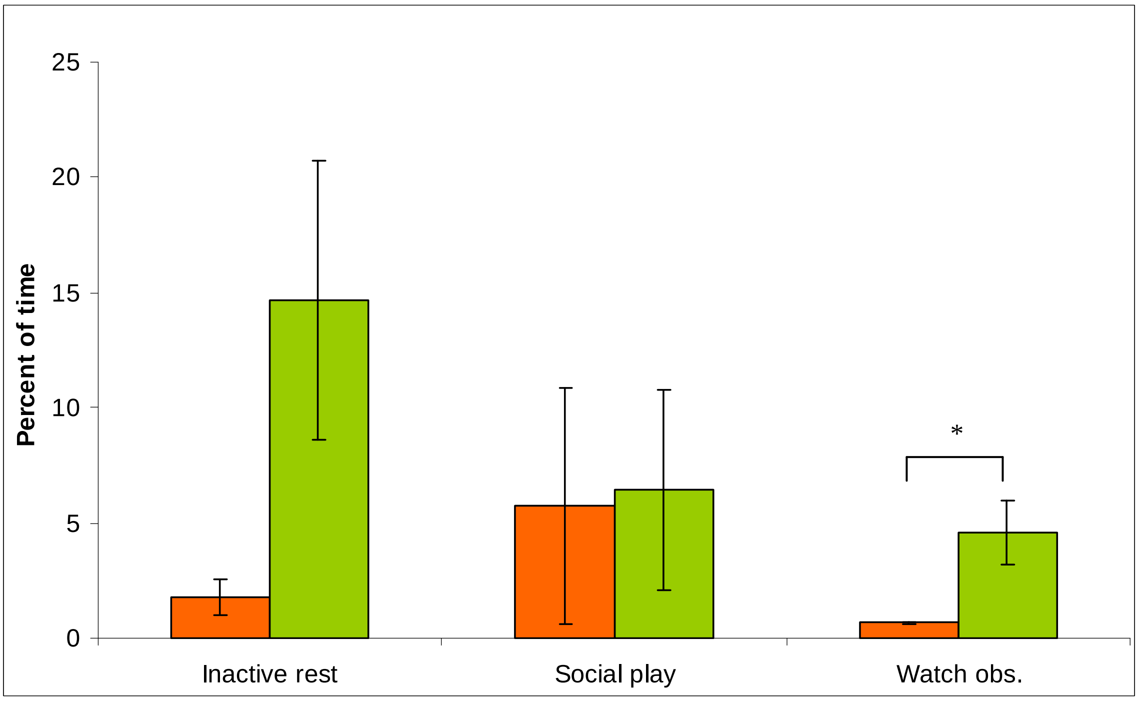
🟩 Light on 🟦 Light off

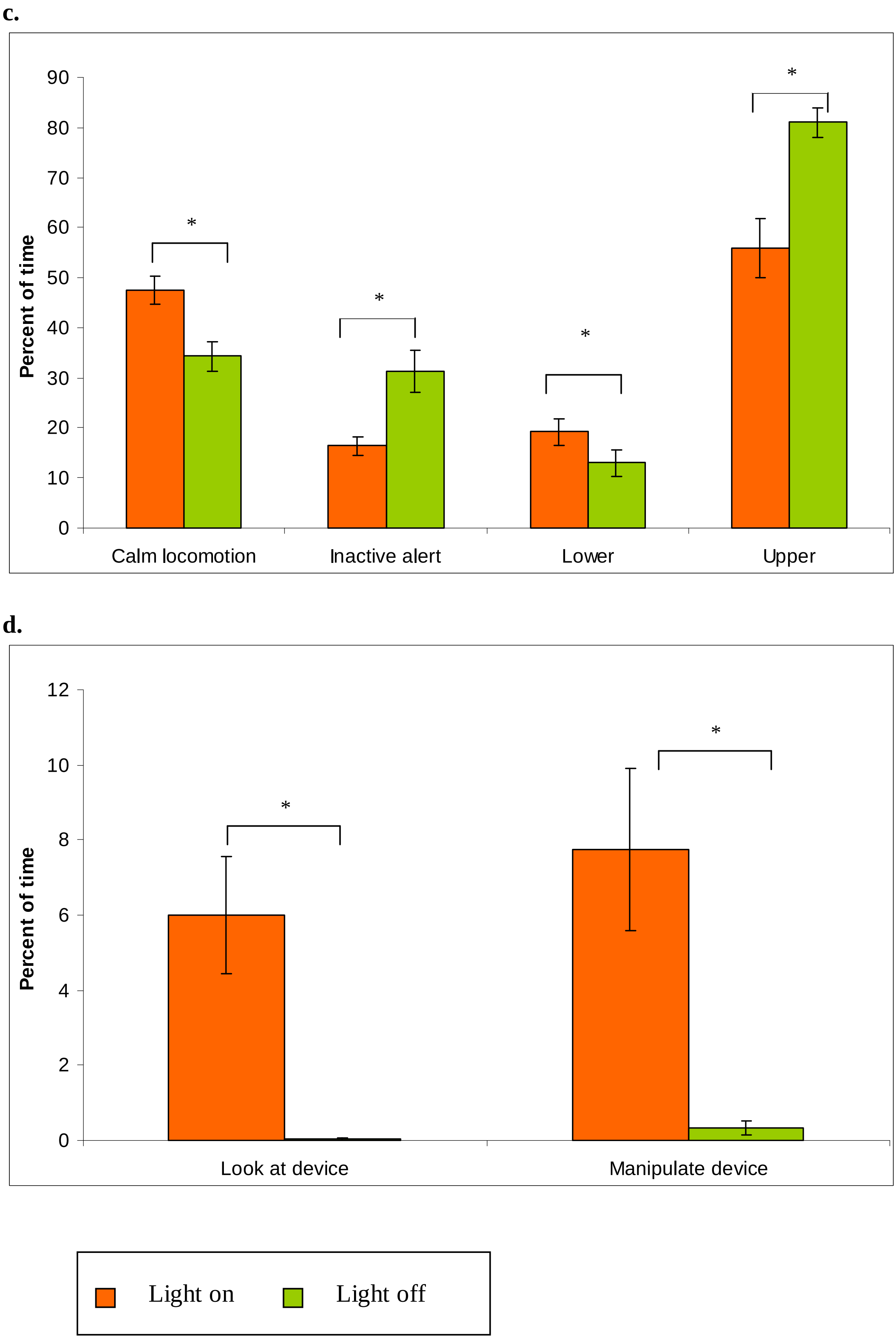
Figure 8.3: Mean percentage time (±SE bars) spent in behaviours and cage locations for youngsters in Master groups when the lights were on and off (*P<0.05)

a.



b.





8.3.3 Effects of control over coloured lights on behaviour

The effects of controllability were explored using two-way ANOVAs. Three results might indicate an effect of control: behavioural differences between the study groups during the Test phase, differences between the study phases in the behaviour of Master individuals, and interactions between study groups and study phases.

8.3.3.1 Differences between Master and Unaffected groups during the Test phase

Although there were only two groups in the study, Tukey post-hoc tests were applied whenever a significant main effect of study group was found in order to examine whether this difference resulted from differences during the Test phase (only results of post-hoc tests are presented in figures). Results show that adults in Master groups spent significantly more time in calm locomotion than adults in Unaffected groups during the Test phase (t=-3.39, P=0.03). Tukey post-hoc tests were carried out for calm locomotion since significant interaction between study group and study phase was found for this behaviour ($F_{2,20}$=3.91, P=0.037; see Table 8.7 and Figure 8.4 a, b and c).

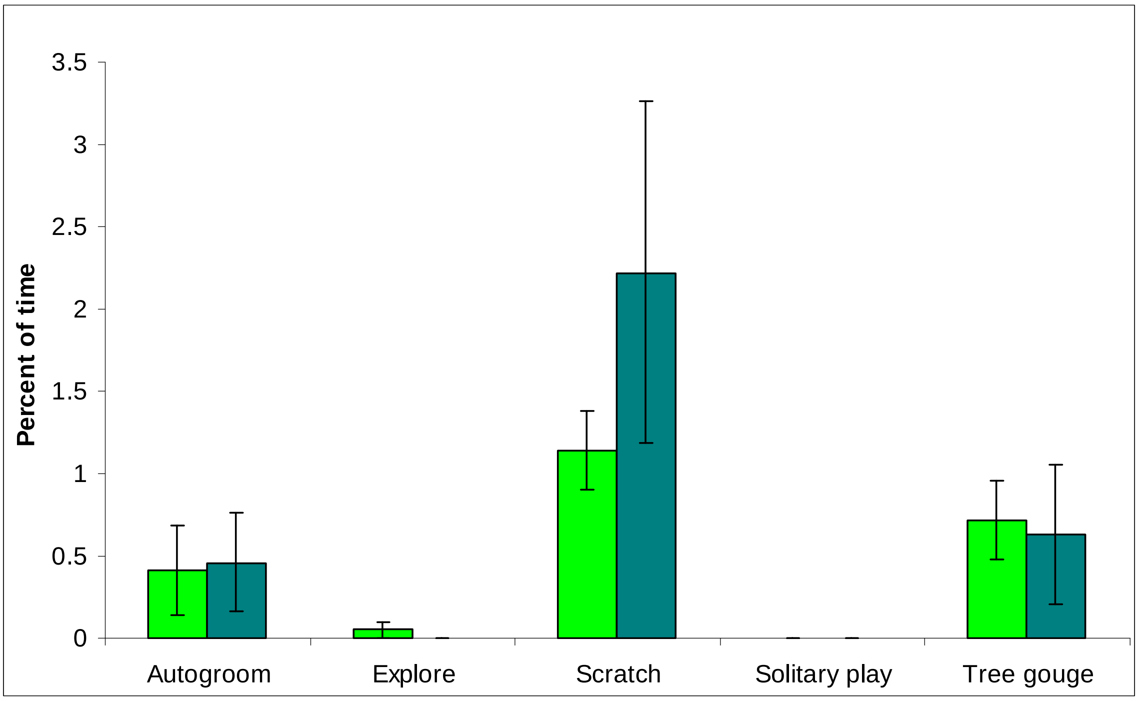
Table 8.7: Results of ANOVAs for effects of study condition on behaviour and cage locations of adults and youngsters (*P<0.05; **P<0.01; ***P<0.001)

	Adults	**Adults**	**Youngsters**	**Youngsters**
	d.f.=1,10		d.f.=1,10	
	F	**P**	**F**	**P**
Agitated locomotion	1.93	0.195	0.53	0.484
Allogroom	0.01	0.929	0.02	0.890
Autogroom	0	0.953	1.61	0.233
Calm locomotion	1.35	0.272	2.72	0.130
Contact	0.66	0.434	0.12	0.741
Explore	1.45	0.257	5.91	0.035*
Inactive alert	0.02	0.985	0.93	0.357
Inactive rest	2.02	0.185	0.84	0.382
Scent mark	0.98	0.345	0.24	0.635
Scratch	3.32	0.098	1.87	0.201
Social play	2.03	0.185	4.99	0.050*
Solitary play	no data	no data	2.98	0.115
Tree gouge	1.31	0.279	0.02	0.884
Watch observer	0.15	0.705	6.20	0.032*
Lower	0.50	0.494	0.44	0.521
Upper	3.54	0.089	1.66	0.227

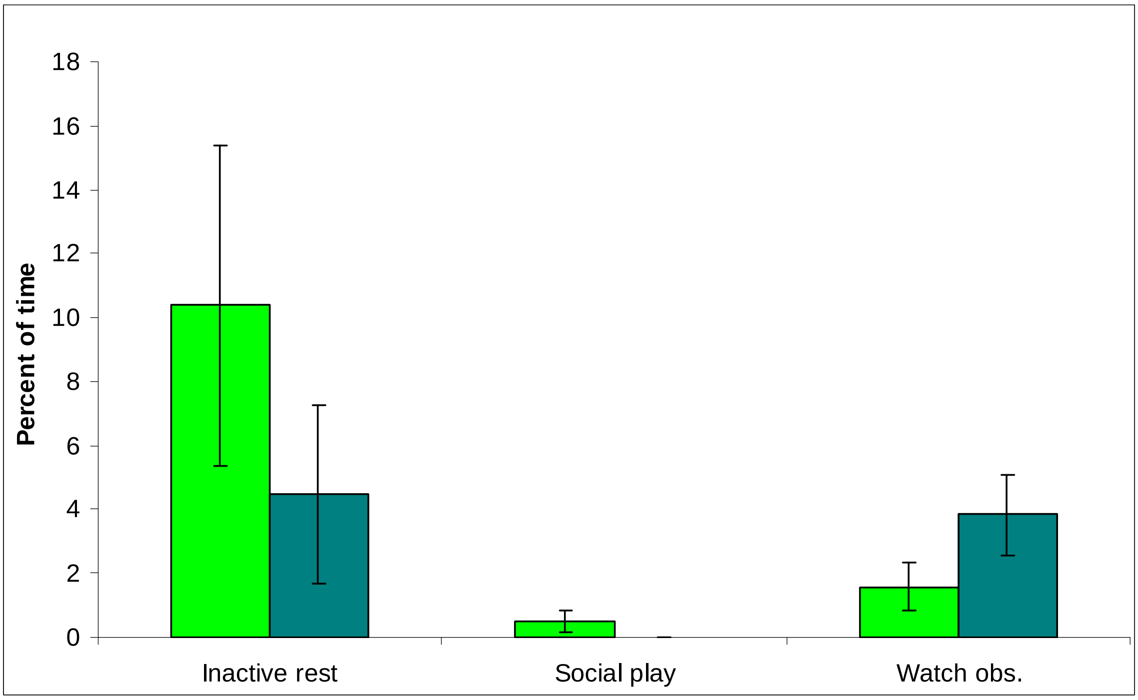
Youngsters in Master groups showed significantly higher levels of social and solitary play than youngsters in Unaffected groups. Further, they watched the observer less and showed lower levels of inactive alert behaviour. Although a significant main effect of study group was found for exploratory behaviour, post-hoc tests revealed no significant differences between the study groups during the Test phase (see Tables 8.7 and 8.8 and Figure 8.5 a, b and c).

Figure 8.4: Mean percentage time (±SE bars) spent in behaviours and cage locations for adults in Master and Unaffected groups during the Test phase (*P<0.05)

a.



b.



c.

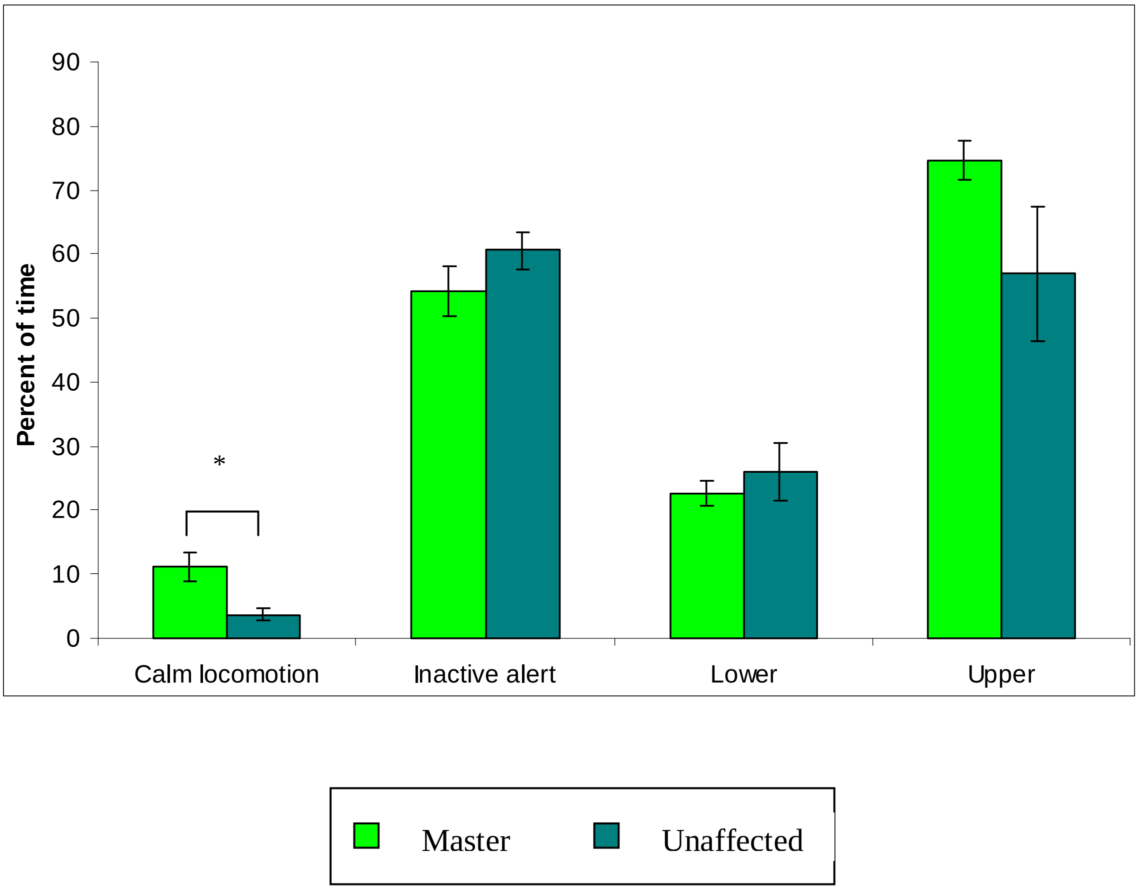
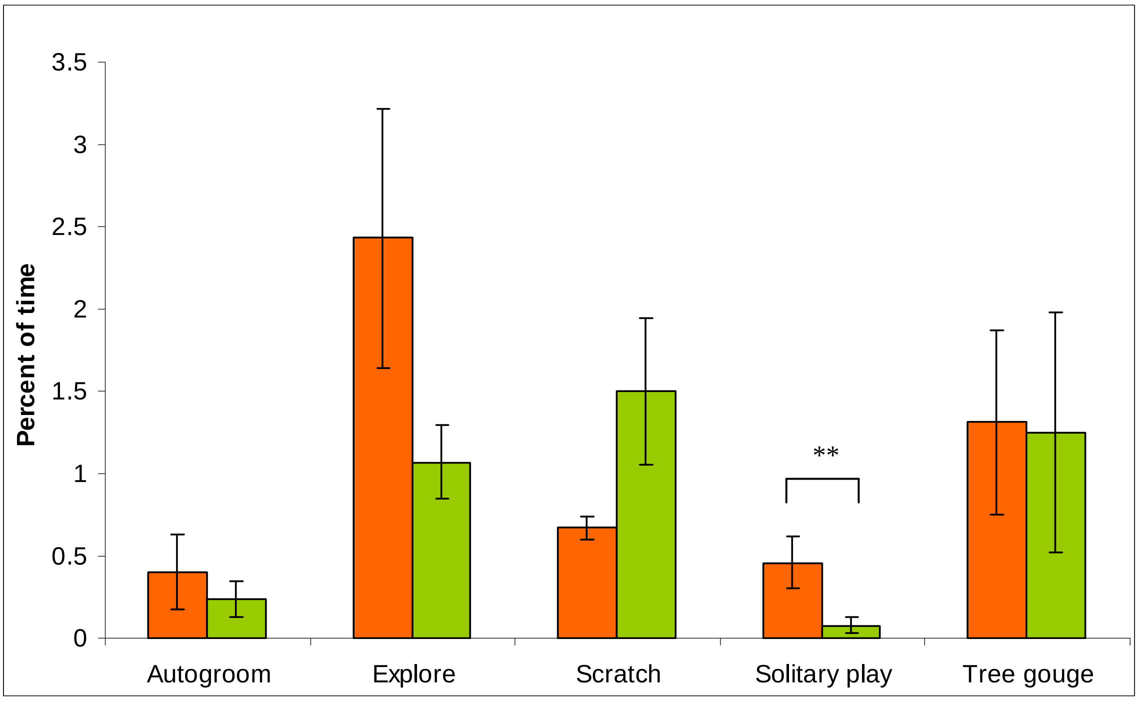


Table 8.8: Results of Tukey post-hoc tests for effects of study condition on behaviour of youngsters during the test phase (*P<0.05; **P<0.01)

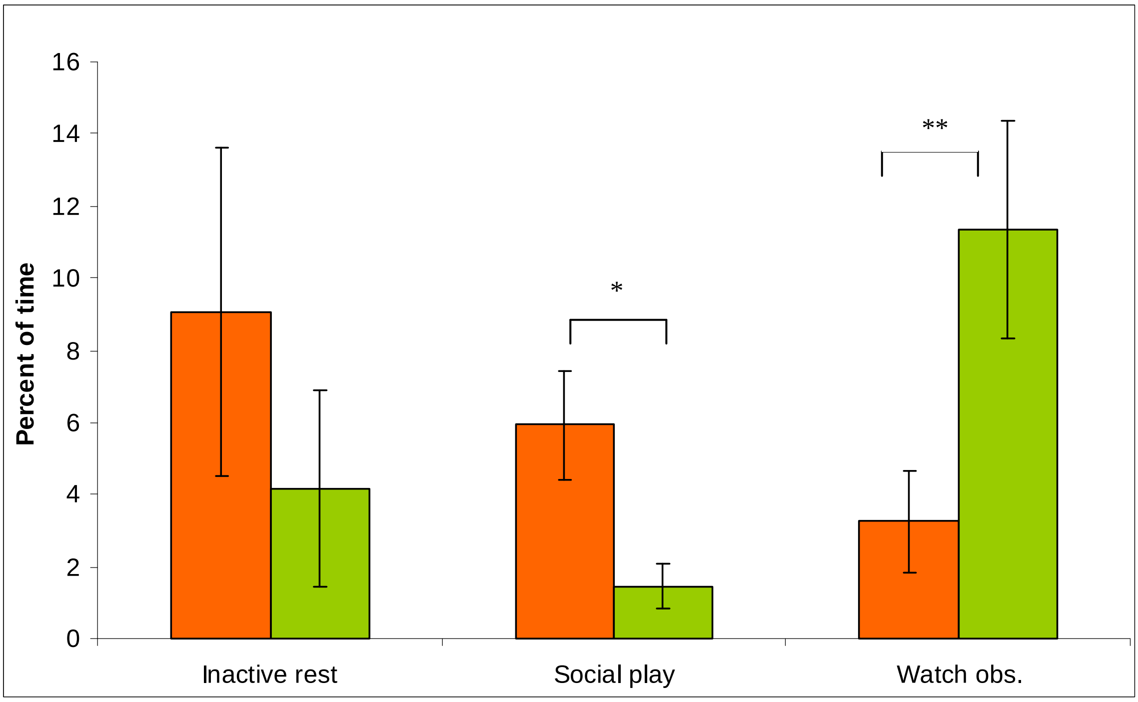
	t	**P**
Explore	-1.93	0.415
Inactive alert	3.13	0.052*
Social play	-3.16	0.049*
Solitary play	-4.10	0.006**
Watch observer	4.17	0.005**

Figure 8.5: Mean percentage time (±SE bars) spent in behaviours and cage locations for youngsters in Master and Unaffected groups during the Test phase (*P<0.05; **P<0.01]

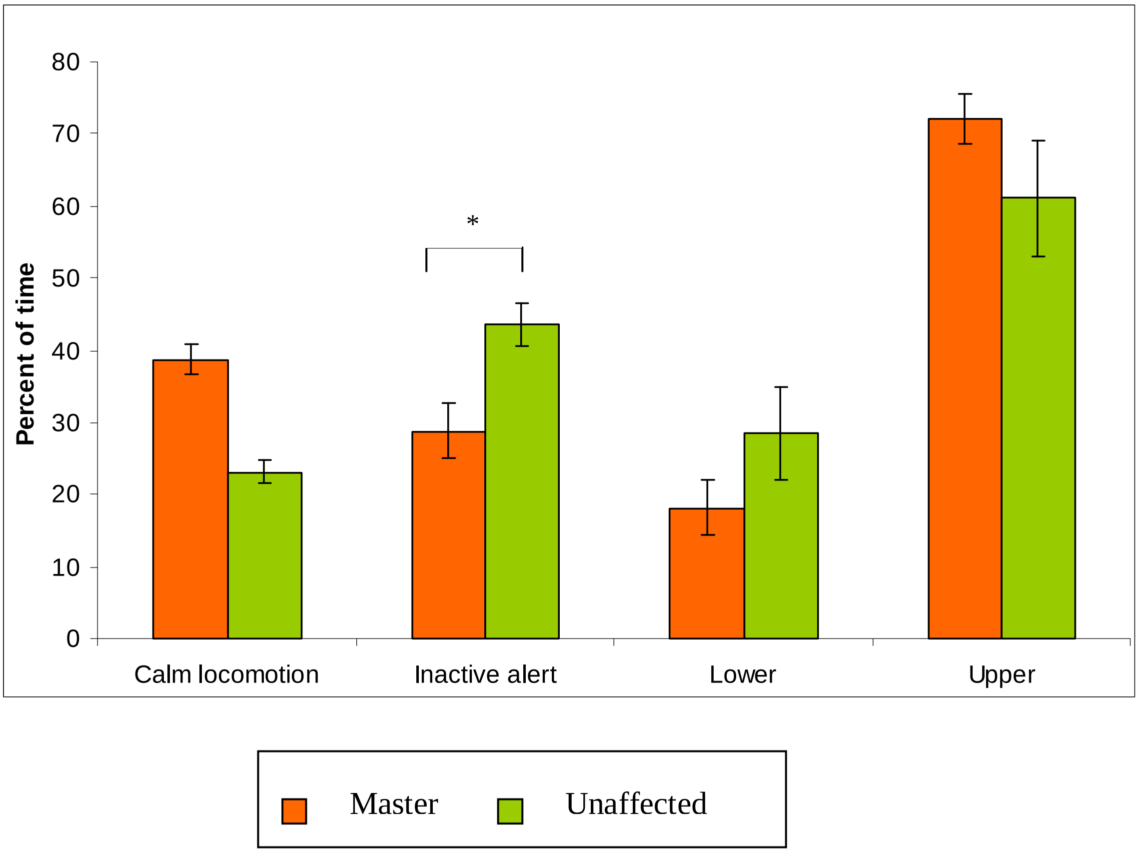
a.



b.



c.



8.3.3.2 Effects of study phase on behaviour for Master groups

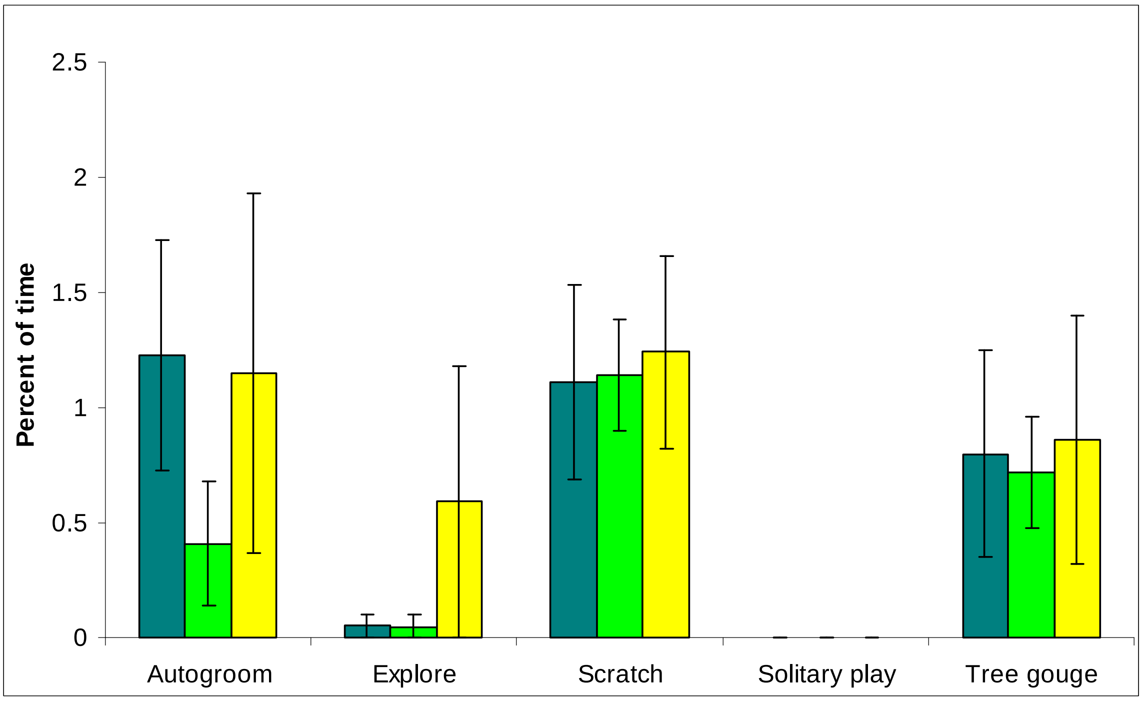
Another method used to investigate the effects of controllability was to compare the data from the three study phases. Results of ANOVAs for adults showed a significant main effect of study phase in inactive rest. However, no significant differences between study phases were found in post-hoc tests (see Table 8.9 and Figure 8.6 a, b and c).

Table 8.9: Results of ANOVAs for effects of study phase on behaviour and cage locations of adults and youngsters (*P<0.05; **P<0.01; ***P<0.001)

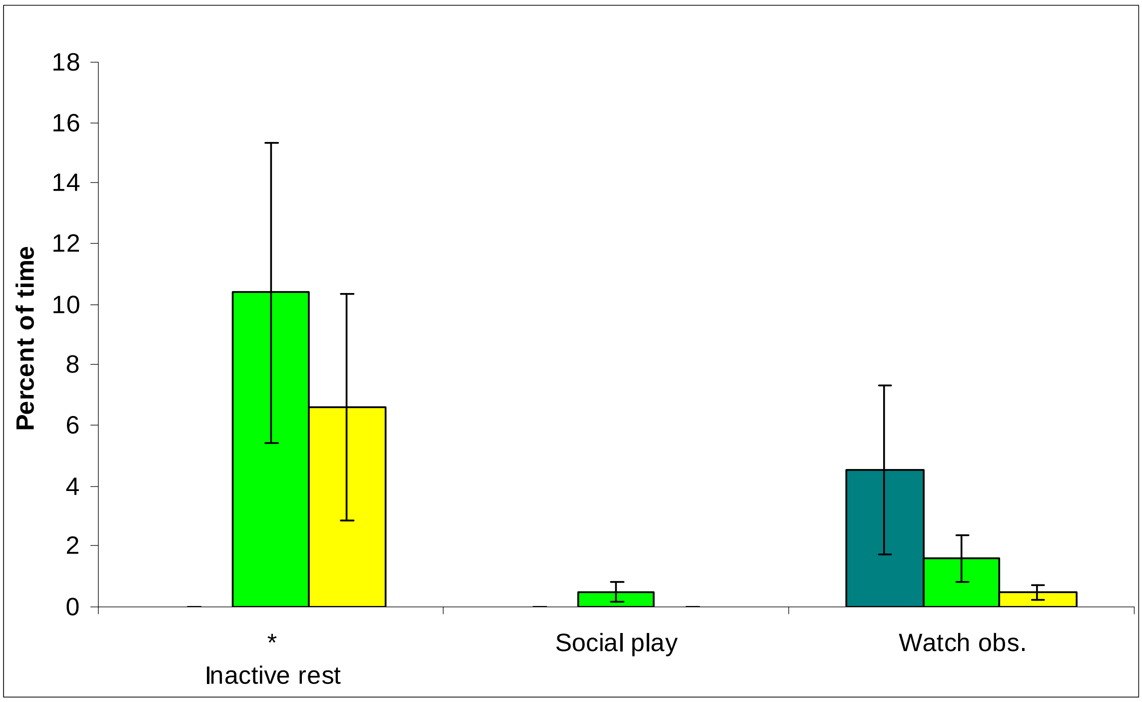
	Adults d.f.=2,20	**Adults**	**Young** d.f.=2,20	**Young**
	F	**P**	**F**	**P**
Agitated locomotion	2.28	0.128	1.40	0.270
Allogroom	1.49	0.249	0.14	0.873
Autogroom	1.11	0.350	4.20	0.030*
Calm locomotion	0.43	0.657	1.12	0.345
Contact	0.01	0.987	2.07	0.153
Explore	0.79	0.465	2.33	0.123
Inactive alert	2.07	0.153	2.67	0.094
Inactive rest	4.25	0.029*	2.23	0.133
Scent mark	1.63	0.222	0.95	0.403
Scratch	1.06	0.366	0.76	0.480
Social play	2.03	0.158	6.62	0.006**
Solitary play	no data	no data	7.92	0.003**
Tree gouge	0.22	0.804	1.63	0.220
Watch observer	3.18	0.063	31.89	<0.001***
Lower	1.87	0.181	0.66	0.530
Upper	1.49	0.249	0.24	0.786

Figure 8.6: Mean percentage time (±SE bars) spent in behaviours and cage locations for adults in three study phases (*P<0.05)

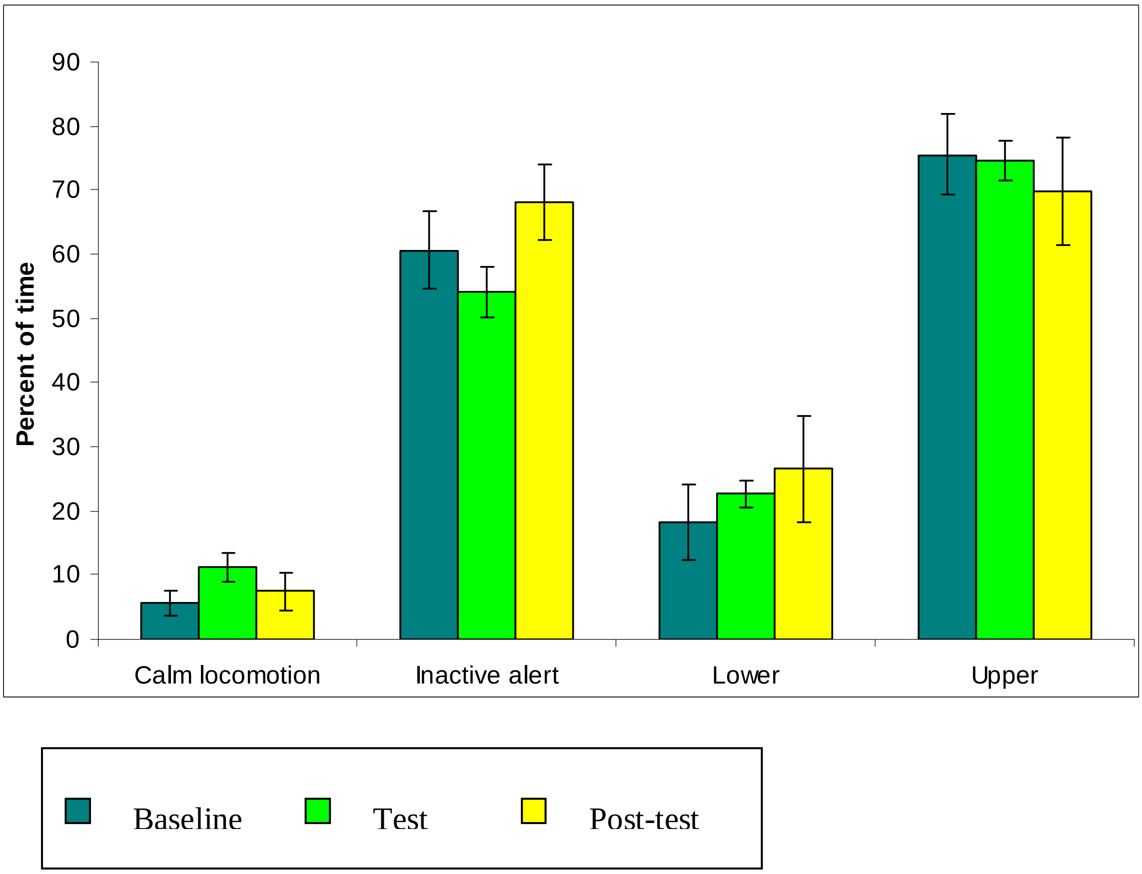
a.



b.



c.



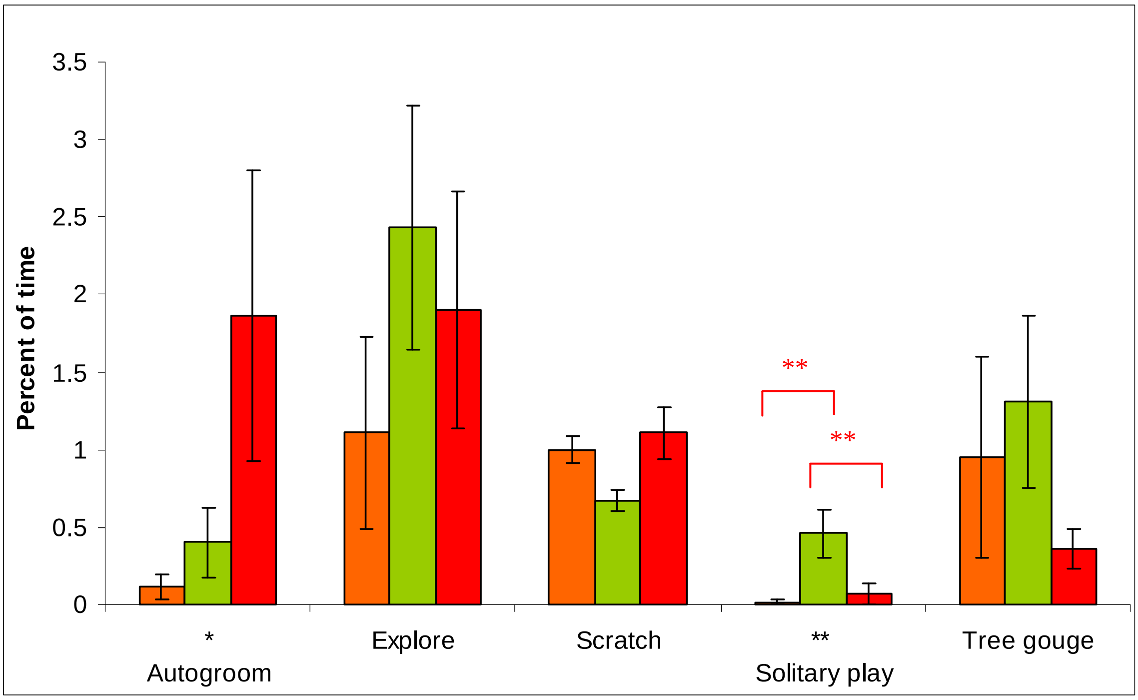
For youngsters, significant main effects of study phase was found in autogrooming, social and solitary play and for time youngsters watched the observer (see Table 8.9 and Figure 8.7 a, b and c). Tukey post-hoc tests showed that youngsters spent significantly more time in solitary play and less time in inactive alert (checked due to a significant interaction between study group and study phase) during the Test phase compared to the other two phases. In addition, they watched the observer significantly more, and engaged in social play less during the Baseline phase compared to both Test and Post-test phases (see Table 8.9 and 8.10 and Figure 8.7 a, b and c).

Table 8.10: Results of Tukey post-hoc tests for effects of study phase on behaviour of youngsters in Master groups (*P<0.05; **P<0.01)

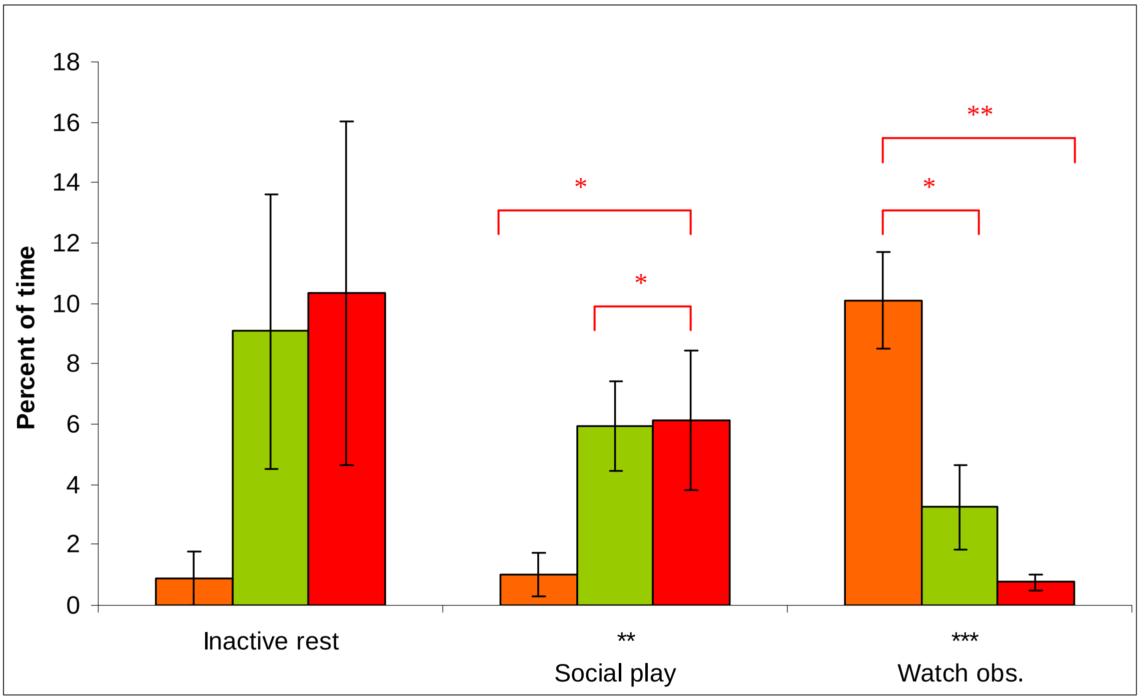
	Baseline	**vs. Test**	**Post-test**	**vs. Test**	**Baseline vs.**	**Post-test**
	t	**P**	**t**	**P**	**t**	**P**
Autogroom	0.47	0.997	-2.45	0.19	2.92	0.078
Inactive alert	-3.36	0.032*	-3.15	0.049*	-0.21	0.999
Social play	3.48	0.025*	-0.14	1.00	-3.16	0.049*
Solitary play	4.74	0.002**	4.14	0.006**	0.61	0.989
Watch observer	-3.53	0.022*	1.28	0.791	-4.81	0.002**

Figure 8.7: Mean percentage time (±SE bars) spent in behaviours and cage locations for youngsters in three study phases [one-way ANOVA with repeated measures (black marks) and Tukey post-hoc tests (red marks) *P<0.05; **P<0.01]

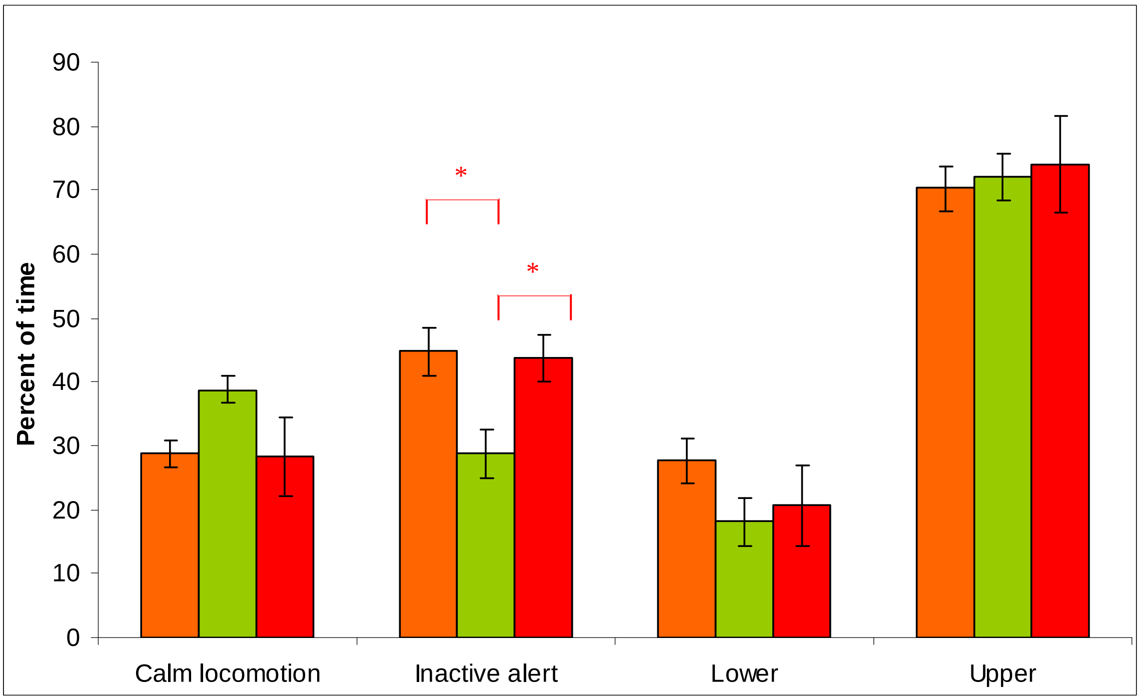
a.



b.



c.



🟧 Baseline 🟩 Test 🟥 Post-test

8.3.3.3 Interaction between study groups and phases

Interactions between study conditions and phases were found for adults in calm locomotion (see Table 8.11 and Figure 8.8). For youngsters significant interactions were found in inactive alert and solitary play (see Table 8.11 and Figure 8.9 a and b). All significant interactions resulted from differences between study phases that were shown for marmosets in Master groups (although only for youngsters were those differences significant), while levels of these behaviours were barely changed for marmosets in Unaffected groups.

Table 8.11: Results of ANOVAs for interactions between study groups and study phases
(*P<0.05)

	$F_{2,20}$	**P**
ADULTS		
Calm locomotion	3.91	0.037*
YOUNGSTERS		
Inactive alert	4.59	0.023*
Solitary play	5.53	0.012*

Figure 8.8: Interaction between study group and study phase for adults

a. Calm locomotion

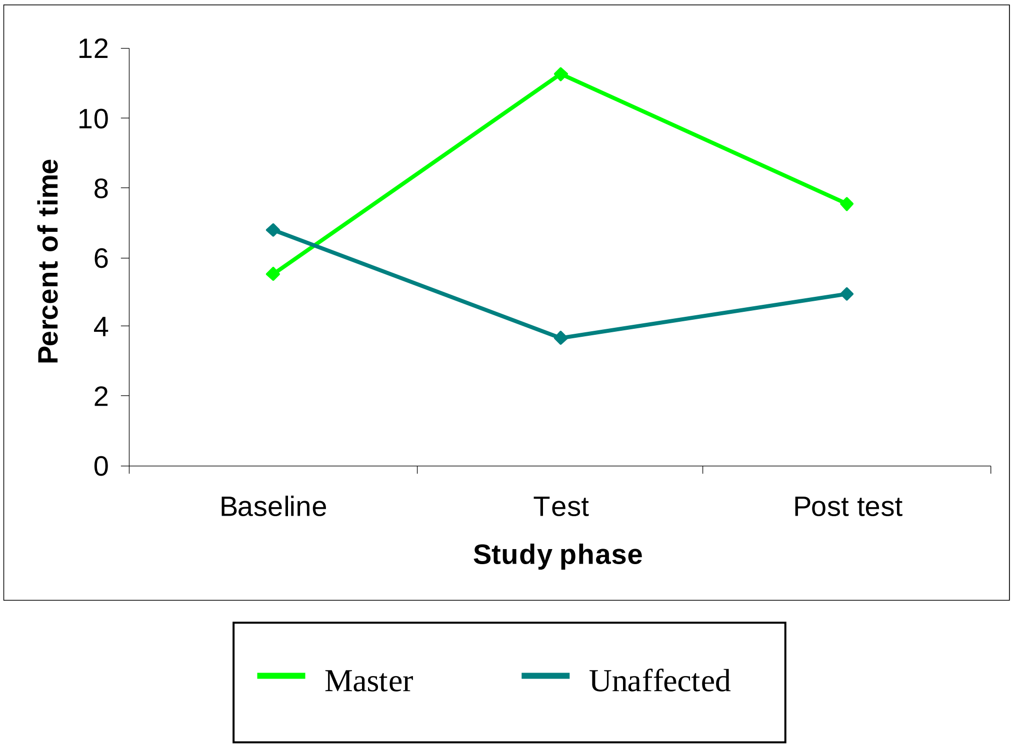
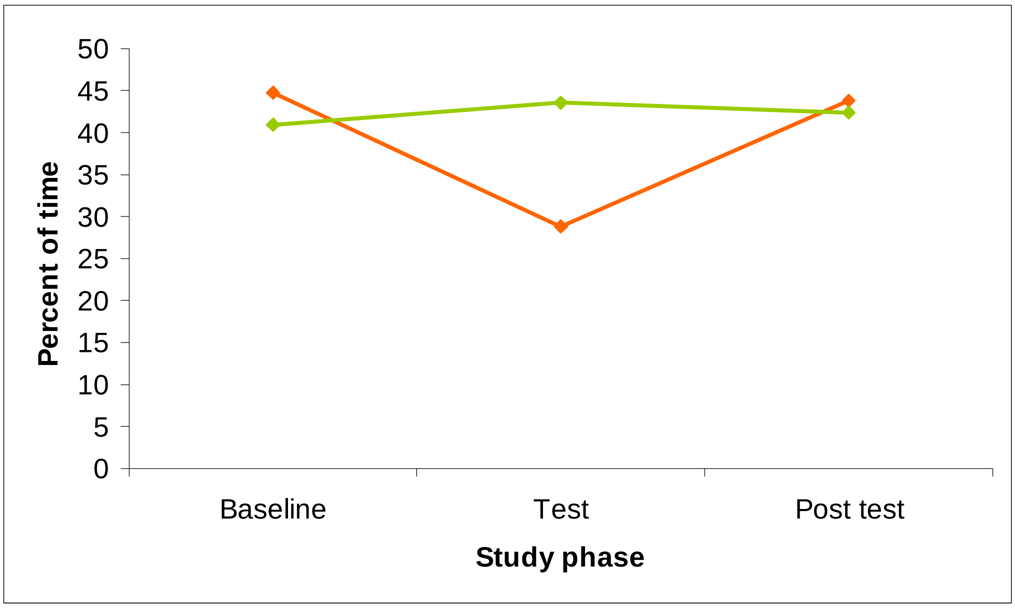
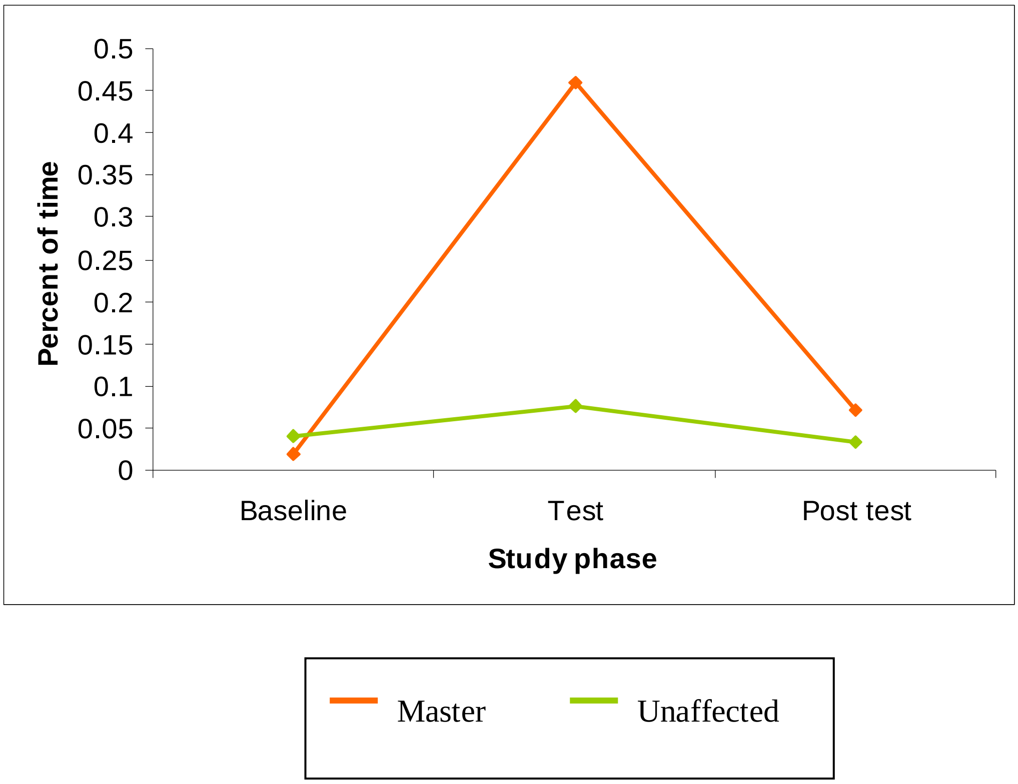


Figure 8.9: Interaction between study group and study phase for youngsters

a. Inactive alert



b. Solitary play



8.3.4 Effects of loss of control (or of visual stimulus) on behaviour

Adults showed few behavioural changes in reaction to the visual stimulus or to the ability to control it; therefore they were not affected by the loss of these factors. Youngsters showed higher levels of social play during the Post-test phase compared to the Baseline phase. Further, they watched the observer significantly less during the Post-test phase compared to the Baseline phase. None of these changes may be seen as a negative effect of loss of control or stimulus. As significant differences between the Baseline and Post-test phases were found only in these behaviours, this topic will not be addressed in the Discussion.

8.4 DISCUSSION

The results of this study show that the visual stimulus and the ability to control it had positive effects on the behaviour of captive common marmosets, even though they did not use it for a considerable amount of time. As with the opportunity to control the cage’s illumination, the visual stimulus had a greater impact on young marmosets than it did on adults.

8.4.1 Measures of coloured lights usage

None of the groups in the present study used the coloured light sequences regularly or consistently. The average time that the device was on never exceeded 19 percent for any of the Master groups. This is in contrast to the amount of usage of additional white light in the previous study (see Chapter 7), which was, on average, of over 44 percent of the total time. Moreover, in the previous study, some groups showed a very constant usage of the light. In fact, this contrast was expected, as the effect of coloured lights on the home environment of the marmosets was much more dramatic and unnatural for them.

The marmosets showed a significant decrease in button touches after the first four days of the study, but they did not show a significant decrease in the percentage of time that the lights were on. However, the marmosets never showed a consistent pattern of use of the coloured lights. Therefore, these results may indicate habituation to controlling the device. The impact of the coloured lights may also be reduced after extended exposure.

Previous studies have also shown a decrease in device usage when the reward was visual stimulus (Harris et al., 1999; Brannon et al., 2004). However, when primates were exposed to visual stimuli for shorter or fewer sessions, they showed greater interest in the stimulus (Swartz & Rosenblum, 1980; Novak & Drewsen, 1989). One possible reason for the difference between studies is that sensory stimuli may attract primates for short periods only. If the stimulus is available for too long, primates may lose interest and stop activating it. Indeed, studies have shown that a change in the stimulus (e.g. new content of videotapes) increases monkeys’ interest (Andrews & Rosenblum, 2001, 2002).

Although sensory enrichment seems to attract primates for relatively short periods, and despite previous findings that primates prefer food rewards over visual stimuli (e.g. Washburn et al., 1997; Brannon et al., 2004), it is important to provide primates with non-food enrichment for at least two reasons. First, primates may become obsessed with food enrichment (e.g. Line et al., 1990a, 1991a) which may lead to the performance of undesirable behaviours. Second, many primates in captivity are overweight and food enrichment (which in many cases uses favoured foods) exacerbates this problem.

8.4.2 Effects of coloured lights on behaviour

In common with the previous study on control over cage illumination (Chapter 7), youngsters were affected by the coloured lights much more than adults. Adult marmosets spent less time in the upper part of the cage and engaged less in tree gouging behaviour when the lights were on. However, the interpretation of tree gouging behaviour in relation to welfare is not clear and will be addressed in the General Discussion. Youngsters showed increased calm locomotion when the coloured lights were on. Further, when the coloured lights were activated they showed decreased levels of undesirable behaviours such as scratching and inactive alert.

Young marmosets also watched the observer less when the lights were on. The interpretation of changed levels of this behaviour will be addressed in the General Discussion. In addition, youngsters spent more time manipulating the device and looking at the lights or the device when the lights were on. Finally, youngsters spent more time in the lower part and less time in the upper part of the cage when the lights were on. These findings suggest that the marmosets responded to the stimulus in a positive exploratory way. Although the marmosets still spent more time in the upper part of the cage, they showed a significant change in this tendency. This result is in line with the results of Kissinger and Bouwens (2006) that showed that gorillas preferred to stay in a room where coloured lights were projected rather than moving to a separate room.

The results of the present study contradict those of Schapiro and colleagues (Schapiro & Bloomsmith, 1995; Schapiro et al., 1995), in which sensory enrichment was found to be less effective than feeding and physical enrichments on the behaviour of yearling rhesus monkeys. This may be due to species differences, and/or the use of different sensory stimuli (videotapes in the Schapiro et al.'s studies). Additionally, Schapiro and his colleagues did not separate the three enrichment types (sensory, feeding and physical) when they compared the behaviour to that of non-enriched monkeys. Their results showed that sensory enrichment was less effective than the other two enrichment types; however, no data were published relating to the exact effects of the sensory enrichment on behaviour. On the other hand, the results of the present study are in agreement with those of Platt and Novak (1997) regarding the effects of videotapes and computer task stimuli on the behaviour of adult rhesus monkeys. Similar to the marmosets in the present study, the rhesus monkeys showed higher levels of locomotion. However, the impact of visual stimuli on adult rhesus monkeys in Platt and Novak's study, were more analogous to the impact of coloured lights (in the present study) on youngsters than to their impact on adults.

8.4.3 Effects of control over coloured lights on behaviour

Although the marmosets in the present study did not operate the coloured light sequencer frequently, their behaviour (especially that of youngsters) during the whole Test phase of the study was affected. The behaviour of Master marmosets during the Test phase was significantly different to the behaviour of Unaffected marmosets during the same phase, as well as to their own behaviour during both Baseline and Post-test phases.

Locomotion and inactivity

Significant interactions between study group and phase were found in inactive alert behaviour for youngsters and calm locomotion for adults. These interactions resulted from differences in the behaviour of Master and Unaffected marmosets throughout the study period. Unaffected marmosets hardly changed their behaviour between the study phases. In contrast, youngsters in Master groups showed decreased levels of inactive alert behaviour in the Test phase compared to the other two phases of the study. Adults in Master groups showed more changes in calm locomotion compared to Unaffected adults, however, these changes were not significant. In addition, youngsters in Master groups showed lower levels of inactive alert and adults in Master groups showed higher levels of calm locomotion than adults in Unaffected groups. These changes and differences in activity patterns suggest that Master marmosets were more relaxed and more active when they could control the visual stimulus in their cage. In common with the youngsters in the present study, Baker and co-workers (2001) showed that captive chimpanzees spent less time inactive when they could control computer tasks. However, only those chimpanzees that spent significantly more time watching the monitor compared to yoked animals, showed a significant decrease in inactivity.

Social and solitary play

In the present study, youngsters showed significantly higher levels of social play when compared to Unaffected individuals during the Test phase of the study. Further, they showed significantly more solitary play in the Test phase compared to both Baseline and Post-test phases, and significantly higher levels of social play in the Test phase than in the Baseline phase. In addition, an interaction between study group and phase was found for solitary play. This interaction resulted from the significant change in levels of solitary play that were shown by Master youngsters, while for youngsters in Unaffected groups levels of this behaviour remained low throughout the whole study. These findings may indicate positive effects of control on behaviour, and therefore on the welfare of Master youngsters. The present results are in agreement with previous research, in which captive chimpanzees and orangutans performed higher levels of solitary play when they were allowed to control videotape and computer tasks, respectively (Bloomsmith et al., 2000a; Baker et al., 2001; Tarou et al., 2004). In contrast, Bloomsmith and colleagues (2000b) found that solitary play levels were reduced when captive chimpanzees could control computer tasks.

Watch the observer

Young marmosets in Master groups watched the observer more during the Baseline phase compared to the Test and the Post-test phases. In addition, they watched the observer during the Test phase less than youngsters in Unaffected groups did. These results will be addressed in the General Discussion.

To sum up, the findings of the present study agree with conclusions of the previous study; controllability has positive effects on the welfare of captive marmosets, with no major difference between different controllable objects. However, differences in the amount of device usage between the studies suggests that additional white light is more effective for longer periods than coloured lights. Further, the results support the argument regarding the importance of stimulation for captive primates, even if the stimulus is unnatural and unfamiliar to the monkeys.

8.5 CONCLUSIONS

The effects of visual stimuli and the control over these stimuli on the behaviour of family-housed marmosets were studied. The main results are presented in Table 8.12.

The conclusions made from this study are:

5) Exposure to a visual stimulus (coloured lights) has positive effects on the welfare of captive marmosets.
6) The ability to control a visual stimulus has positive effects on welfare.
7) Young marmosets are more influenced than adults both by exposure to visual stimulus and/or the ability to control it.
8) Loss of control over visual stimuli and/or the loss of the stimuli themselves have no impact on the behaviour of marmosets.

In the next chapter the effects of control over white light are studied again, however several factors are added to the study. First, the composition of the groups is adult pairs instead of family groups. Second, the marmosets are housed in single cages in two tiers. Third, a yoked condition is added to dissociate the effects of the light intensity from those of controllability.

Table 8.12: Summary of the main results of Chapter 8

	Adult marmosets		**Young marmosets**	
	Elevated levels	**Reduced levels**	**Elevated levels**	**Reduced levels**
Effects of visual stimulus		Tree gouging Usage of upper part of cage	Calm locomotion Usage of lower part of cage Look at device Manipulate device	Inactive alert Scratching Watch observer Usage of upper part of cage
Effects of control over visual stimulus (study group comparison)	Calm locomotion		Social play Solitary play Explore (only main effect)	Inactive alert Watch observer
Effects of control over visual stimulus (study phase comparison)	Inactive rest (only main effect)		Social play Solitary play	Inactive alert Watch observer
Effects of loss of control over visual stimulus			Social play	Watch observer

Chapter 9

Effects of Control over Light on the Welfare of Common Marmoset Pairs Housed in Two Tier Cages

9.1 INTRODUCTION

The study in Chapter 7 showed that light intensity in their home cage, as well as the option to control it, had a considerable impact on the welfare of common marmosets housed in family groups. The aim of the present study is to extend these findings in three directions. Firstly, the results of Chapter 4 showed minor behavioural differences between marmosets in lower and upper tiers, despite the differences in light intensity between these two housing conditions. However, previous research has shown an influence of light intensity on primates (e.g. Isaac & DeVito, 1958; Erkert & Gröber, 1986; Heger et al., 1986). The first aim of the present study is therefore to investigate whether cage level has an impact on the responses of marmosets to control over light. Secondly, the results of Chapter 4 showed effects of group composition on the behaviour of adult marmosets. Previous studies have also suggested that social conditions may affect the reaction of marmosets to the same stimuli. Hence the second aim of this study is to investigate control over light in a different social structure, that of adult pairs. Thirdly, in previous studies (Chapters 7 and 8) the effects of control and light were confounded. In the present study a Yoked condition is added to the two previous study conditions (Master and Unaffected). This study design will distinguish between the impact of the light intensity and that of the control itself on the behaviour of the marmosets.

The following questions were asked:

1) Does cage level affect the responses of the marmosets in relation to controlling light?
2) How does light intensity affect the welfare of pair-housed marmosets?
3) How does the opportunity to control light intensity in the cage affect the welfare of pair-housed marmosets?
4) Does loss of control affect the welfare of the monkeys?

It was hypothesized that marmosets in lower tiers would use the lights more than their conspecifics in upper tiers. Further, as adult marmosets in different group compositions behave differently (see Chapter 4), differences in their responses to control over light were also expected. Finally, based on previous findings, no effects of loss of control were expected.

9.2 METHODS

9.2.1 Study animals and housing

The study animals were 72 common marmosets housed in single cages in female-female (n=14), male-male (n=11), and female-male (n=11) pairs. The study included three conditions, with twelve pairs in each condition: Master pairs, Yoked pairs (who were given identical lighting conditions to those of Master pairs, without the ability to control the light) and Unaffected pairs. In each condition six pairs were housed in lower tiers, and six in upper tiers. Pair details and individuals' ages and sexes are presented in Table 9.1. There were no significant differences in mean age of marmosets between Master, Yoked and Unaffected pairs ($F_{(2,69)}$=0.961, P=0.387).

Mean age for animals in Master pairs on the first day of the study was 1356 days (±S.E. 184.2 days; n=24), 1073 days (±S.E. 145.4 days; n=24) for animals in Yoked pairs, and 1109 days (±S.E. 139.1 days; n=24) for those in Unaffected pairs. There was also no significant difference in mean age between marmosets in lower and upper tiers ($F_{(1,70)}$=1.022, P=0.316).

Table 9.1: Pair and individual details (sex, date of birth (D.O.B), age on first day of the study). Individuals that were used twice are shown in red.

Pair type	**Pair identifier**	**Individual**	**D.O.B.**	**Age (days)**
Master Upper tier	a-2RaU	111Y (♀)	19/12/2001	979
		184Y (♀)	13/03/2003	530
	a-3RaU	904R (♀)	22/7/1998	2225
		150Y (♀)	30/07/2002	756
	b-4RaU	676R (♀)	25/03/1993	4184
		5G (♂)	09/03/2002	913
	c-2LbU	914R (♀)	03/09/1998	2254
		847BK (♂)	23/11/1998	2173
	c-4LbU	863BK (♂)	19/04/1999	2026
		84G (♂)	08/08/2003	454
	6-2LbU	877BK (♂)	24/06/1999	1979
		6G (♂)	14/03/2002	985
Master Lower tier	a-2RaL	865BK (♂)	22/04/1999	1951
		78G (♂)	24/07/2003	397
	b-4RaL	20W (♀)	26/11/2000	1381
		176Y(♀)	26/02/2003	559
	b-1RaL	822BK (♂)	18/06/1998	2273
		71G (♂)	09/06/2003	456
	c-1LbL	980R (♀)	21/09/1999	1871
		177Y (♀)	26/02/2003	617
	6-1LbL	122Y (♀)	13/03/2002	986
		53G (♂)	21/02/2003	641
	6-3LbL	981BK (♂)	09/11/2001	1110
		147Y (♀)	22/07/2002	855
Yoked Upper tier	a-2RbU	104Y (♀)	09/11/2001	1019
		138Y (♀)	29/05/2002	818
	a-3RbU	95G (♂)	02/12/2002	631
		66G (♂)	22/05/2003	460
	b-4RbU	215Y (♀)	09/08/2003	395
		211Y (♀)	04/08/2003	400

Continuation of Table 9.1

Pair type	Pair identifier	Individual	D.O.B.	Age (days)
Yoked	c-2LaU	782R (♀)	22/08/1996	2996
Upper tier		210Y (♀)	04/08/2003	458
	c-4LaU	842BK (♂)	10/09/1998	2247
		134Y(♀)	16/05/2002	903
	6-2LaU	966BK (♂)	10/07/2001	1232
		7G (♂)	14/03/2002	985
Yoked	a-2RbL	137Y (♀)	29/05/2002	818
Lower tier		173Y (♀)	24/02/2003	547
	b-4RbL	864BK (♂)	22/04/1999	1965
		72G (♂)	23/06/2003	519
	b-1RbL	75Y (♀)	09/05/2001	1217
		187Y (♀)	11/04/2003	515
	c-1LaL	169Y (♀)	05/01/2003	669
		196Y (♀)	09/06/2003	514
	6-1LaL	870BK (♂)	04/05/1999	2030
		13Y (♀)	15/04/2000	1683
	6-3LaL	872BK (♂)	21/05/1999	2013
		160Y (♀)	02/10/2002	783
Unaffected	a-1RaU	131Y (♀)	16/04/2002	861
Upper tier		156Y (♀)	18/09/2002	706
	a-1RbU	96Y (♀)	29/09/2001	1060
		123Y (♀)	03/04/2002	874
	b-4LbU	863BK (♂)	19/04/1999	1968
		84G (♂)	08/08/2003	396
	c-3LbU	959BK (♂)	05/06/2001	1248
		848R (♀)	05/09/1997	2617
	c-3LaU	4G (♂)	09/03/2002	971
		81G (♂)	04/08/2003	458
	6-2RaU	55Y (♀)	02/01/2001	1421
		943BK (♂)	05/02/2001	1387
Unaffected	a-4LbL	914R (♀)	03/09/1998	2182
Lower tier		847BK (♂)	23/11/1998	2101
	b-3RbL	842BK (♂)	10/09/1998	2189
		134Y (♀)	16/05/2002	845
	b-3RaL	169Y (♀)	05/01/2003	611
		199Y (♀)	09/06/2003	456
	c-3RaL	192Y (♀)	03/05/2003	551
		193Y (♀)	03/05/2003	551
	6-4LaL	72G (♂)	23/06/2003	442
		88G (♂)	20/08/2003	461
	6-4LbL	889BK (♂)	28/02/2000	1730
		943M (♂)	19/08/2003	462

Mean age for animals in lower tiers was 1089 days (±S.E. 111.7 days; n=36), and 1273 days (±S.E. 143.3 days; n=36) for those in upper tiers. Significant differences were found between the mean ages of marmosets in the three pair compositions ($F_{2,63}$=5.59, P=0.06). Marmosets in female-male pairs were significantly older than those in female-female and male-male pairs (t=707.29, P=0.006; t=585.51, P=0.038, respectively). Due to this potential confound, no differences between marmosets in different pair compositions are discussed. All marmosets in this study were more than 300 days old; hence, no discrimination between age groups was made.

9.2.2 Experimental design

The 36 study pairs were housed in four colony rooms each containing three Master pairs, three Yoked pairs and three Unaffected pairs. The study was carried out in four repetitions (each corresponding to a separate colony room) at different times, due to restrictions in the quantity of apparatus. The experimental schedule is described in Table 9.2. Some pairs were used twice; in each of these cases the marmosets were used first as an Unaffected pair and then as a Yoked or Master pair. In one case only one individual (72G) was used twice, as his cage mate was changed between the study repetitions. As no significant behavioural differences were found between the study conditions during the Baseline phase of the study (even in the percentage time that monkeys watched the observer) re-use of individuals did not confound results.

An Unaffected pair was defined as a pair to which no manipulation was applied in any of the study phases. Master and Yoked pairs were defined as pairs to which a manipulation was applied during the Test phase of the study. During the morning of the fifth day of the study, a controllable additional white light was hung on each Master and Yoked pair’s cage (for more details about the light box, see Chapter 7). The only difference between Master and Yoked pairs was that Yoked pairs could not control the additional light, which was controlled by the Master pair in the neighbouring cage (i.e. when Master pairs turned their own light on, their Yoked partners’ light also went on). In the present study, the cages’ height was 1.15m (half the height of the cages in Chapter 7). The light boxes were hung on the upper part of the cage and influenced the light intensity in the whole cage. Therefore, no measurements were taken with reference to the individual’s location inside the cage.

Table 9.2: Study protocol, describing the three study phases, together with details of number of focal observations

	Days	**1-4**	**Days**	**5-22**	**Days**	**23-27**
	Baseline	**phase**	**Test**	**phase**	**Post-test**	**phase**
	light	**observations**	**light**	**observations**	**light**	**observations**
Master pairs	no	3 focal obs. per individual	yes	10 focal obs. per individual	no	3 focal obs. per individual
Yoked pairs	no	3 focal obs. per individual	yes	10 focal obs. per individual	no	3 focal obs. per individual
Unaffected pairs	no	3 focal obs. per individual	no	10 focal obs. per individual	no	3 focal obs. per individual

Illumination measures were taken using a Jessop light-meter and showed that the light intensity inside the cage with the additional light was more than twice as high as normal (see Table 9.3). However, the difference was greater in the lower tiers, as the non-manipulated light intensity was greater in the upper tiers. European regulations (Council of Europe, 2004) require light intensity that allows the monkeys to be observed during their active periods, and to enable routine husbandry tasks to be carried out safely. They also recommend a light intensity that satisfies the monkeys' needs. However, there is no clear information about marmosets' light intensity preferences, or required levels to satisfy needs. On the other hand, the United States' regulations require that "lighting must be uniformly diffused throughout animal facilities" (USDA, 1991). This requirement was not implemented in the present colony rooms; however, with the additional light the differences between lower and upper tiers decreased.

Table 9.3: Light measures (in EV) in two different locations of the cage with the additional light on and off

Tier	Additional light	Centre of the cage	Back of the cage
Upper	on	11	10
	off	6	5.5
Lower	on	10	9
	off	4	3.5

The light also produced heat and increased the temperature within its very near environment (up to 15cm from the light) from around 23ºC to around 34ºC. However, this thermal change did not affect the whole cage as the source of the heat was very small.

9.2.3 Data collection

Behavioural observations were recorded in each phase of the study for each study condition. Focal animal sampling was used with four-minute observation sessions per animal. During the Baseline and the Post-test phases of the study, each individual was observed three times (total observation time of 4 hours and 48 minutes for each one of the study conditions) and ten times during the Test phase (total of 16 hours for each study condition), see Table 9.2. All other methods of data collection were the same as in Chapter 7.

9.2.4 Statistical analysis

Separate statistical tests were carried out in order to examine the effects of different factors of the study (see Table 9.4).

Table 9.4: Statistical analyses used in the present study

Research question	Statistical test	Factors	Levels	Analysis
Habituation to device (percentage time on)	One-way ANOVA	Period	first 4 days/ middle/ last 4 days	Within subjects
Habituation to device (frequency of button touches)	One-way ANOVA	Period	first 4 days/ middle/ last 4 days	Within subjects
Effects of cage level on light usage	Independent sample t-test	Cage level	Upper/lower	Between subjects
Effects of light condition in different cage levels	Two-way ANOVA mixed design	Light condition	On/off	Within subjects
		Cage level	Upper/lower	Between subjects
Effects of light condition in different study conditions	Two-way ANOVA mixed design	Light condition	On/off	Within subjects
		Study condition	Master/Yoked	Between subjects
Effects of control and loss of control	Two-way ANOVA mixed design	Study phase	Base/Test/Post	Within subjects
		Study condition	Master/Yoked/ Unaffected	Between subjects

9.3 RESULTS

The results of the present study are analysed in relation to three factors:

1) Usage of light in general and in two different cage levels
2) Effects of light intensity on the animals' welfare in general, in Master and Yoked pairs and in two cage levels
3) Effects of control on the animals' welfare

9.3.1 Measures of light usage

Four groups kept the cage lit for relatively large percentages of time, showing quite a consistent pattern of light usage (see Tables 9.5 and 9.6 and Figures 9.1 and 9.2). The frequency of button touches reduced throughout the study (see Tables 9.7 and 9.8). A significant main effect of Test phase period was found for frequency of button touches ($F_{2,22}$=13.76, P<0.001), but not for percentage time of light usage. The frequency of button touches was significantly greater during the first four days of the Test phase compared to the middle period of the Test phase (t=-4.13, P=0.001) and compared to the last four days of the Test phase (t=-4.87, P<0.001).

Table 9.5: Mean (±S.E.) percentage time per day of device usage in six Master groups in upper cages during the Test phase

	a-3RaU	**b-2RaU**	**b-4RaU**	**c-4LbU**	**c-2LbU**	**6-2LbU**
All Test phase	83.68±3.4	83.71±4.3	10.38±4.1	3.57±3.1	4.94±3.6	39.82±8.5
First 4 days	67.91±10.2	59.94±13	24.79±13.1	16.08±13.4	22.25±14.5	45.27±18.8
Middle period	86.17±3.1	88.57±2.4	8.76±4.4	0	0	21.98±9.7
Last 4 days	92.97±2.5	95.33±2.4	0	0	0	78.98±3.6

Table 9.6: Mean (±S.E.) percentage time per day of device usage in six Master groups in lower cages during the Test phase

	a-2RaL	**b-4RaL**	**b-1RaL**	**c-1LbL**	**6-3LbL**	**6-1LbL**
All Test phase	5.83±3.9	70.36±5	36±6.5	26.03±5.4	46.05±6.5	73±7.5
First 4 days	26.25±14.7	54.11±19.1	27.4±13.1	42.64±14.9	42.62±12.9	29.11±11.2
Middle period	0	70.81±3.5	36.56±9.4	25.13±6.3	45.8±9.1	81.16±7.4
Last 4 days	0	85.48±3.9	43.17±14.6	11.67±6.7	50.19±17.3	96.49±0.6

Figure 9.1: Percentage time of light usage for Master groups in upper tiers during the Test phase

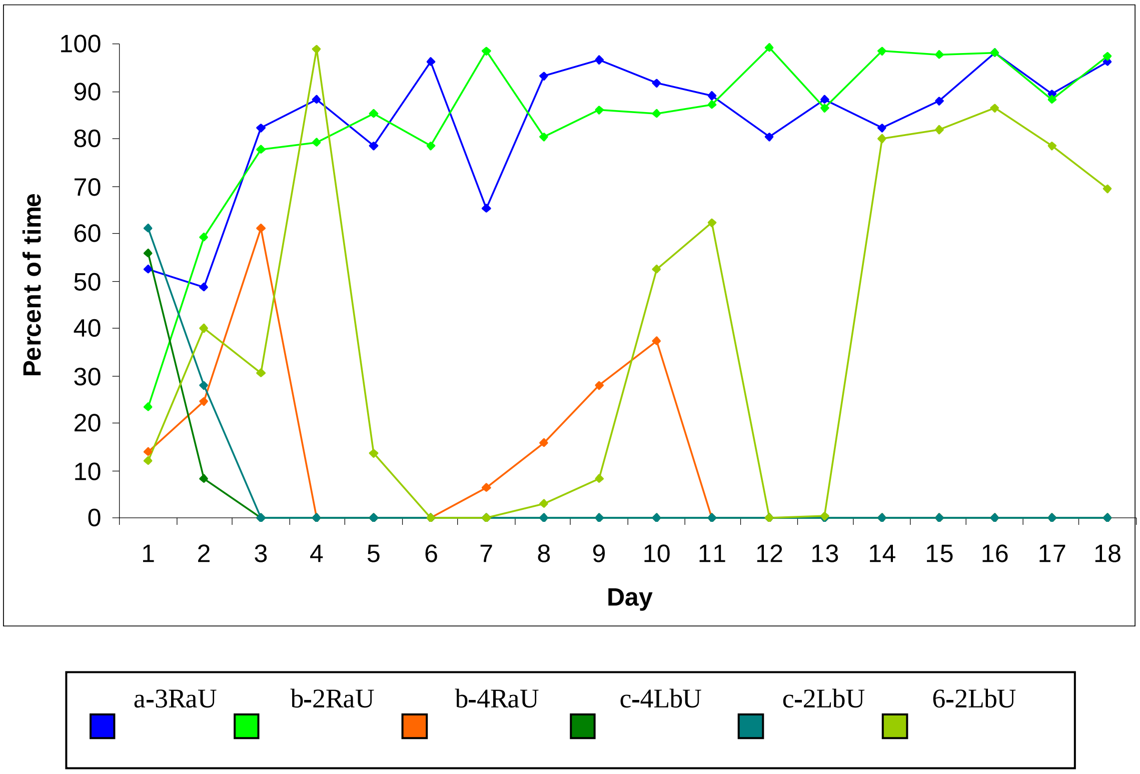


Figure 9.2: Percentage time of light usage for Master groups in lower tiers during the Test phase

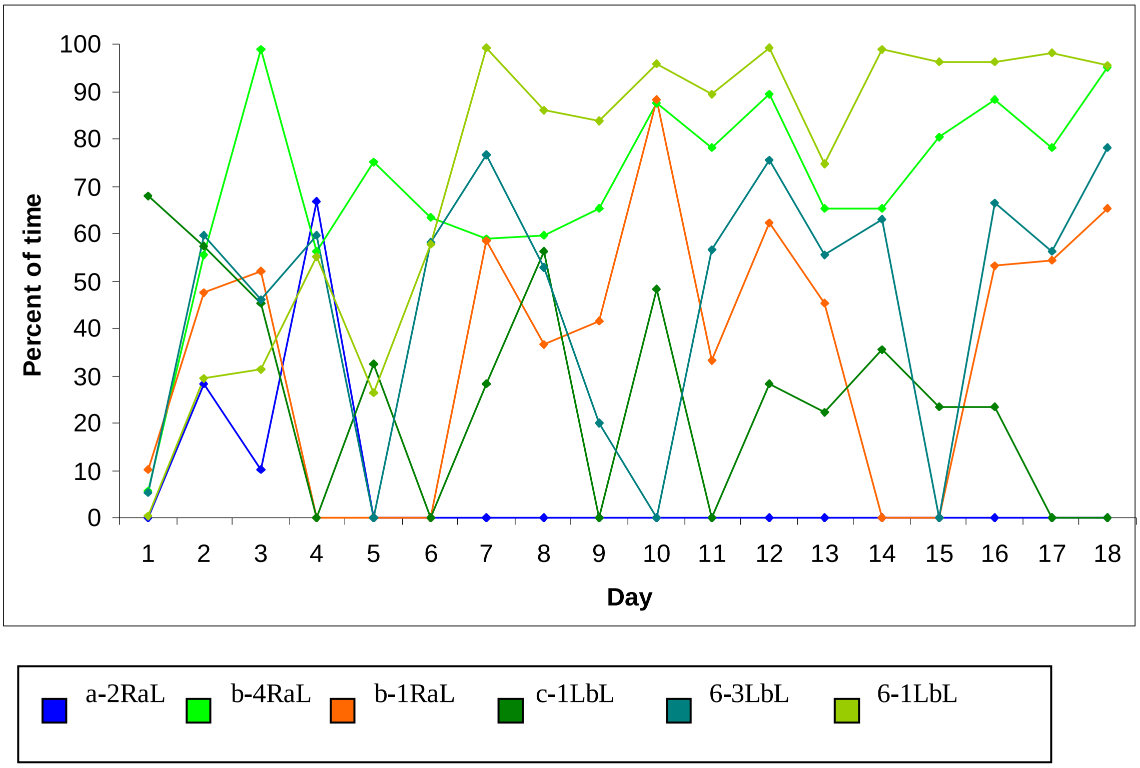


Table 9.7: Mean (±S.E.) frequency per day of device usage in six Master groups in Upper cages during the Test phase

	a-3RaU	b-2RaU	b-4RaU	c-4LbU	c-2LbU	6-2LbU
All Test phase	1.67±1	2.44±1	2.22±0.7	2.61±1	3.44±2	8±2.8
First 4 days	15±6.9	26.75±9	3.75±2.4	3.75±2.3	5.5±3.2	10±6.4
Middle period	2.9±0.2	6.6±1.3	1.3±0.3	0	0	8.6±0.2
Last 4 days	2.5±0.3	3.75±1.4	0	0	0	1.5±0.3

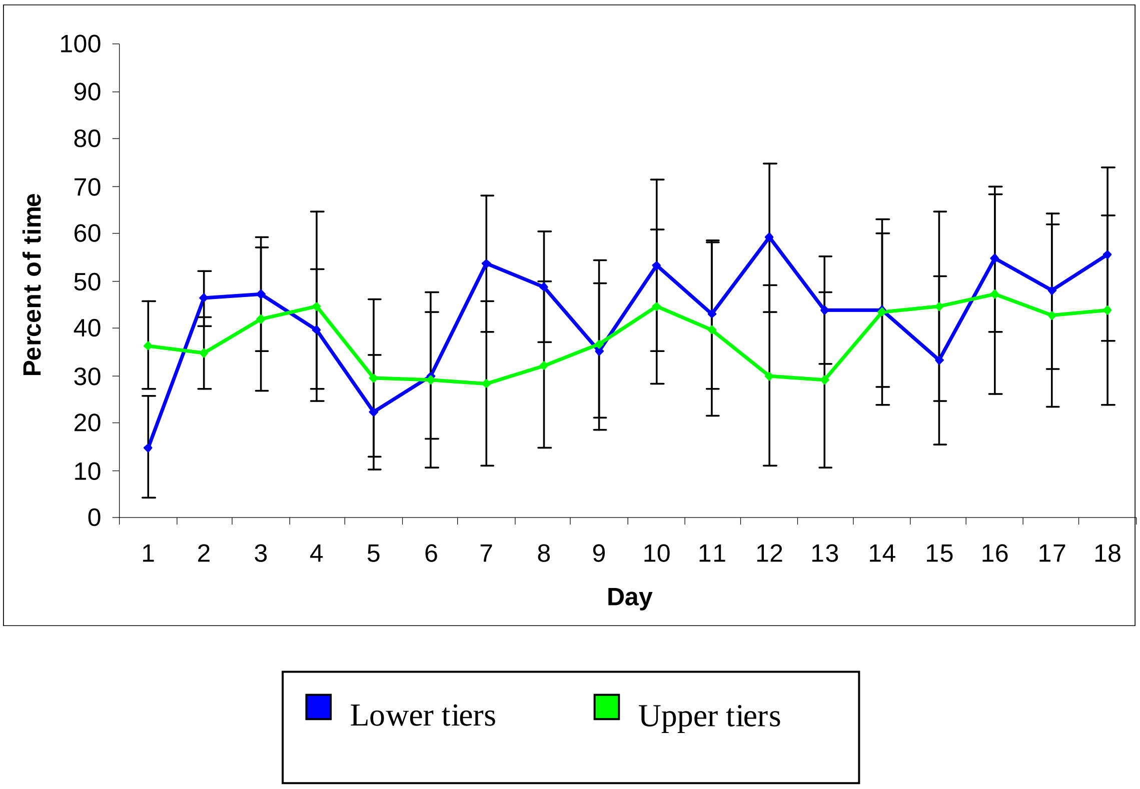
Table 9.8: Mean (±S.E.) frequency per day of device usage in six Master groups in lower cages during the Test phase

	a-2RaL	b-4RaL	b-1RaL	c-1LbL	6-3LbL	6-1LbL
All Test phase	0.89±0.2	5.5±2	10.4±2.9	1.56±1	5.72±2	1.78±0.3
First 4 days	1.75±0.5	11±7.4	1.5±0.3	3.25±1.25	8.25±4.6	22.25±10.7
Middle period	0	4.6±2.4	2.2±0.4	2.4±1.1	1±0.2	4.4±0.6
Last 4 days	0	3.25±0.5	1±0	0.75±0.25	1±0.4	2.75±0.5

9.3.2 Effects of cage level on light usage

There were no significant differences between marmosets in the two cage levels in percentage time of light usage (t=0.28, P=0.787, see Figure 9.3) nor in the frequency of button touches (t=-0.36 P=0.727). The variation in light usage was very high. Only four out of twelve pairs kept the light on for more than 60% of the time; two of these pairs were housed in lower tier cages and two in upper tier cages. Four other pairs kept the light on for more than 20% of the time; one of them was from upper tier cages and the other three pairs from lower tier cages. The other four pairs used the light for less than 20% of the time. Although three out of the four pairs that used the light for the lowest percents of the total available time were upper tier pairs, no significant differences were found between lower and upper tiers in light usage.

Figure 9.3: Mean percentage time of light usage (± SE bars) for lower and upper tiers during the test phase of the study



9.3.3 Effects of light intensity on behaviour

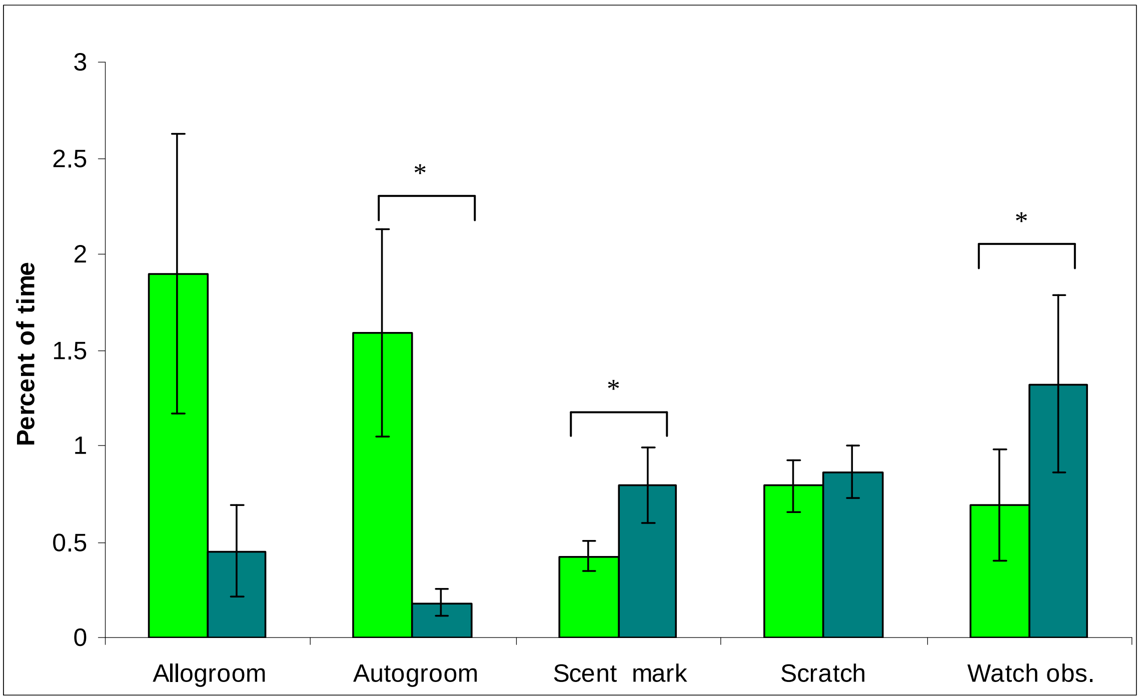
Both Master and Yoked pairs were included in the analysis of the effects of light on the animals' behaviour during the Test phase. With additional light, marmosets showed significantly more calm locomotion and autogrooming, and spent significantly more time close to the light box. In addition, with the light on, the monkeys spent significantly less time watching the observer and showed less inactive alert, agitated locomotion and scent marking behaviour (see Table 9.9 and Figure 9.4 a, b and c).

Table 9.9: Results of ANOVAs for effects of light on behaviour of Master and Yoked pairs (*P<0.05; **P<0.01; ***P<0.001)

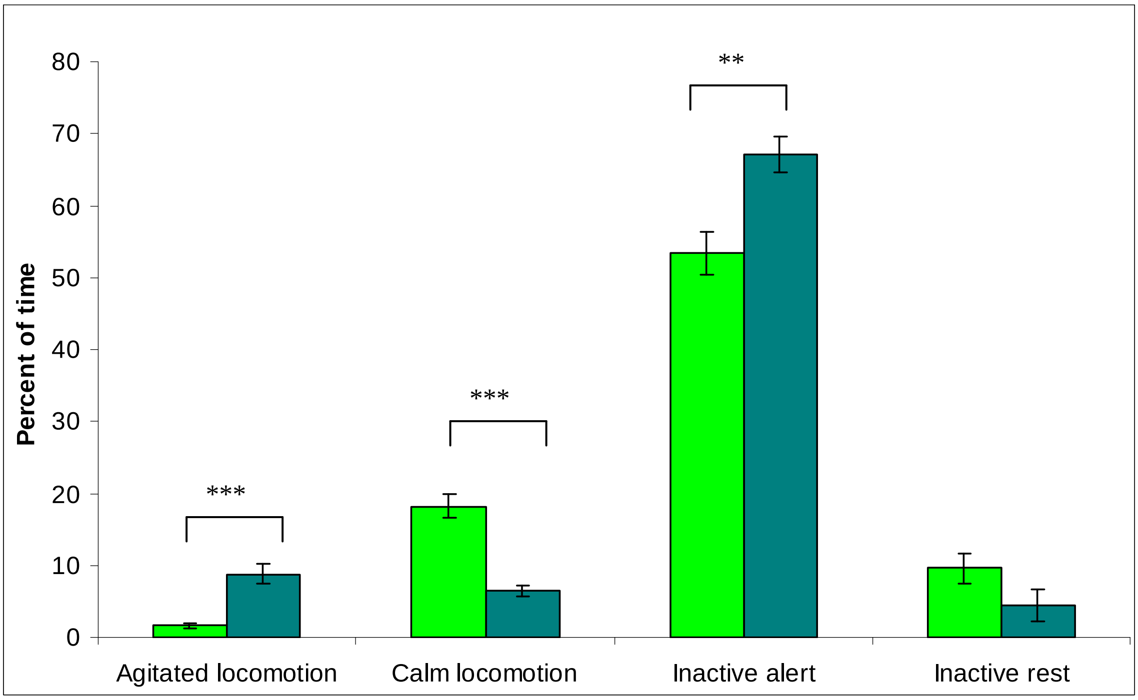
	F (d.f.=1,22)	**P**
Agitated locomotion	27.82	<0.001***
Allogroom	4.04	0.057
Autogroom	6.70	0.017*
Calm locomotion	61.17	<0.001***
Contact	0.11	0.739
Explore	0.09	0.771
Inactive alert	14.50	0.001**
Inactive rest	2.45	0.132
Scent mark	6.73	0.017*
Scratch	0.16	0.695
Social play	0.93	0.344
Solitary play	2.07	0.164
Tree gouge	2.27	0.146
Watch observer	4.60	0.043*
Close to device	67.97	<0.001***
Manipulate device	1.87	0.186

Figure 9.4: Percentage time (± SE bars) spent in behaviours for marmosets in Master and Yoked pairs during the two light conditions (*P<0.05; **P<0.01; ***P<0.001)

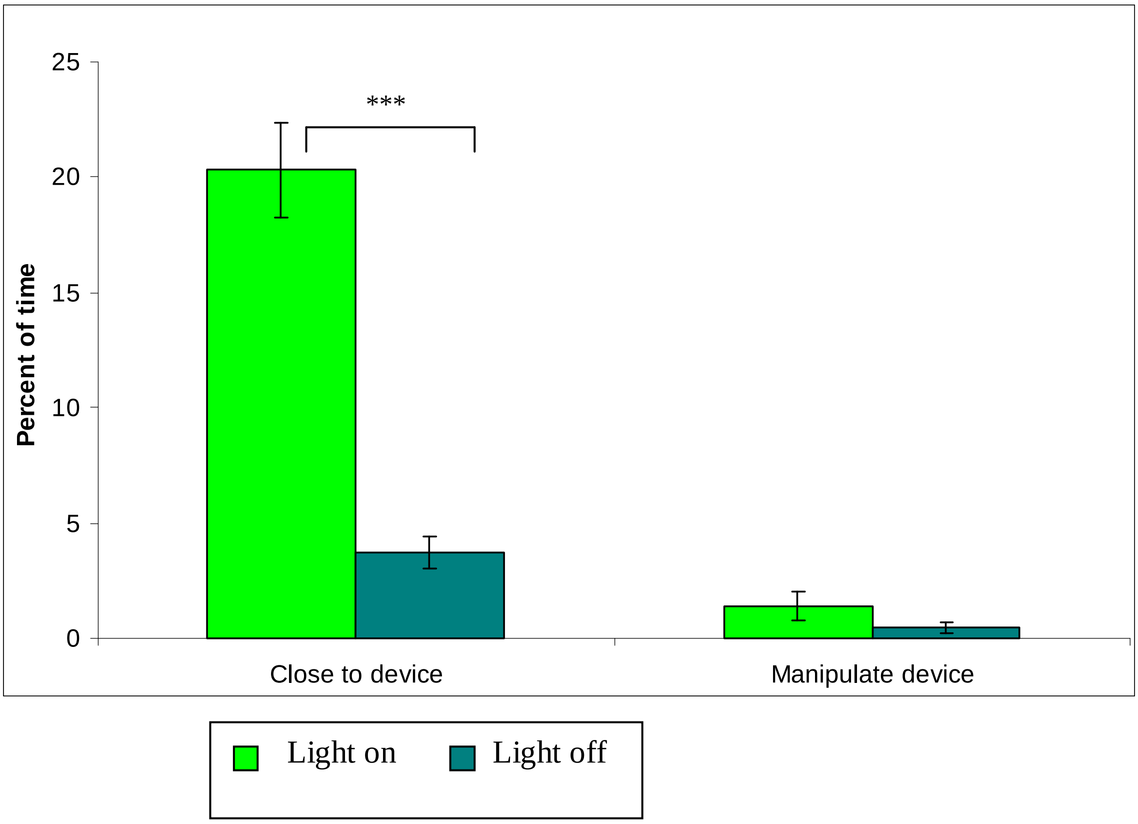
a.



b.



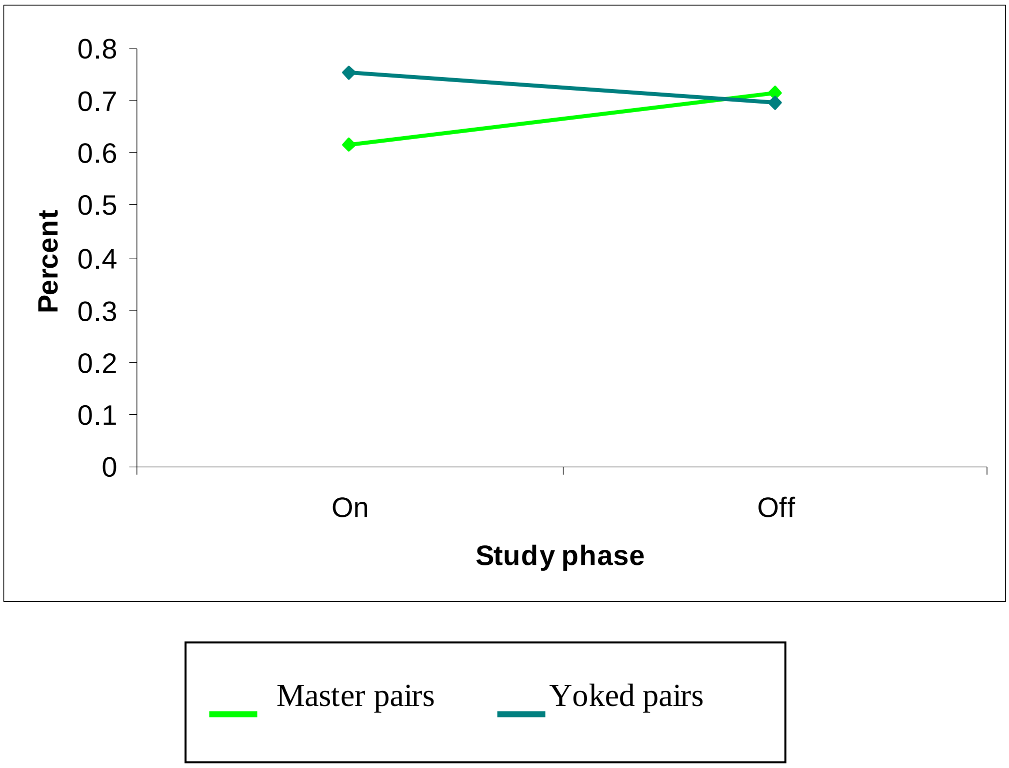
c.



9.3.3.1 *Effects of light intensity in relation to study condition*

In order to separate the effects of the light intensity from those of control over the additional light, the responses of Master and Yoked pairs to the changes in light intensity were compared. A significant interaction between light condition and study condition was found for scratching only ($F_{(1,22)}$=4.85; P=0.038). Master pairs showed a decrease in time spent scratching when the light was on, while Yoked pairs showed an increase in this behaviour when the light was on (see Figure 9.5). Tukey post-hoc tests showed no significant differences between Master and Yoked pairs in either of the light conditions. However, when the light was on the difference between the percentage time Master and Yoked pairs spent scratching approached significance (t=2.663; P=0.063).

Figure 9.5: Interaction between study conditions and light conditions for scratching behaviour



9.3.3.2 Effects of light intensity in relation to cage level

As the change in the light intensity between the two light conditions was greater for lower tiers, it was expected that the increase in light intensity would have a greater impact on the behaviour of marmosets in lower tiers compared to those in upper tiers. Nevertheless, no significant interactions were found between light condition and cage level. Hence, no further analyses were applied.

9.3.4 Effects of control and loss of control on behaviour

In order to examine the effects of control on the behaviour of Master pairs, their behaviour during the Test phase was compared to that of Yoked and Unaffected pairs. Further, the behaviour of Master and Yoked pairs during the Test phase was compared to their behaviour during the Baseline and the Post-test phases. Finally, interactions between study phase and study condition were investigated. The results of these analyses are described separately.

9.3.4.1 Effects of study condition on behaviour

In order to study the effects of control, Master pairs were compared to both Yoked and Unaffected pairs. The results showed significant main effects of study condition on agitated locomotion, calm locomotion and inactive rest behaviour (see Table 9.10 and Figure 9.6 a, b and c). Moreover, Tukey post-hoc tests showed that, in the Test phase of the study, significant differences between Master pairs and either Yoked and Unaffected pairs were greater than those between Yoked and Unaffected pairs. In particular, Unaffected pairs were significantly more agitated than either Master or Yoked pairs. Further, Master pairs showed significantly more calm locomotion compared to both Yoked and Unaffected pairs, and Yoked pairs showed significantly more calm locomotion than Unaffected pairs. In addition, Master pairs performed significantly more inactive rest behaviour compared to both Yoked and Unaffected pairs (see Tables 9.11 and Figure 9.6 a, b and c).

Table 9.10: Results of ANOVAs for effects of study condition on behaviours (*P<0.05; ***P<0.001)

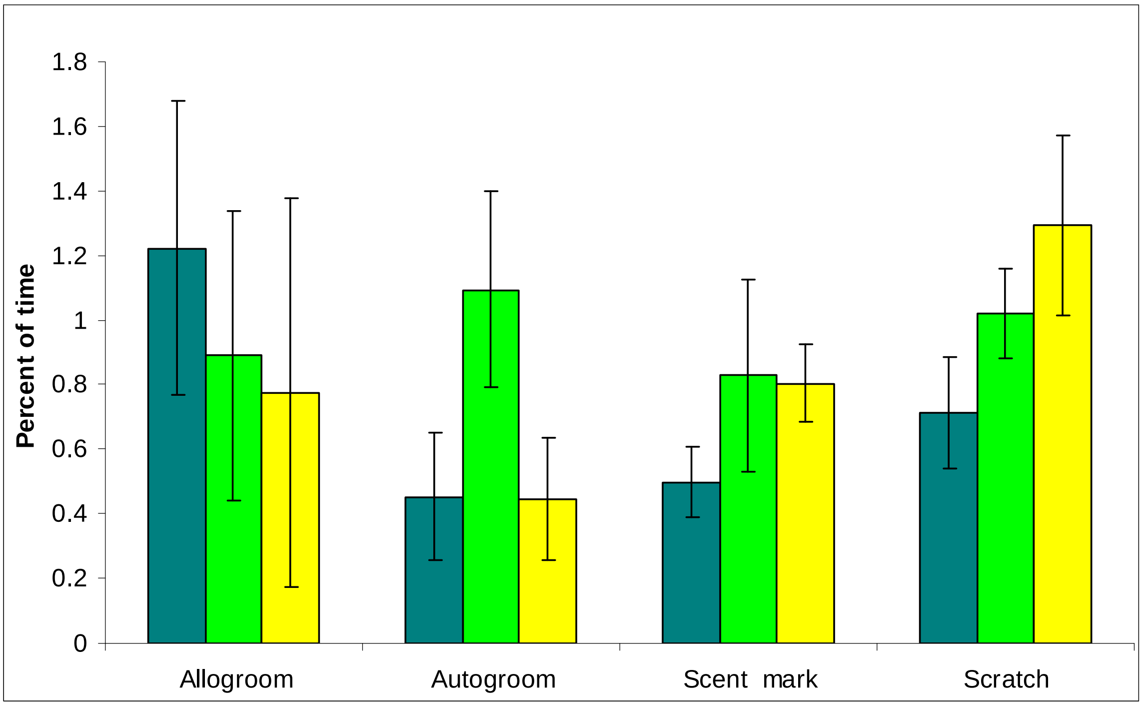
	F (d.f.=2,23)	**P**
Agitated locomotion	4.21	0.023*
Allogroom	0.35	0.710
Autogroom	0.01	0.985
Calm locomotion	22.80	<0.001***
Contact	0.55	0.583
Explore	1.72	0.195
Inactive alert	1.34	0.275
Inactive rest	4.47	0.019*
Scent mark	0.01	0.994
Scratch	0.84	0.440
Social play	0.48	0.623
Solitary play	1.45	0.249
Tree gouge	2.27	0.146
Watch observer	0.78	0.467

Table 9.11: Results of Tukey post-hoc tests for effects of study condition on behaviours (**P<0.01; ***P<0.001)

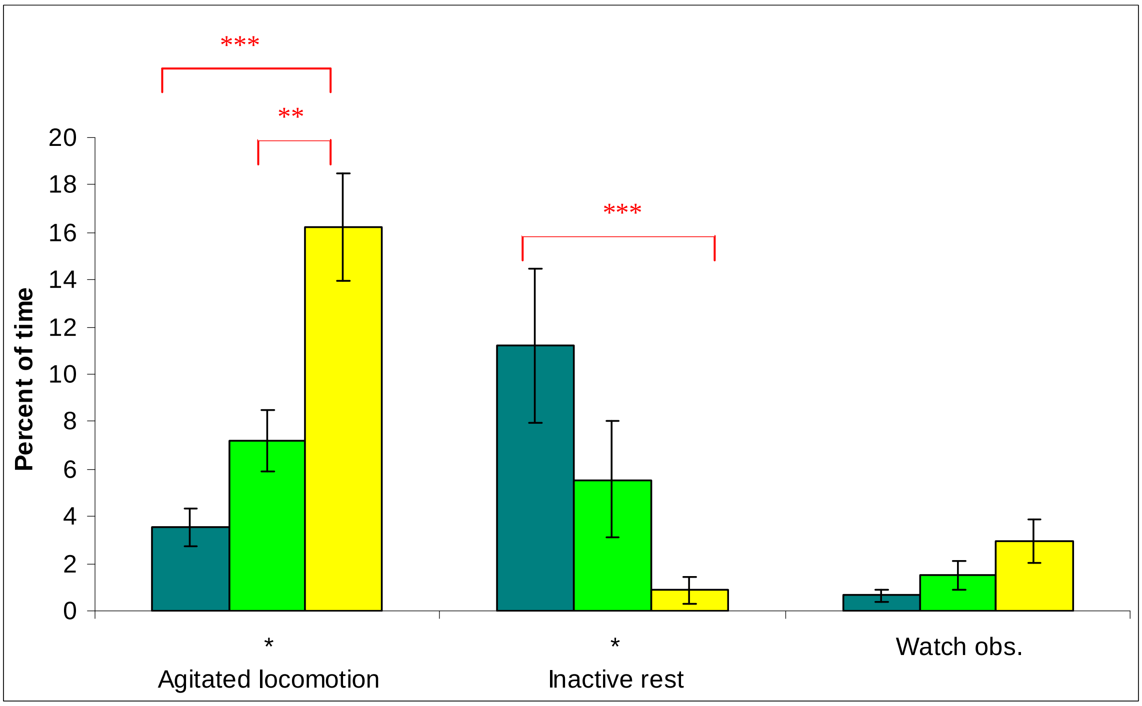
	Master vs. Yoked		**Master vs. Unaffected**		**Yoked vs. Unaffected**	
	t	**P**	**t**	**P**	**t**	**P**
Agitated locomotion	1.68	0.75	5.84	<0.001***	4.16	0.003**
Calm locomotion	-4.65	<0.001***	-12.07	<0.001***	-7.42	<0.001***
Inactive rest	-2.99	0.08	-5.47	<0.001***	-2.47	0.26

Figure 9.6: Percentage time (± SE bars) spent in behaviours for marmosets in Master, Yoked and Unaffected pairs during the Test phase of the study [Two Way ANOVA with repeated measures (black marks), Tukey post-hoc tests (red marks) P<0.05; **P<0.01; ***P<0.001]

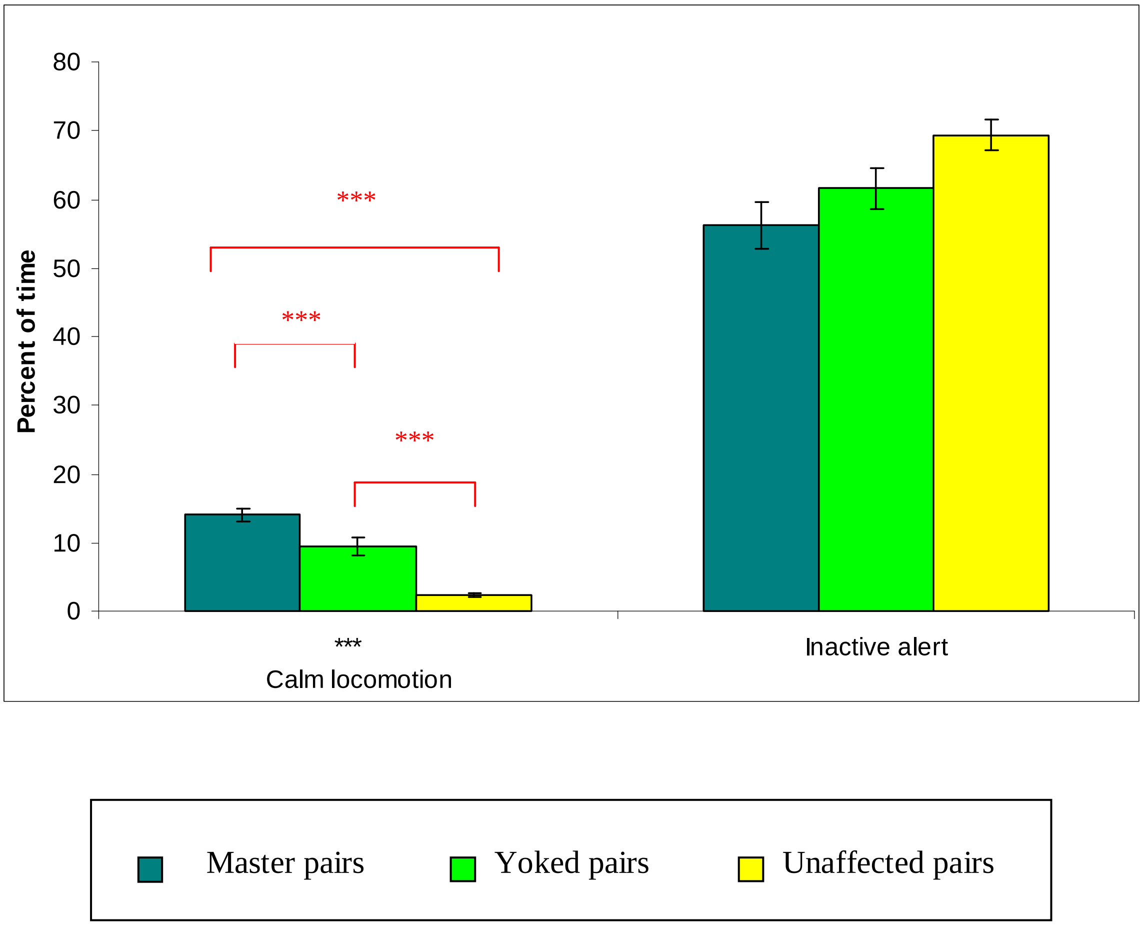
a.



b.



c.



9.3.4.2 Effects of study phase on behaviour

Another method used to examine the effects of control was to compare the different study phases for each study condition separately. Significant main effects of study phase were found for agitated locomotion, calm locomotion, inactive alert and inactive rest behaviours, as well as for scratching and watching the observer (see Table 9.12 and Figures 9.7 a, b and c and 9.8 a, b and c).

Table 9.12: Results of ANOVAs for effects of study phases on behaviours of Master and Yoked pairs (**P<0.01; ***P<0.001)

	F (d.f.=2,66)	P
Agitated locomotion	7.77	0.001**
Allogroom	0.09	0.917
Autogroom	0.19	0.825
Calm locomotion	74.96	<0.001***
Contact	0.00	0.996
Explore	2.93	0.060
Inactive alert	11.70	<0.001***
Inactive rest	16.36	<0.001***
Scent mark	2.19	0.120
Scratch	9.09	<0.001***
Social play	0.45	0.639
Solitary play	0.88	0.419
Tree gouge	1.59	0.211
Watch observer	14.93	<0.001***

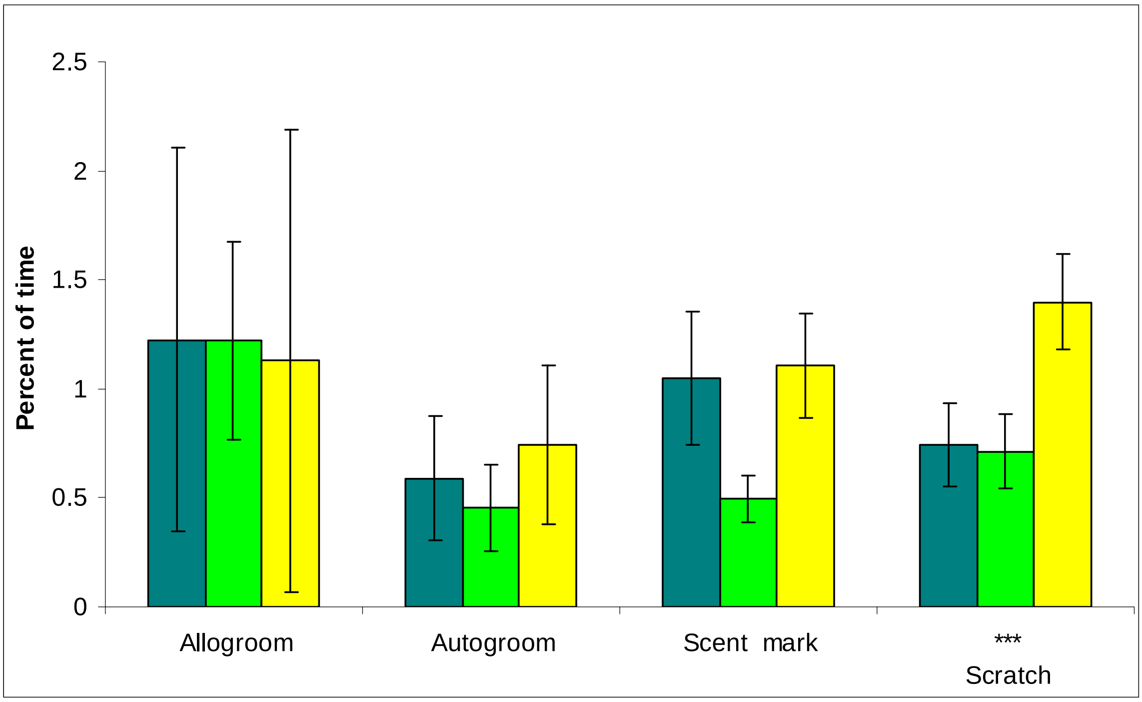
Tukey post-hoc tests showed no significant differences between study phases for Unaffected pairs. Moreover, there were more significant differences between the study phases for Master pairs than for Yoked pairs. Master pairs showed significantly less agitated locomotion in the Test phase of the study compared to both Baseline and Post-test phases. In addition, only Master pairs watched the observer significantly more during the Baseline phase compared to both the Test and the Post-test phases. Master pairs also spent significantly more time in inactive rest during the Test phase compared to both Baseline and Post-test phases. Both Master and Yoked pairs spent significantly more time in calm locomotion during the Test phase compared to both Baseline and Post-test phases and less time in inactive alert behaviour during the Test phase compared to the Post-test phase. No significant differences between the study phases were found in scratching for any study condition (see Table 9.13 and Figures 9.7 a, b and c and 9.8 a, b and c).

Table 9.13: Results of Tukey post-hoc tests for effects of study phases on behaviours of Master and Yoked pair separately (*P<0.05; **P<0.01; ***P<0.001)

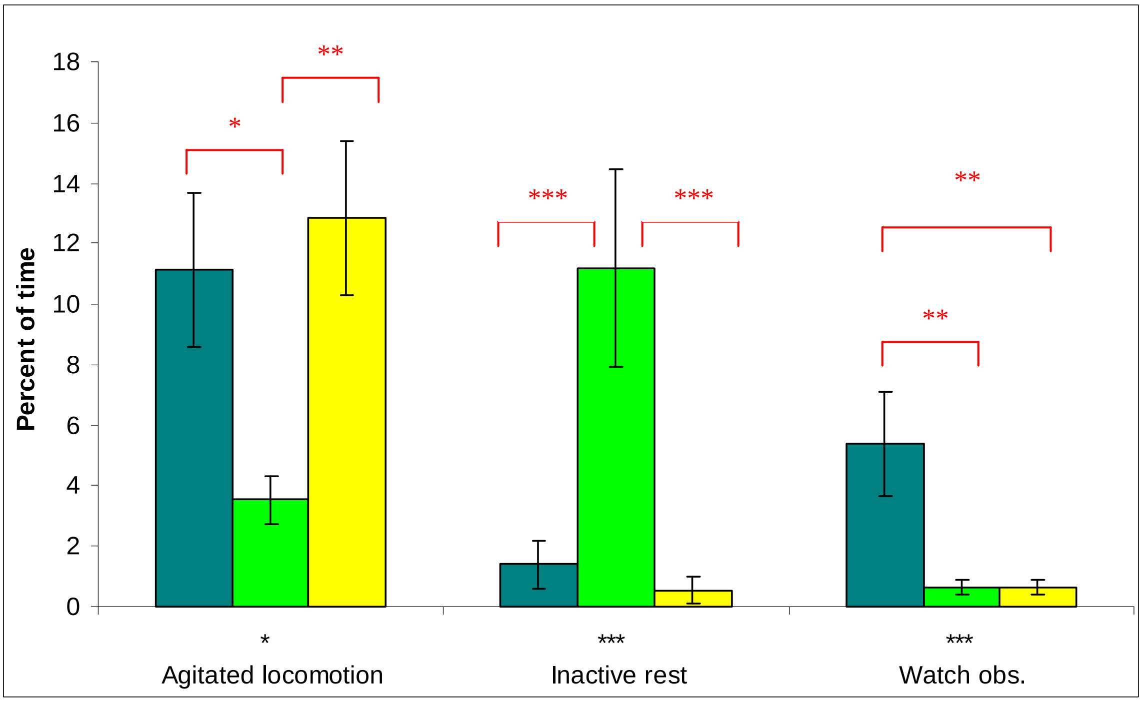
	Baseline vs. Test		Test vs. Post-test		Baseline vs. Post-test	
	t	**P**	**t**	**P**	**t**	**P**
Agitated locomotion						
Master	-3.50	0.022*	-4.29	0.002**	0.79	0.99
Yoked	-2.66	0.182	-1.27	0.936	-1.39	0.90
Calm locomotion						
Master	9.88	<0.001***	12.43	<0.001***	-2.55	0.227
Yoked	5.79	<0.001***	7.88	<0.001***	-2.09	0.487
Inactive alert						
Master	-1.52	0.842	-3.96	0.006**	2.44	0.282
Yoked	-1.56	0.824	-3.84	0.008**	2.28	0.368
Inactive rest						
Master	5.20	<0.001***	5.65	<0.001***	-0.45	0.99
Yoked	2.94	0.10	2.78	0.141	0.16	1.00
Watch obs.						
Master	-3.80	0.009**	0.002	1.00	-3.80	0.009**
Yoked	-1.89	0.625	-0.17	1.00	-1.72	0.733

Figure 9.7: Percentage time (± SE bars) spent in behaviours for Master pairs in three study phases [Two Way ANOVA with repeated measures (black marks) and Tukey post-hoc tests (red marks) *P<0.05; **P<0.01; ***P<0.001]

a.



b.



c.

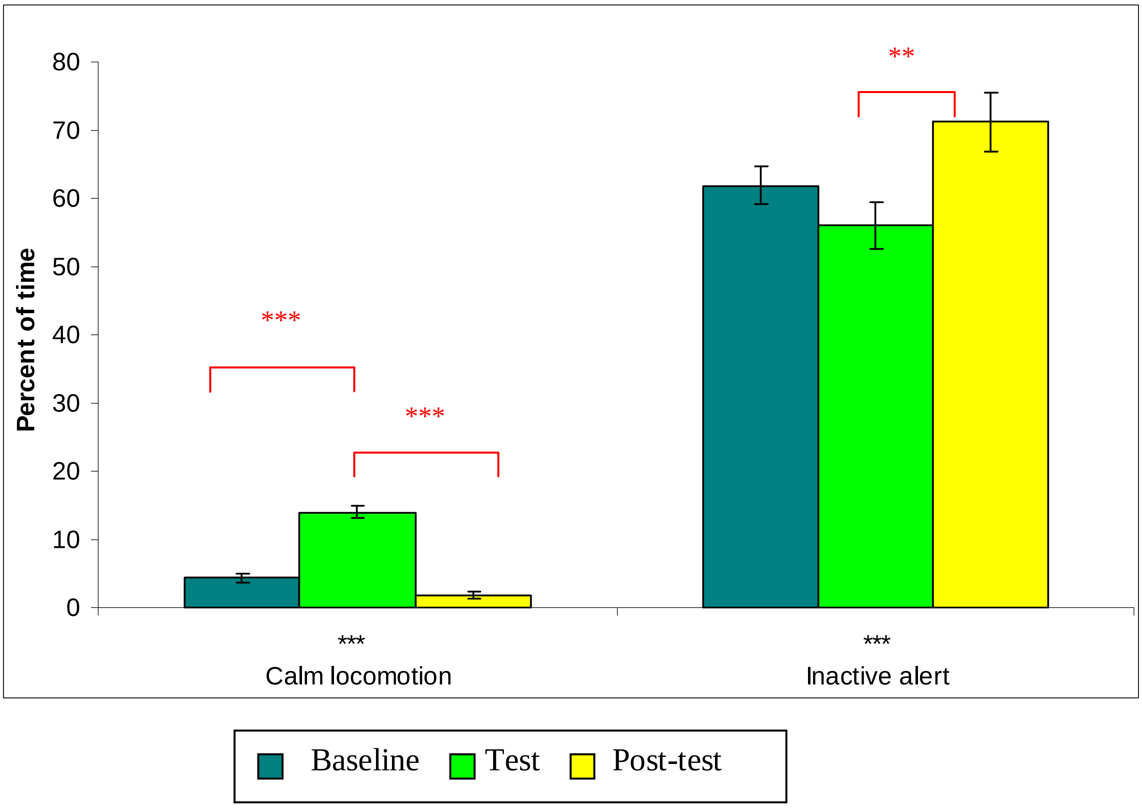
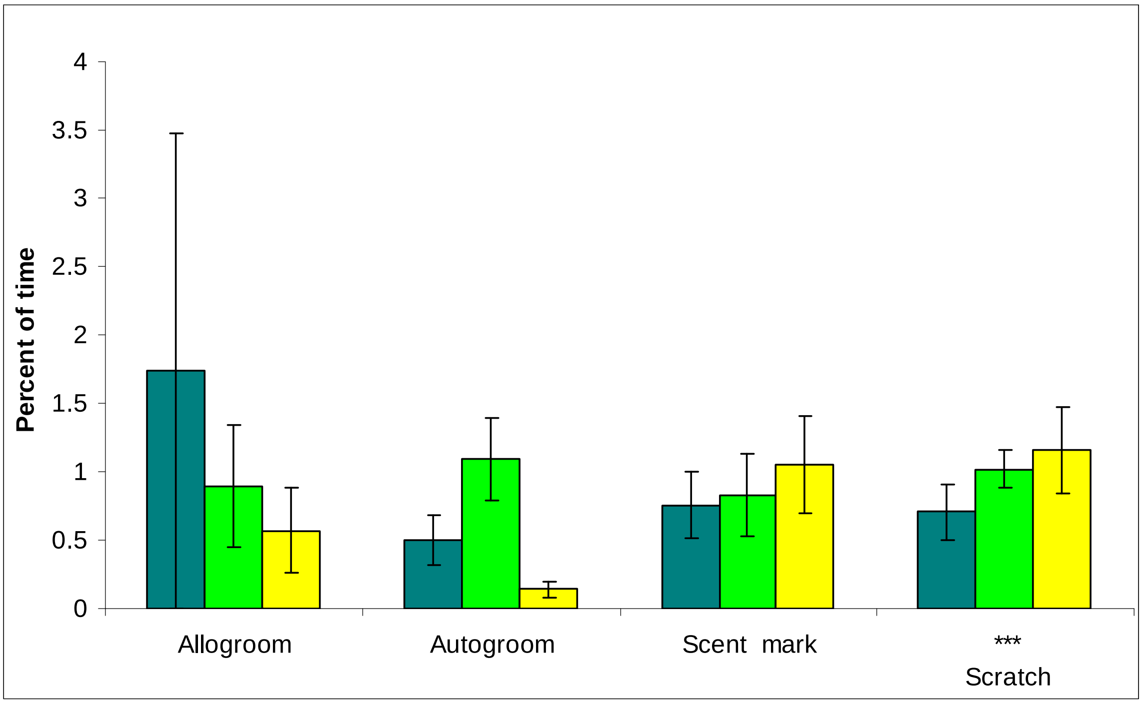
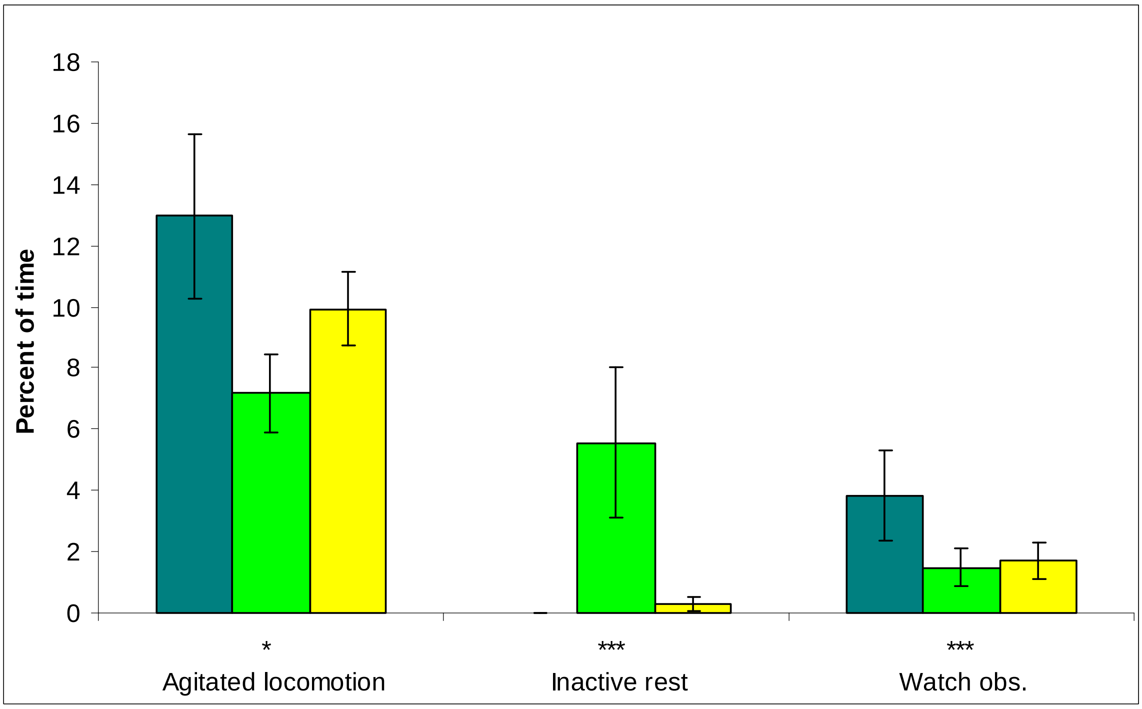

Percent of time
80
70
60
50
40
30
20
10
0
***
***
**
***
Calm locomotion
***
Inactive alert
Baseline
Test
Post-test

Figure 9.8: Percentage time (± SE bars) spent in behaviours for Yoked pairs in three study phases [Two Way ANOVA with repeated measures (black marks) and Tukey post-hoc tests (red marks) *P<0.05; **P<0.01; ***P<0.001]

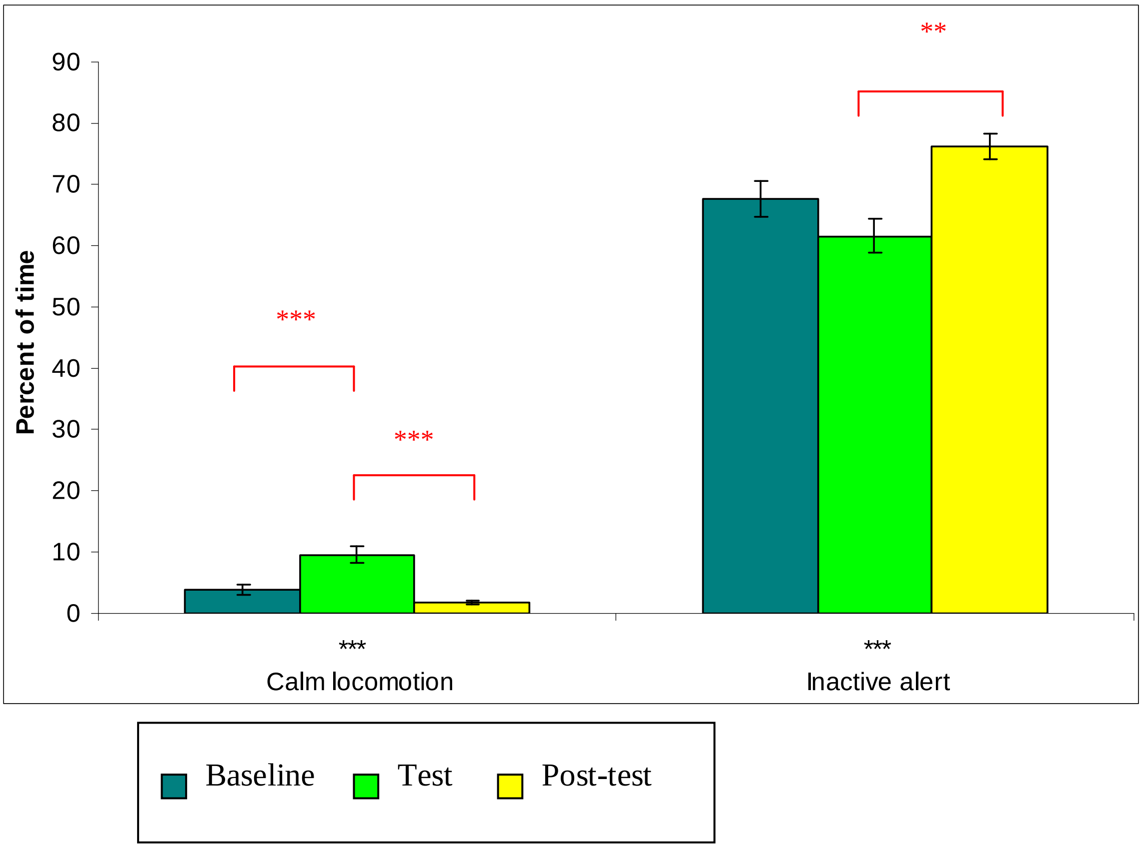
a.



b.



c.



9.2.4.3 *Interactions between study phase and study condition*

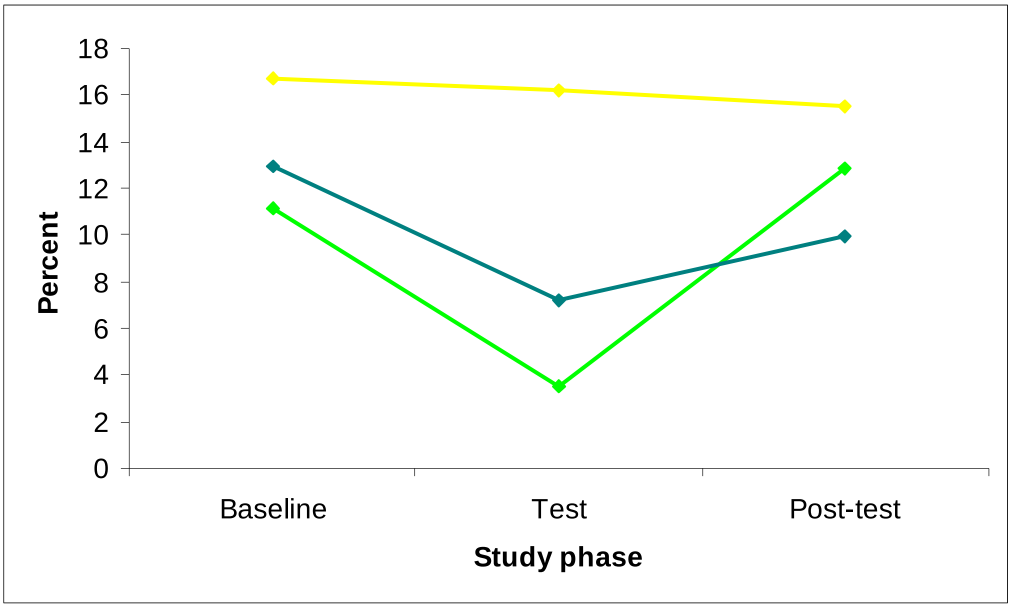
ANOVAs revealed several interactions between study condition and study phase. Master and Yoked pairs showed a decrease in agitated locomotion and inactive alert behaviours in the Test phase of the study, following by an increase in the Post-test phase, while Unaffected pairs showed no major changes between the three study phases (see Table 9.14 and Figure 9.9 a and b). In calm locomotion and inactive rest behaviours, Master and Yoked pairs showed a significant increase in the Test phase of the study, with a decrease in the Post-test phase. Here again, the Unaffected pairs showed no significant changes along the whole study period (see Table 9.14 and Figure 9.9 c and d).

Table 9.14: Results of ANOVAs for interactions between study phase and study condition (*P<0.05; **P<0.01; ***P<0.001)

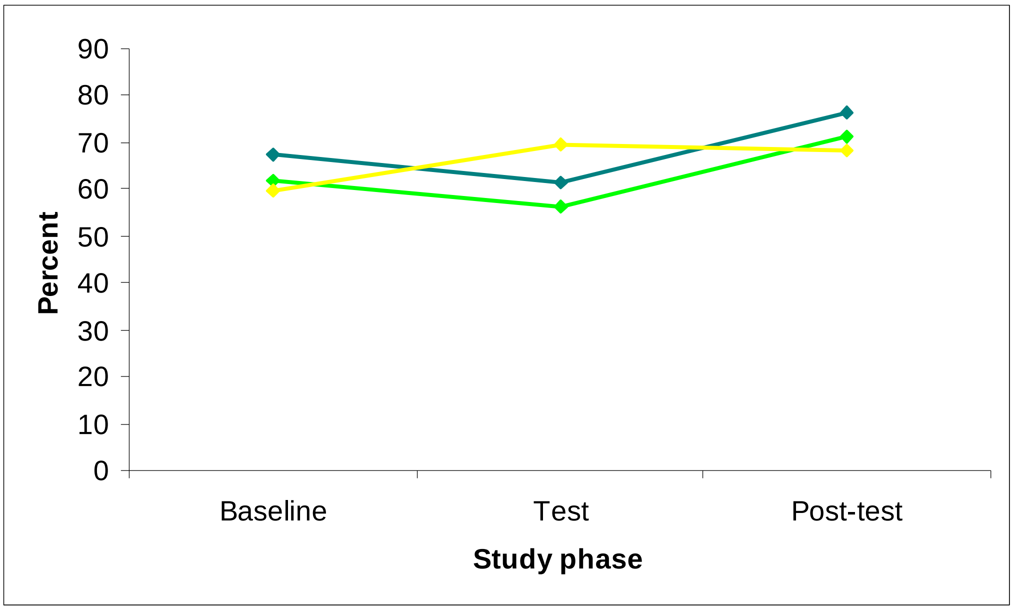
d.f.= 2,66	**F**	**P**
Agitate locomotion	3.18	0.019*
Calm locomotion	22.72	<0.001***
Inactive alert	3.80	0.008**
Inactive rest	4.46	0.003**

Figure 9.9: Interactions between study condition and study phase

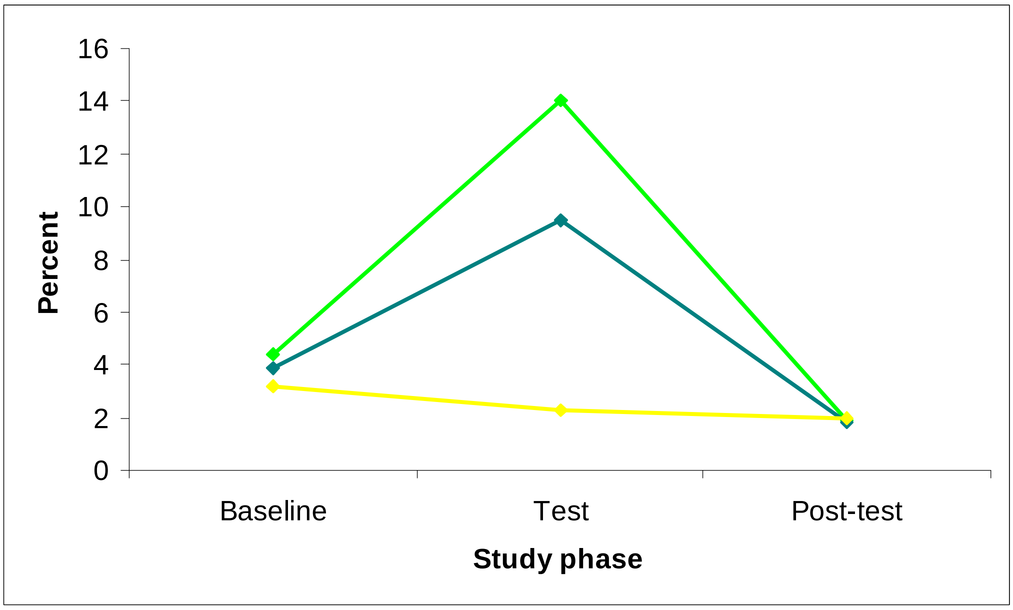
a. Agitated locomotion



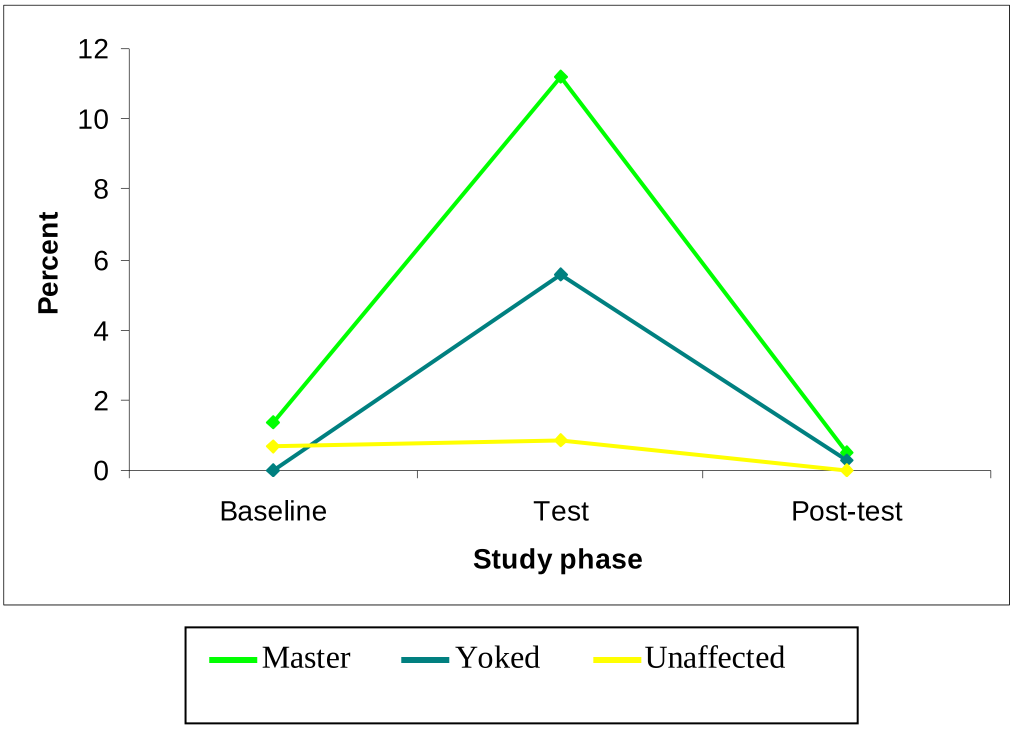
b. Inactive alert



c. Calm locomotion



d. Inactive rest



Similarly to previous studies in this thesis, no effects of loss of control, or loss of additional light and/or heat source were found. Therefore, this issue is not discussed further in the present chapter.

9.4 DISCUSSION

The results of the present study support the conclusions of the previous study (Chapter 7); that both enhanced light intensity and the opportunity to control it improve the welfare of captive common marmosets. This study not only replicates the results of the previous study, with a different housing system and group composition, but also shows that when marmosets are allowed to control the light intensity inside their cage they show a greater change in their behaviour than yoked individuals that experienced the improved light intensity alone. In the present study, in common with the previous one, no significant effects of loss of control were found. In addition, the results show that there are no significant differences in the behaviour of monkeys housed in lower compared to upper tier cages. Further, there were no differences in the way marmosets in lower and upper tiers used the light or responded to it.

9.4.1 Measures of light usage

Marmosets in the present study touched the button significantly less after the first four days of the study, but kept the cage lit for similar percentages of time during the whole Test phase. This reaction to the light is similar to the reaction of family-housed marmosets when allowed control over coloured lights (Chapter 8). Nevertheless, the cause for this reaction appears to be different in the two studies. Figures 9.1 and 9.2 show that at least some of the pairs in the present study used the light consistently for high percentages of the available time. In contrast, such a consistent pattern of the use of the coloured lights was not seen in the previous study. These findings suggest that the marmosets in the present study learnt to associate the button and the additional light in their cage and touched the button only when needed. That is to say, although they showed reduced frequencies of button touches, the additional light was still rewarding for them.

9.4.2 Effects of light intensity on behaviour

As the marmosets in this study were all adults, no age differences are discussed. However, these adults were much more affected by the light intensity inside the cage than were the adults in previous studies (Chapters 7 and 8). These differences between the studies may be the result of different social situations. The results of Chapter 4 showed that adult marmosets behave differently when housed in different group compositions. Further, Box (1984a) found that parent and non-parent adult common marmosets behaved significantly differently to each other in reaction to a novel environment. Further, she found that the variability of behaviour among non-parent pairs was greater than among parent pairs. However, in contrast to these findings, Vignes and co-workers (2001) studied the reactions of common marmosets to novel food enrichment, and found no significant differences between adults in three different social settings (singly housed, same sex pairs and family groups). For further discussion of this issue see Chapter 10.

Locomotion and inactivity

Both Master and Yoked marmosets in this study spent more time in calm locomotion, and less time in agitated locomotion and inactive alert, when the light was on. These changes in the nature of activity patterns are considered to be signs of better welfare (for rationale see Chapter 3).

Scent marking

High levels of scent marking are considered to be stress related (see Chapter 3). In the present study, marmosets scent marked significantly more when the light was off than they did when it was on. This difference suggests that a lighter cage environment was less stressful for the monkeys.

Scratching

There was only one interaction between light condition (on/off) and study condition (Master/Yoked), in scratching behaviour. Animals in Master pairs scratched themselves more when the light was off, while marmosets in Yoked pairs scratched themselves more when it was on. The monkeys showed opposite tendencies in this behaviour in the two different light conditions. The interpretation of this is unclear.

Autogrooming

Marmosets were found to autogroom more when the light was on. Autogrooming is a natural behaviour for nonhuman primates, although it could be considered to be a stress related behaviour when shown at high rates (Barros et al., 2000). However, in the present study the rates of appearance of this behaviour were relatively low (0.5% when the light was off and 1.5% when the light was on). Furthermore, the conclusion that these higher rates of autogrooming reflect poorer welfare, are not consistent with other behavioural changes in this study.

Watch the observer

It was also found that marmosets watched the observer more when the light was off. This finding will be addressed in the General Discussion.

Proximity to the light box

In common with the adults in the previous study, the marmosets (both in lower and upper tiers) spent significantly more time close to the light box when the light was on. This difference may be due to the light itself, or to the heat that the light produced. The possibility that the marmosets preferred to sit close to the device so they would be able to control it is not supported by this study, as individuals in Yoked pairs showed the same behaviour to those in Master pairs, yet they could not control the light at any time.

In summary, the light intensity inside the cage affected the welfare of the marmosets in this study. However, contrary to the predictions, it affected individuals in the lower and upper tier cages similarly, although the improvement in illumination was greater for the lower tier housed monkeys. It is possible that there was a considerable improvement in the light intensity in both cage levels; hence, all marmosets were affected in the same way from this change. In addition, there were no significant differences between Master and Yoked animals, in their reaction to the enhancement in the cages' illumination. This finding is more logical, as the monkeys in both conditions benefited from the same lighting improvement. It also supports the conclusions of the previous study (Chapter 7), which suggested that better lighting conditions enhance the welfare of common marmosets in captivity. The fact that Yoked marmosets were affected by the improved lighting conditions in the same way as Master marmosets, even though they were unable to control them, emphasizes the beneficial effects of the light *per se*.

9.4.3 Effects of control over light on behaviour

The effects of controllability on the welfare of the Master pairs in this study were investigated in relation to two study factors: condition and phase. The results show a greater behavioural change throughout the study phases in Master marmosets compared to both Yoked and Unaffected marmosets, and a greater behavioural change in Yoked marmosets compared to Unaffected animals. No significant differences were found between the different study phases for Unaffected individuals, in any behaviour. Consequently, all differences between the different study phases that appeared in the behaviour of Master and Yoked pairs may be related to the improved lighting conditions and/or the opportunity to control light. Here again, the impact of control over light on behaviour was greater on pair-housed adult marmosets than on family-housed adults.

Locomotion and inactivity

Significant differences in levels of calm locomotion were found between all three study conditions. During the Test phase of this study, Master marmosets were significantly more active compared to both Yoked and Unaffected individuals, and Yoked monkeys were more active compared to Unaffected individuals. This finding suggests that Master marmosets were most affected by the study manipulation, although Yoked marmosets were also positively affected. In addition, individuals in both Master and Yoked pairs showed significantly more calm locomotion during the Test phase of the study compared to both Baseline and Post-test phases.

Further results show that during the Test phase of the study, Unaffected marmosets spent significantly more time in agitated locomotion compared to both Master and Yoked individuals. However, the difference between Unaffected and Master marmosets was more significant than the difference between Unaffected and Yoked animals. Further, only Master marmosets showed significantly less agitated locomotion during the Test phase compared to the Baseline and the Post-test phases. This result indicates again a superior impact on Master compared to Yoked marmosets.

Both Master and Yoked pairs also showed significantly less inactive alert behaviour during the Test phase of the study compared to the Post-test phase. During the Test phase, Master pairs also spent significantly more time in inactive rest behaviour compared to Unaffected pairs. In addition, only Master marmosets showed significantly higher levels of inactive rest during the Test phase than during the other two phases.

Several significant interactions were found between study phases and conditions. All these interactions were found in locomotion and inactivity patterns: calm locomotion, agitated locomotion, inactive alert and inactive rest. All these interactions stemmed from the considerable differences between the study phases shown by Master and Yoked marmosets. Unaffected individuals, which did not experience any environmental changes, did not show any major changes in the performance of these behaviours during the whole study period. All these differences in the locomotion and activity patterns of the marmosets suggest that marmosets in Master pairs were the most positively affected by the study manipulation; marmosets in Yoked pairs were more positively affected than those in Unaffected pairs.

Watch the observer

Master marmosets were the only ones that showed a significant reduction in the amount of time they spent watching the observer during the study period. Several explanations may be suggested for this reduction, as well as for the finding that only Master marmosets showed this behavioural tendency. These possible explanations will be presented in the General Discussion.

There are different methods for studying the effects of control on behaviour and welfare. One method is to compare the behaviour of animals when exposed to the manipulation with their own baseline and post-test data (e.g. Line et al., 1990a, 1991a), or with the behaviour of unaffected counterparts. When using this method, it is however, difficult to separate the effects of the environmental change from those resulting from the opportunity to control it. Another way to study the effects of control is to compare the manipulated animals to yoked counterparts (e.g. Joffe et al., 1973; Mineka et al., 1986; Taylor et al., 2001). This method gives a much better discrimination between the effects of the environmental change and control over this change. In order to cover all aspects of the study it is best to use as many comparisons as possible (e.g. Hanson et al., 1976; Jones & Nicol, 1998). In the previous studies (Chapters 7 and 8), the behaviour of Master groups during the Test phase was compared to that of Unaffected groups, as well as to their own behaviour during the Baseline and Post-test phases. In the present study, the Yoked condition was added and more comparisons were performed. These combined studies and analyses ensure that the most reliable results are achieved.

9.5 CONCLUSIONS

The effects of light, and the control over it, on the behaviour of pair-housed marmosets in two different cage levels were studied. The main results are presented in Table 9.15. In addition, a comparison between the results of the present study and the results of Chapter 7 is presented in Table 9.16. This comparison brings out the greater influence that control over light had on the behaviour of pair-housed adult marmosets compared to family-housed adults.

The conclusions made from this study are:

9) An increase in illumination intensity has positive effects on the welfare of captive marmosets.
10) The increase in light intensity have a similar impact on marmosets in lower and upper tiers.
11) The ability to control light has positive effects on welfare.
12) The effects of control over light are greater than the effects of the increased light intensity *per se*.
13) The loss of control over cage illumination and/or the loss of increased light intensity and heat, does not affect the welfare of marmosets.
14) The ability to control additional light in the home cage has a greater impact on adult marmosets when housed in pairs than when housed in family groups.

Table 9.15: Summary of the main behavioural results of Chapter 9

	Yoked pairs		**Master pairs**	
	Elevated levels	**Reduced levels**	**Elevated levels**	**Reduced levels**
Effects of increased light intensity	Calm locomotion Close to device	Agitated locomotion Scent marking	Calm locomotion Close to device	Agitated locomotion Inactive alert
Effects of study condition	Calm locomotion	Agitated locomotion	Calm locomotion Inactive rest	Agitated locomotion
Effects of Test phase (vs. Baseline and Post-test)	Calm locomotion	Inactive alert	Calm locomotion Inactive rest	Agitated locomotion Inactive alert Watch observer

Table 9.16: A comparison between the results of Chapters 7 and 9

	Family -housed	**adults**	**Pair-housed**	**adults**
	Elevated levels	**Reduced levels**	**Elevated levels**	**Reduced levels**
Effects of increased light intensity (on both Master and Yoked individuals)	Close to device		Calm locomotion Autogroom Close to device	Agitated locomotion Inactive alert Scent mark Watch observer
Effects of study condition	Calm locomotion		Calm locomotion Inactive rest	Agitated locomotion
Effects of Test phase (vs. Baseline and Post-test)	Calm locomotion		Calm locomotion Inactive rest	Agitated locomotion Inactive alert Watch observer

Chapter 10

General Discussion

Animal welfare research is well established and the main three approaches (biological, natural and subjective: Duncan & Fraser, 1997) were discussed thoroughly in Chapter 1. In the present thesis a behaviourally integrated approach was adopted for the study of three natural aspects that wild animals experience as a result of their own behaviour: complexity, choice and control. Each of these features of natural environments has been frequently recommended as significant for the welfare of captive animals in general and captive primates in particular (complexity: e.g. Snowdon & Savage, 1989, Novak & Drewsen, 1989; Carlstead & Shepherdson, 1994; choice: e.g. Markowitz, 1982; Hutchinson, 2005; control: e.g. Bayne, 1989a; Scott, 1991; Warburton, 1991; Rosenblum & Andrews, 1995; Buchanan-Smith, 1997b). Nevertheless, there is little empirical support for these recommendations. The two approaches to animal welfare that have been used in this thesis are the natural living and the subjective experience approaches. Preference tests were used in some of the studies (Chapters 4 and 6); however, the main methods to examine the effects of complexity, choice and control on the welfare of the marmosets used behavioural measurements, both comparatively and in response to changes in the environment.

The assumption that the captive environment should mimic the salient features of the natural habitat of its occupants has become commonly accepted even in the absence of extensive empirical data to support it (Novak & Suomi, 1988). However, there are arguments that contradict, or at least weaken this assumption. First, wild environments are clearly not uniform and not always ideal. Many wild environments may actually be characterized as impoverished or stressful, to the whole population in general or to specific individuals in particular (Novak & Suomi, 1988; Bayne et al., 1991; Rosenblum, 1991). Second, it has been suggested that captive animals may express biobehavioural adaptations or coping strategies to their environment and housing conditions. In such cases, modification of the captive environment to a more naturalistic one may result in interference with the adjustments that the animals have made to their captive conditions (Bayne et al., 1991). Nevertheless, many captive facilities, especially zoos, attempt to replicate the natural habitat of the animals and build enclosures that are similar to the wild environment of the animals. However, as human beings are able to perceive the animals' environment only from a human's point of view, in many cases, only aesthetic aspects of the natural habitat are replicated. Many environmental characteristics are therefore likely to be overlooked by the human eye. One such characteristic is the high number of contingencies to which animals must learn to respond effectively. As has been suggested by Markowitz (1982; Markowitz & Aday, 1998), when natural characteristics cannot be replicated, unnatural ones may serve to provide the animals with natural contingencies, such as the power to make choices or to control their environment. In some of the studies in the present thesis the marmosets were required to present unnatural behaviours (i.e. touch a button to turn on a light) to gain a natural contingency (control over their environment).

10.1 NORMAL BEHAVIOUR OF CAPTIVE PRIMATES

While the adaptation of natural features to captive environments is easier said than done, the valid comparison of the behaviour of animals in captivity to that of their wild conspecifics may be even more problematic (see Veasey et al., 1996a, 1996b).

Furthermore, what constitutes ‘normal’ and ‘abnormal’ behaviour may be different for captive and wild animals because of the considerable differences in environmental conditions (Erwin & Deni, 1979). The terms ‘normal’ and ‘abnormal’ behaviour are frequently used in the research of animal welfare without exact definition (e.g. Meyer-Holzapfel, 1968; Paulk et al., 1977; Bayne et al., 1992a; Laule, 1993; Bollen & Novak, 2000; Lutz et al., 2000; Hook et al., 2002; Kaufman et al., 2002). First, it is necessary to define ‘natural’ and ‘unnatural’ behaviours as these terms are usually used in relation to definitions of ‘normal’ and ‘abnormal’ behaviours.

‘Natural’ behaviour has been defined as a behaviour that is “typically observed in the wild; it is adaptive in the evolutionary sense…(i.e.) has evolved by natural selection which allows an individual to survive more easily in its particular environment and so gives it a better chance of leaving offspring than an animal not so adapted (Poole, 1988b, p. 3).

‘Unnatural’ behaviour is defined as a behaviour that is not “seen in the wild. Not all unnatural behaviours are regarded as abnormal, however, as they may promote success within the captive environment” (Poole, 1988b, p. 3-4).

As mentioned above, ‘normal’ behaviour depends on environmental conditions and varies between natural and captive settings. Definitions for these behaviours in captive situations follow.

'Normal' behaviour will "promote the success and survival of the individual and its genetic contribution to the population" and is "clearly appropriate to the particular situation". It may also "be either natural or unnatural" (Poole, 1988b, p. 4).

'Abnormal' behaviour is defined as a behaviour that is 'rarely seen in wild populations and does not promote the success and the survival of the individual or its close relatives (i.e. it does not increase fitness). It appears not to be goal-oriented, so that its function is not apparent'. It 'may include elements of normal activities, but they are performed in an inappropriate fashion' (Poole, 1988b, p. 4).

As the behavioural ethogram of captive populations is apparently different from that of wild populations both qualitatively and quantitatively, an assessment of 'normal' behaviour of captive animals is required (Erwin & Deni, 1979). However, such an evaluation must take into account many variables such as species, age and sex differences as well as temperament and prior experience. In Chapter 3, I drew a picture of desirable and undesirable behaviours for captive common marmosets; however, such a general distribution of behaviours into 'desirable' and 'undesirable' is not enough, and more accurate assessment of 'normal' qualities and quantities for each behavioural pattern is needed. In this chapter I will try to establish the normal quantities of locomotion, inactivity and scent marking for captive adult common marmosets. These behaviours were chosen given their relevance to welfare and because comparative data were available.

Although various behaviours may be described as desirable or undesirable for marmosets in captivity (see Chapter 3), the interpretation of some behavioural patterns in relation to welfare is ambiguous. The results of this thesis do not provide a more definite understanding of the significance of autogrooming and contact between group members in relation to welfare. On the other hand, the significance of tree gouging now seems to be clearer. In addition, watching the observer showed a consistent pattern across studies, and this behaviour is also discussed below.

Tree gouging

Tree gouging is a natural behaviour of wild marmosets (Stevenson & Rylands, 1988). However, in captivity this behaviour appeared to be performed out of context, as in captive conditions no gum exuded from the gouged holes. The occurrence of a natural behaviour out of context may be explained as an expression of animal needs (Dawkins, 1983) or, especially when performed in high frequencies, as a displacement activity (Schino et al., 1991, 1996; Maestipieri et al., 1992). In the present thesis, results of two different studies show that marmosets tree gouged significantly more when conditions were poorer. In Chapter 7 young marmosets gouged significantly more following a loss of control. In Chapter 8, adult marmosets (during the Test phase) gouged significantly more when the device was off. These results suggest that tree gouging (without gum) may be a displacement activity and therefore be indicative of reduced welfare in captive marmosets.

Watching the observer

Significant differences between study conditions in time spent watching the observer were found in all studies in this thesis. In some of these cases the change was time dependent (i.e. marmosets watched the observer significantly less after the Baseline phase) which may suggest that the habituation period of around one week prior to each study was not enough. In other cases, an interaction between study conditions and time spent watching the observer was found. In Study III in Chapter 4, family group-housed adults watched the observer more than pair-housed adult marmosets. This finding suggests that when adult marmosets are housed with their offspring they pay more attention in relation to ‘predator’ risks. In addition, in Chapters 7, 8 and 9, Master marmosets spent more time watching the observer during the Test phase when the device was off. In Chapter 8, Master marmosets watched the observer significantly less than Unaffected individuals during the Test phase and in Chapter 9, only Master marmosets spent significantly less time watching the observer after the Baseline phase. All these findings show that the marmosets watched the observer significantly less when they were able to control lights, which may indicate positive effects of control and/or stimulation (i.e. marmosets were less bored). It is important to emphasize that even when animals do not react to the observer with anti-predator behaviours an assumption that animals are not affected by the presence of a familiar observer (e.g. Stevenson & Poole, 1976) might frequently turn out to be mistaken (Martin & Bateson, 1993) and any change in the observer’s appearance (or odour) might affect the animals’ reaction to him/her. For example, in Chapter 6, during the Outdoor phase, the marmosets watched the observer more than during Test phases in other studies, possibly because the observer’s clothes were different when outdoors from her indoor clothing.

10.1.1 The behaviour of captive and wild marmosets

The behaviour of the marmosets in the present thesis was compared with the behaviour of wild marmosets as a first step in the assessment of the behaviour of captive marmosets in different situations (see Figure 10.1). The activity budget of wild common marmosets has been described in only three studies (see Table 10.1). There is considerable variation between the different studies in the amount of time that wild marmosets spent stationary and feeding. This variation illustrates the difficulties in comparing captive and wild populations, and suggests that any attempt to describe normal behaviour is likely to necessitate using a range of values of several different activities, obtained from studies in a wide variety of environmental contexts.

Table 10.1: The activity budget of wild common marmosets (percentages of time)

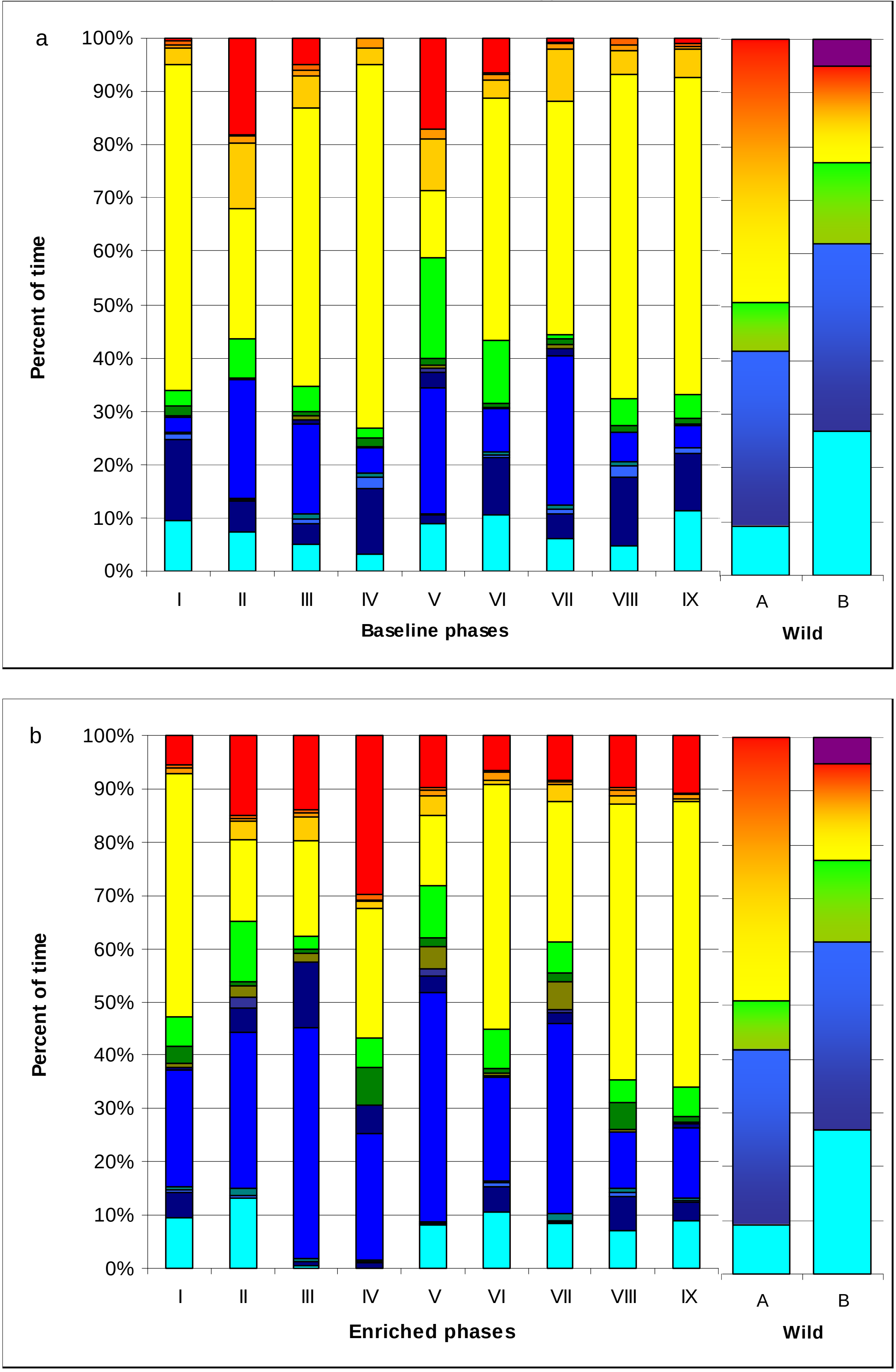
	Stevenson & Rylands, 1988	**Alonso & Langguth, 1989**	**Ferrari & Digby, 1996**
Moving	35% (including foraging)	11%	
Foraging		24%	
Feeding	10%	27%	
Stationary (resting)	53%	18%	
Social activities	10%	15% (grooming)	
Resting+ socializing			37%
Interactions with other groups		5%	

The results of two of these studies (Stevenson & Rylands, 1988; Alonso & Langguth, 1989) are presented in Figure 10.1, in order to compare the activity budgets of the marmosets in the different studies in this thesis with the activity budgets of wild marmosets. Table 10.2 describes the main characteristics of the studies in Figure 10.1.

Figure 10.1 shows that the activity budgets of captive marmosets are in fairly good agreement with those of their wild conspecifics, especially when housing conditions are improved (see columns I, IV and VI in Figure 10.1 b). Erkert (1997) also found similarities in behavioural data obtained under laboratory and natural conditions (although no actual data on the activity budget of captive marmosets are provided in the study). However, the activity budget of captive marmosets remains different (albeit similar) from that of wild populations. In particular, wild marmosets spend more time foraging and feeding than their captive conspecifics, as it requires less time to feed on dry pellets and chopped fruits that are served virtually into the monkeys' palm just once or twice daily. The differences between wild and captive animals emphasize the necessity of establishing a 'normal activity budget' for captive marmosets, to allow the comparison between various captive situations and improve the assessment of welfare.

A noteworthy point that is illustrated very clearly in Figure 10.1 is that even though overall levels of locomotion and inactivity were not considerably affected by the manipulations in some of the studies, patterns of these behaviours were changed. In the Enriched phases of all studies the marmosets appeared to be more relaxed, i.e. showed higher levels of inactive rest and calm locomotion and lower levels of inactive alert and agitated locomotion. This finding emphasizes the necessity of dividing locomotion and activity measures into two different categories. In most enrichment studies (e.g. McKenzie et al., 1986; Schoenfeld, 1989; Kerl & Rothe, 1996; Kitchen & Martin, 1996; Roberts et al., 1999; de Rosa et al., 2002; Pines et al., 2002, 2003, 2005; Bassett et al., 2003; Ventura & Buchanan-Smith, 2003; Chamove & Scott, 2005) such a discrimination is missing, which may explain the lack of significant differences between different conditions (e.g. Kitchen & Martin, 1996; de Rosa et al., 2002; Pines et al., 2003; Ventura & Buchanan-Smith, 2003).

Figure 10.1: Activity budget of marmosets during Baseline (a) and Enriched (b) phases in the present thesis compared with that of wild marmosets (A-Stevenson & Rylands, 1988; B-Alonso & Langguth, 1989)



Legend to Figure 10.1

	Feed	**Moving + foraging**	**Social activities**	**Stationary**	**Interaction with other groups**
Captive animals	🟦 Forage + feed	🟦 Solitary play	🟩 Contact	🟥 Inactive rest	
		🟦 Explore	🟩 Allogroom	🟧 Autogroom	
		🟦 Calm locomotion	🟩 Social play	🟧 Scratch	
		🟩 Tree gouge		🟨 Watch observer	
		🟦 Scent mark		🟨 Inactive alert	
		🟦 Agitated Locomotion			
Wild animals	🟦	🟦	🟩	🟧	🟪

Table 10.2: Description of the studies in Figures 10.1 and 10.6

Column in Figures	**Study, Chapter**	**Natural aspect**	**Manipulation**	**Housing and age of individuals**
I	II, 4	Complexity/choice	Cage size and complexity	Pairs
II	5	Complexity/choice	Cage size and complexity	Family (all individuals)
III	II, 6	Complexity/choice	Free access to outdoors	Family (youngsters)
IV	II, 6	Complexity/choice	Free access to outdoors	Family (adults)
V	7	Control	Additional light	Family (youngsters)
VI	7	Control	Additional light	Family (adults)
VII	8	Control	Coloured lights	Family (youngsters)
VIII	8	Control	Coloured lights	Family (adults)
IX	9	Control	Additional light	Pairs

10.1.2 Activity budget of captive common marmosets

In order to establish an improved understanding of the ‘normal’ behaviour of captive common marmosets, quantitative data on locomotion, inactivity and scent marking from several studies were compared. Only data from adult marmosets (or whole family groups, if impossible to separate) were used as there are few studies that provide data on young individuals in the literature (but see Epple, 1970b; Box, 1975a, for data on scent marking). By and large, the comparison of data from different studies is very difficult for several reasons. First, in many studies no comparable data are provided (e.g. Box, 1975a, 1988; Vignes et al., 2001; Ventura & Buchanan-Smith, 2003). Second, in some studies data collection methodology is so different that comparisons are not valid (e.g. Chamove & Rohrhuber, 1989; Schoenfeld, 1989; Pines et al., 2002, 2003). Third, behavioural definitions are inconsistent between studies. Despite all these difficulties, a comparison between data from some studies which provide data that may be validly compared is given below.

Locomotion

A comparison between quantities of locomotion of captive marmosets in different conditions is provided in Figure 10.2. Table 10.3 describes the studies in this Figure. Data are given for baseline and enriched captive conditions as well as for wild marmosets. Data are given for different types of activity and locomotion and therefore comparisons are not straightforward.

Figure 10.2: Mean durations of locomotion of captive and wild marmosets (description of the different studies is given in Table 10.3; F- Family housed; P- Pair housed; S- Socially housed, exact composition is unknown)

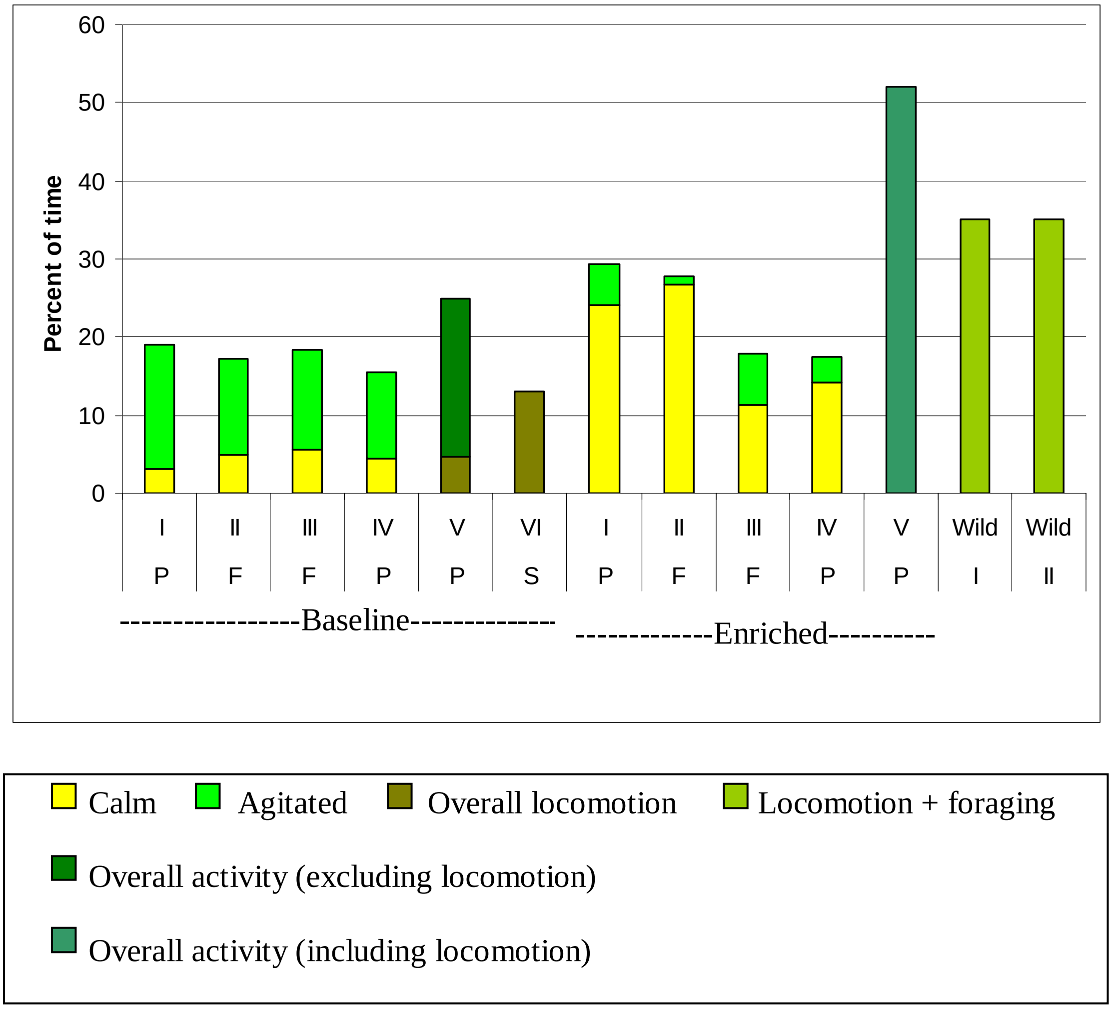


Table 10.3: Description of the studies in Figure 10.2

Column in Figure 10.2	**Study**	**Sample size**	**Enrichment**
I	Study II, Chapter 4	19 pairs	Larger and more complex cage
II	Study II, Chapter 6	8 groups	Outdoor cages (complexity, choice)
III	Chapter 8	6 groups	Control over coloured lights
IV	Chapter 9	18 pairs	Control over white light
V	Kitchen & Martin, 1996	5 pairs	Larger and more complex cage
VI	Chamove & Scott, 2005	unknown	No behavioural data when enriched
Wild I	Stevenson & Rylands, 1988;	6 groups	Natural conditions
Wild II	Alonso & Langguth, 1989	unknown	Natural conditions

Total time spent in locomotion varies from 13%-19% (25% overall activity including locomotion, but unclear as to which behaviours are included, Kitchen & Martin, 1996) in baseline (non-enriched) conditions and from 18%-29% (52% overall activity, Kitchen & Martin, 1996) in enriched conditions.

The wild comparison is 35%. It is clear that larger, more complex enclosures encourage higher proportions of locomotion. However, what is arguably more important is the proportion of calm locomotion to agitated locomotion that is illustrated in Studies I-IV and which changes markedly between housing conditions. The results of these studies show that the mean proportion of calm locomotion to overall locomotion is 0.26 in baseline conditions and 0.80 in enriched conditions.

Inactivity

Figure 10.3 compares percentages of time that marmosets spent inactive in different captive and natural settings (studies are described in Table 10.4). Data on inactivity are varied for both captive and natural settings and hence are very difficult to compare. It is important to emphasize again that in most welfare studies, no discrimination is made between different types of inactivity. Total time spent inactive varies from 33%-68% in baseline conditions and from 24%-56% in enriched conditions. Despite the decrease in mean levels of inactivity, differences between baseline and enriched conditions are less obvious than they are for locomotion.

Figure 10.3: Mean durations of inactivity of captive and wild marmosets
(description of the different studies is given in Table 10.4; F- Family housed; P- Pair housed; S- Singly housed; So- Socially housed, exact composition is unknown)

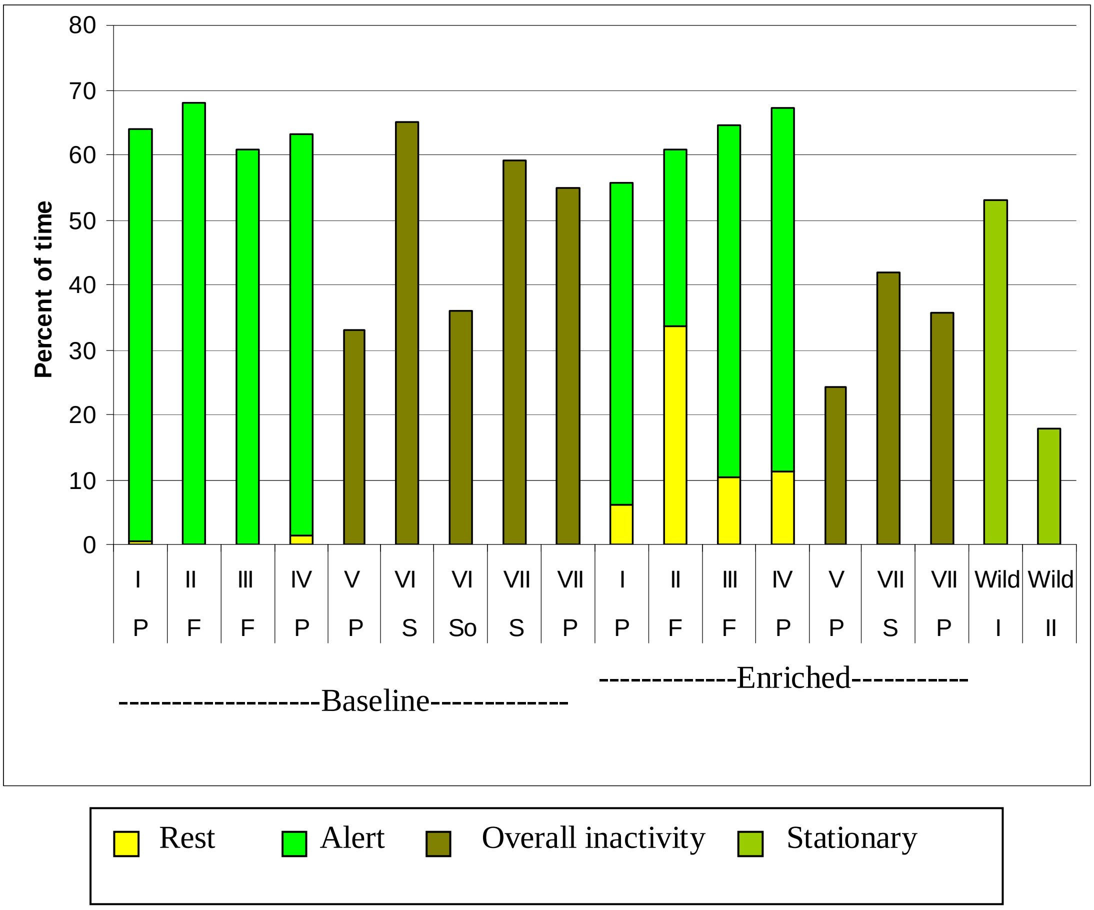


Table 10.4: Description of the studies in Figure 10.3

Column in Figure 10.3	**Study**	**Sample size**	**Enrichment**
I	Study II, Chapter 4	19 pairs	Larger and more complex cage
II	Study II, Chapter 6	8 groups	Outdoor cages (complexity, choice)
III	Chapter 8	6 groups	Control over coloured lights
IV	Chapter 9	18 pairs	Control over white light
V	Kerl & Rothe 1996	1 male	Larger and more complex cage
VI	Chamove & Scott, 2005	unknown	No behavioural data when enriched
VII (single)	Roberts et al., 1999	16	Feeding enrichment
VII (pairs)	Roberts et al., 1999	12 pairs	Feeding enrichment
Wild I	Stevenson & Rylands, 1988	6 groups	Natural conditions
Wild II	Alonso & Langguth, 1989	unknown	Natural conditions

There is a great variation between studies from wild populations of marmosets in recorded levels of time spent inactive (18%-53%) probably due to inconsistent definitions. The results of studies I-IV show that only small proportions of overall inactivity were defined as inactive rest. Nevertheless, differences between housing conditions in proportions of inactive rest to inactive alert are still shown. In baseline conditions the mean proportion of inactive rest to overall inactivity is 0.008 while in enriched conditions inactive rest occupies 0.25 of overall inactivity.

It is concluded from these comparisons that it is not necessarily the total quantity of locomotion and inactivity that is critical for welfare, but the type of locomotion and inactivity. Attempts should be made to provide captive conditions in which marmosets show decreased levels of agitated locomotion and increased levels of inactive rest (inalert). Providing larger and more complex cages is clearly one way to encourage this, but changes in care staff routine and interactions may also be critical.

Scent marking

Levels of scent marking have been recorded for both wild and captive common marmosets and data for adult individuals are compared in Figure 10.4 (Table 10.5 provides a description of the studies). Data are provided in mean frequencies per hour for baseline, enriched, post-stress and wild situations (in the different studies data for only some of these conditions are available). In all studies data required further analysis in order to obtain the comparable mean frequencies necessary for this comparison.

Figure 10.4: Mean frequencies/hour of scent marking of captive marmosets (description of the different studies is given in Table 10.5; F- Family housed; P- Pair housed)

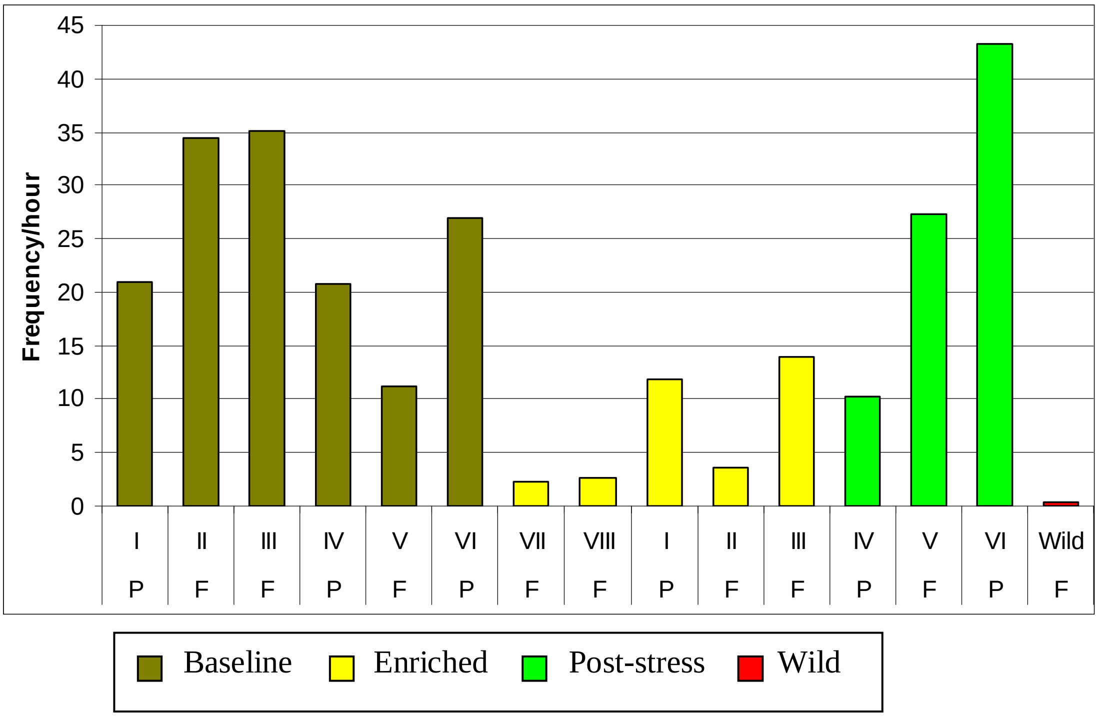


Table 10.5: Description of the studies in Figure 10.4

Column in Figure 10.3	Study	Sample size	Enrichment/ stress
I	Study II, Chapter 4	19 pairs	Larger and more complex cage
II	Study II, Chapter 6	8 groups	Outdoor cages (complexity, choice)
III	Chapter 8	6 groups	Control over coloured lights
IV	Chapter 9	18 pairs	Control over white light
V	Epple, 1970b	1 group	Male or female intruders
VI	Bassett et al., 2003	6 pairs	Capture and weighing
VII	Nogueira et al., 2001	6 groups	Natural outdoor cages
VIII	de Sousa et al., 2006	8 groups	Natural outdoor cages
Wild	Lazaro-Perea et al., 1999*	5 groups	Natural habitat

* Results are giving as a mean of all group members and not for adults only

It can be seen that frequencies of scent marking are much lower in wild populations (range 0.19/h-0.45/h) than in their captive conspecifics. However, for wild marmosets data are given as mean frequencies of whole family groups (and not adults only as in data from captive populations). It is likely that a small part of the difference between wild and captive rates stem from the difference in the available data as rates of scent marking for adults are higher than for young animals, as has been shown in captivity (de Sousa et al., 2006). In captivity, rates of scent marking are highest in post-stress situations (range 27.3/h-43.2/h) and lowest in outdoor conditions, when marmosets have only olfactory and auditory contact with neighbouring groups (2.2/h-3.6/h). This finding is in agreement with previous research regarding effects of proximity to other groups on levels of scent marking (Stevenson & Poole, 1976; Box, 1977b, 1984a; Sutcliffe & Poole, 1978; see below). It is noteworthy to emphasize that when studying rates of scent marking it is important to consider the age of the animals together with the time of the day since these factors have been found to significantly affect levels of scent marking in captive marmosets (de Sousa et al., 2006). The effect of sex on levels of scent marking is yet not clear and results of previous studies are contradictory. Some studies have found no significant effect of sex (e.g. Epple, 1970b; Sutcliffe & Poole, 1978; Nogueira et al., 2001), while others found that adult female scent mark significantly more than adult males (de Sousa et al., 2006).

The behaviour of captive marmosets in various housing and experimental conditions was compared in order to establish the ‘normal’ activity budget of common marmosets in captive conditions. This first comparison demonstrates the difficulties in carrying out such a process. However, it is obvious that the establishment of values for the ‘normal’ behaviour of marmosets and other animals in captive conditions is essential for research on animal welfare and to allow cross-laboratory comparisons. For the present thesis data regarding the behaviour of the marmosets in improved conditions (i.e. higher levels of complexity, choice and control) were compared with baseline data from the enriched individuals, together with data from unaffected (in most studies) and sometimes yoked individuals (Chapter 9). The main effects of complexity, choice and control are presented in Table 10.6 and discussed below.

10.2 COMPLEXITY

Natural habitats are more complex and variable than captive environments and therefore provide far more stimulation. The lack of environmental challenge in captive environments may lead to apathy and boredom (Wemelsfelder & Birke, 1997). It has been suggested that the complexity of captive environments has a significant impact on the welfare of captive primates (e.g. Snowdon & Savage, 1989; Novak & Drewsen, 1989). The positive effects of physical complexity on welfare (e.g. Kitchen & Martin, 1996; Kerl & Rothe, 1996), infant development (Ventura & Buchanan-Smith, 2003) and biochemical structure of the brain (Kozorovitskiy et al., 2005) of marmosets have been previously shown. However, the influence of social complexity on the welfare of callitrichids has not been studied extensively. In many studies the effects of different aspects of environmental complexity have been investigated simultaneously. For example, Bayne and colleagues (1992a) studied the behaviour of rhesus macaques in several housing conditions. These housing conditions differed from each other in terms of cage size, cage location (indoors/outdoors) and group composition (individually/socially housed). The results of such a study could not provide clear evidence on the effects of any one of these aspects of environmental complexity. In the present thesis, housing conditions also sometimes differed from each other in several aspects (e.g. cage size and location); however, a comparison between the different studies may enable a clearer evaluation of the effects of each separate factor.

Table 10.6: Effects of complexity, choice and control on the behaviour of common Marmosets: A summary of the main results of the present thesis

Chapter	Study	Group composition	Elevated levels	Reduced levels
4	Cage size & complexity	Pairs	Inactive rest Calm locomotion	Inactive alert Agitated locomotion Watch observer
5	Cage size & complexity	Family group	Explore Solitary play	
6	Complexity, choice & outdoor conditions	Family groups (youngsters)	Calm locomotion Explore Watch observer	Agitated locomotion Inactive alert Scent mark Scratch
6	Complexity, choice & outdoor conditions	Family groups (adults)	Calm locomotion Explore	Inactive alert Contact
6	Occasional access to complexity, choice & outdoor conditions	Family groups (youngsters)	Calm locomotion Explore	Inactive alert Scent mark
6	Occasional access to complexity, choice & outdoor conditions	Family groups (adults)	Calm locomotion Inactive rest Allogroom Explore	Agitated locomotion Inactive alert Scent mark Scratch
7	Control over additional light	Family groups (youngsters)	Calm locomotion Solitary play Social play Usage of lower part of cage	Inactive alert Inactive rest Scent mark Watch observer Tree gouge Usage of upper part of cage
7	Control over additional light	Family groups (adults)	Calm locomotion	
8	Control over coloured light	Family groups (youngsters)	Social play Solitary play Explore (only main effect)	Inactive alert Watch observer
8	Control over coloured light	Family groups (adults)	Calm locomotion Inactive rest	
9	Control over additional light	Pairs	Calm locomotion Inactive rest	Agitated locomotion Inactive alert Watch observer

10.2.1 Physical complexity

The physical complexity of the captive environment includes the size of the enclosure, its furnishings and its location. The size and the furnishings of captive environments are linked together in relation to complexity as larger enclosures allow the provision of more furniture. It has been also argued that only appropriate cage furnishing allows an effective utilization of the entire cage space (e.g. Novak, 1989; Poole, 1990; Buchanan-Smith, 1997a; Reinhardt & Reinhardt, 2001). Physical complexity of a particular enclosure could be measured in relation to the total quantity of furniture or as a function of the number of devices per unit volume. However, reference to the total number of devices seems more logical as the animals make use of their whole enclosure as one unit and the quality of it as a complete environment is what really matters. The effects of each environmental component will now be discussed separately.

Cage size

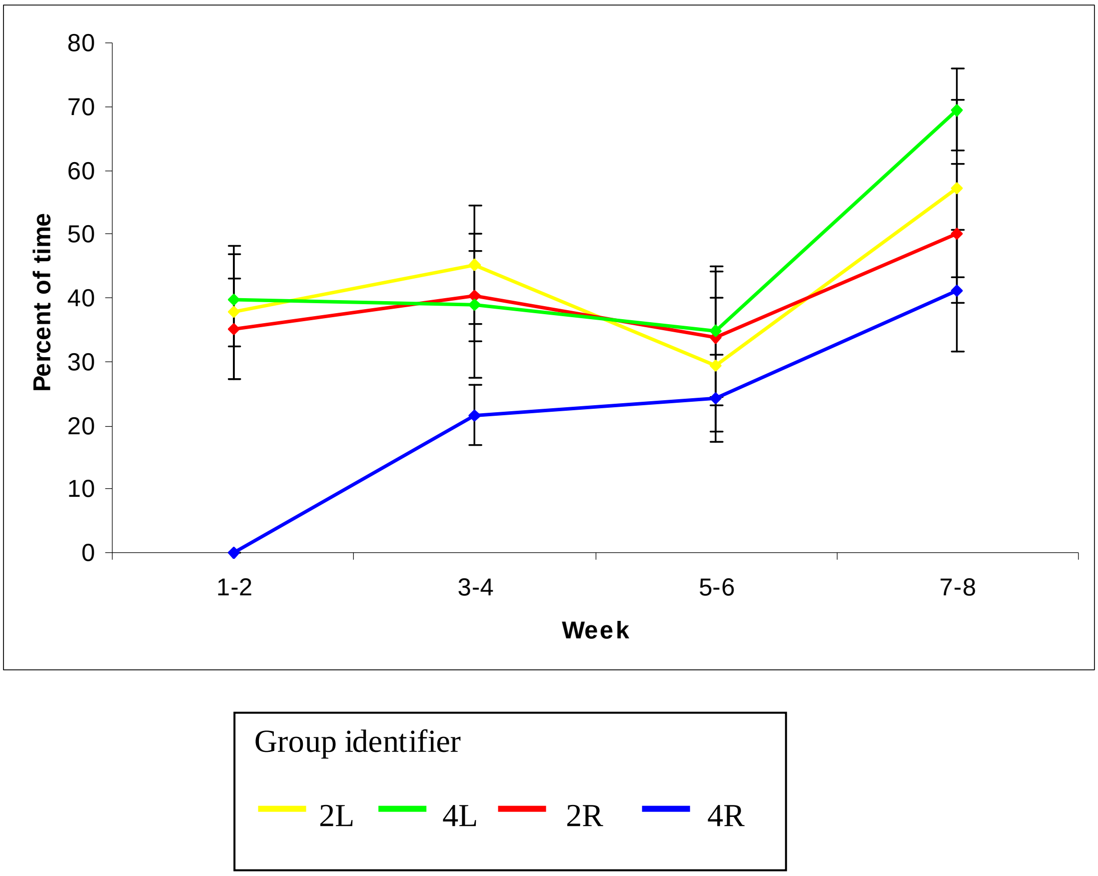
Previous research has shown positive effects of larger cage sizes on the welfare of socially housed callitrichids (e.g. Box & Rohrhuber, 1993; Kitchen & Martin, 1996; Pines et al., 2002, 2003) and other primates (e.g. Southwick, 1967; Alexander & Roth, 1971; Nash & Chilton, 1986). Findings concerning individually housed primates are contradictory and questionable as in some studies all cages were very small (e.g. Line et al., 1990b, 1991a; Crockett et al., 1992, 1993, 1995, 1996) and/or very minimally furnished (e.g. Line et al., 1990b, 1991a; Crockett et al., 1996). The results of all studies in the present thesis are in accord with previous research on socially housed primates, showing positive effects of larger enclosures. However, it is impossible to separate the effects of cage size from those of enclosure furnishings (and location in some studies), as in all studies larger enclosures contained more furniture. In Study II in Chapter 4, double cages were furnished similarly to single cages, only containing more devices of the same type. In this study only locomotion and inactivity patterns were affected, but marmosets were more active and more relaxed in the larger cages.

Cage furnishing

Appropriate furnishings and cage design are good way to increase complexity in captive environments. Any enclosure may become more complex by adding simple equipment, and no vast expense is required (in contrast to the possible costs of enlarging enclosure size or changing locations). Previous studies have shown that furnishing has a greater influence on welfare than increased cage size alone (Kerl & Rothe, 1996; Gaspari et al., 2000). Findings of the present thesis also show positive effects of more equipped enclosures. However, the relatively small impact of a more complex enclosure on the behaviour of a family group of marmosets (Chapter 5) was unexpected. The enriched enclosure in this study was larger and more complex (if the location is not considered) than the outdoor cages in Chapter 6. It is possible that the fewer significant differences stemmed from the small sample size in this study (only one family group). Alternatively, it is possible that the outdoor location of the enriched cages in Chapter 6 and/or the choice that the marmosets were given between the home cages and outdoor enclosures had greater effects on their behaviour than the size and design of the enclosure.

One problem in providing primates with complex environments is that they may habituate to the complex environment after a prolonged exposure to it and its positive influence may weaken (see Kitchen & Martin, 1996). It has been suggested that rotation of enrichment objects may extend the positive effects of enriched environments (Paquette & Prescott, 1988; Line et al., 1991b; Morgan et al., 1998). However, previous findings on the influence of object rotation are unclear (Weld & Erwin, 1990). Bayne (1989a; Bayne & Dexter, 1992) even suggested that the rotation of familiar objects might be stressful to the animals. An alternative way to continue the positive influence of complex environments may be occasional exposure to such environments. This method is usually used due to a restricted budget and/or space limitations (e.g. Bryant et al., 1988; O'Neill, 1989a, 1989b; Salzen, 1989; Kessel & Brent, 1995a, 1995b; Tustin et al., 1996). In Chapter 6 of the present thesis, marmosets were exposed to enriched outdoor enclosures continuously for eight weeks (Study I), or occasionally (Study II) over a similar period. The results of these studies show similar positive effects of exposure to the complex enclosures. An analysis of the usage of these outdoor enclosures by the marmosets in Study I, shows no reduction in use throughout the whole study period (see Figure 10.5). In the last two weeks of the study the marmosets used the outdoor cages even more than they did in the first six weeks. Results of ANOVA show a significant change in mean temperature across two week blocks ($F_{3,15}$=8.26; P=0.006). However, results of Tukey post-hoc tests show that the only significant difference was between the higher mean temperature during the last two weeks of the study and that in the three first two week blocks. The finding that the marmosets did not reduce usage of outdoor cages across the first six weeks of the study shows that there was no habituation to the enriched conditions. However, further analyses and research are required to investigate the effects of time on the influence of this prolonged exposure on the behaviour of the marmosets.

Figure 10.5: Percentage time of outdoor cage usage for marmosets in Study I throughout the study period (Chapter 6)



Cage location

In common with previous findings on callitrichids (e.g. Redshaw & Mallinson, 1991; Pines et al., 2002, 2003), the results of the studies in Chapter 6 show a positive impact of exposure to outdoor conditions. In Chapter 6, more significant differences were found between the study conditions compared with Study II in Chapter 4 and with the study reported in Chapter 5. These differences between the studies emphasize the significance of exposure to outdoor conditions and suggest that this exposure contributes more to the complexity of the environment than cage size and furnishing. However, it is important to stress that in Chapter 6 the marmosets were not only exposed to more complex outdoor enclosures, but they were also allowed to choose between their indoor home cages and these enclosures. Therefore, it is likely that the choice that was experienced also contributed to the improved welfare of the marmosets (see below).

10.2.2 Social complexity

The social environment of captive animals may be more significant, and its ramifications more complicated, than those of the physical environment. Social interaction is of great importance to the welfare of captive primates (e.g. Wolfensohn & Honess, 2005; Rennie & Buchanan-Smith, 2006b). Scientists generally agree that captive primates should be provided with a social environment that is as close as possible to their natural social group composition (e.g. Poole, 1990; Buchanan-Smith, 1994, 1997a; Honess & Marin, 2006). However, the findings of Chapter 4 contradict this approach, indicating that adult marmosets are more relaxed when housed in pairs rather than in family groups (which would be more natural for them, Ferrari & Lopes Ferrari, 1989; Arruda et al., 2005). These results are unexpected and were discussed in Chapter 4.

The composition of the study groups also affected the reactions of adult marmosets to the study manipulations. In Chapters 7 and 9, marmosets were given control over additional light in their home cage. The results of these studies show that adult marmosets were more affected by the additional light, and by controllability, when they were housed in pairs than when in family groups. These findings are in line with Box (1984a) who found that non-parent adult marmosets were faster to respond and more active with respect to novel objects than were parents. In contrast, Vignes and co-workers (2001) found no effects of group composition on the reactions of common marmosets to novel food enrichment. The results of the present thesis and of Box's study (1984a) suggest that adult marmosets are more stressed and less aware of environmental opportunities when housed with their offspring. However, a comparison between columns VI, VIII and IX in Figures 10.1 and 10.6 shows that adults in both group compositions react in a similar way to controllability. This suggests that the more significant differences between study conditions that were found for pairs were due to the larger sample size (6 family groups vs. 18 pairs). It is also important to mention that when family groups of marmosets were given the choice between their home cages and outdoor enclosures all family members, including adult parents, used the outdoor cages and their behaviour was positively affected. Therefore, it may be suggested that the provision of choice and/or exposure to outdoor (more natural) conditions is more significant to the welfare of captive marmosets than cage furnishings, and/or controllability (over unnatural environmental aspects), as even adults in family groups are positively affected by them.

Another aspect of the social environment is proximity to other groups of marmosets, which is usually more intense and frequent in laboratory conditions than in the natural habitat (Stevenson & Poole, 1976; Box, 1984b). Previous studies have shown that marmosets showed decreased levels of scent marking when they were moved to an enclosure where they had no contact with other marmoset groups (Box, 1977b, 1984a), and increased levels of scent marking when they had visual contact with other groups (Sutcliffe & Poole, 1978). In Chapter 6, the marmosets had no visual contact with other groups in the outdoor cages (in contrast to the indoor cages). Further, in the outdoor cages they had less olfactory and auditory contact with other groups than they had in the indoor cages as there were only four groups at a time outdoors, while the indoor colony rooms contained at least eight different family groups. It is possible that the reduction in the amount of contact with neighbouring groups played a role in the positive impact of the outdoor conditions on the welfare of the marmosets. In common with previous studies on the effects of contact with other groups, the marmosets scent marked less outdoors than indoors (although previous presence of other marmoset groups in the same outdoor enclosures may have caused increased levels of scent marking).

Similarly, in Chapter 5, the family group had no contact with other marmoset groups when housed in the enriched enclosure. However, it is impossible to separate the effects of this factor from those of other variations between the different housing conditions. Few significant behavioural differences were found between baseline and enriched conditions in this study. Nevertheless, this family group grew to 17 individuals, which is not only much larger than family groups in colony rooms in the same laboratory (maximum 9 individuals), but is also large compared to marmoset groups in natural habitats, in which the largest group that has been observed has comprised 15 individuals (Scanlon et al., 1989). It is likely that the lack of contact with other groups contributed to the stability of this group as the marmosets were more relaxed.

Interaction with humans is an additional aspect of the social complexity of captive primates. The importance of the human-animal bond has been previously described (e.g. Roberts, 1989; Bayne, 2002; Cosgrove, 2004; Rennie & Buchanan-Smith, 2006a). Although this aspect of social complexity was not formally studied in the present thesis, it is noteworthy to mention the salient influence of housing conditions on the interaction between the marmosets and the laboratory technicians. When housed in the standard laboratory cages (in all sizes) in colony rooms, the marmosets tended to avoid close proximity to technicians and became agitated when they enter the room. In contrast, in the larger enriched enclosures (in Chapters 5 and 6) where humans could walk into the marmoset enclosures (in the enriched enclosure in Chapter 5 they had to do it on a daily basis, in order to feed the animals), the marmosets tended to interact with the technicians (or any other humans who entered their enclosures) voluntarily, showing curiosity and hardly any signs of fear. Further, the care staff enjoyed to being able to interact with the marmosets in such a positive way and their attitude towards the marmosets improved as a consequence. However, this phenomenon was not officially studied and hence will not be discussed any further.

10.3 CHOICE

Complexity and choice are strongly linked; thus, as environmental complexity increases, animals experience more choice. However, it is difficult to investigate the influence of choice *per se* as it is usually confounded with the effects of the choices provided. As a consequence, the impact of choice on the behaviour of animals has not been studied extensively (but see Chapter 2). Animals have many choices in their natural habitats and the provision of choice to captive animals may have various beneficial effects (Huchinson, 2005). Captive marmosets have been given choice between foods (Petto & Devin, 1988), cage locations (Ely et al., 1997) and nest boxes (Hosey et al., 1999). However, in none of these studies was the influence of choice *per se* examined.

In the present thesis, the effects of choice *per se* were also not separated from other aspects of the studies. Whenever the marmosets were housed in complex enclosures (Chapters 4, 5 and 6) they also experienced more choice. In Study II in Chapter 4, marmosets were able to choose between lower and upper parts of their cage. All marmosets, regardless of their familiarity with cage location, chose to spend significantly more time in the upper part of the cage. This finding suggests that doubling vertical space does not double utilizable space as marmosets use the upper half of the cage for more than 80% of the time. The level of the single cage that the marmosets had previously occupied did not appear to affect the behavioural changes in the marmosets after they were moved to the double cages. These findings suggest that both the size of the cage and the ability to choose location affected the marmosets' welfare positively. Further, Kitchen and Martin (1996) found that marmosets used the lower part of high cages more when the cages were more complex. Ely and colleagues (1997) also found that marmosets used the upper part of their cage more than the lower part of it. The authors suggested that monkeys prefer to avoid the lower part of their cage when insufficient furniture is provided to allow them to perform vertical flight behaviour. In this study, lower and upper parts of the cages were furnished identically and the furniture provided the marmosets with relatively easy access between cage locations. However, the marmosets preferred the upper part of the cage and used the lower part of it only occasionally (to get food for instance). To sum up, the complexity (furnishings) of the cage may affect the animals' choice between different locations inside the cage.

Similarly, in Chapter 6, the marmosets had a choice between their indoor home cages and the outdoor enclosures (which also allowed more choice as they were more complex). Here again, one could argue that it is useless to provide marmosets with access to outdoor enclosures in cold weather, as it was found that they utilized the outdoor enclosures significantly less when the temperature was under 18ºC. However, marmosets were observed outdoors even when the temperature was 10ºC (formal data) and lower (informal data). Previous research has also shown that primates used outdoor enclosures in extreme weather conditions (Bernstein, 1980; O'Neill-Wagner & Price, 1995). These findings suggest that the choice between different enclosure locations remains beneficial even when the monkeys do not use all enclosures at the same rates. Access to an additional enclosure may be used at least as a refuge from agonistic encounters and as an opportunity to control proximity to other group members (Rumbaugh et al., 1989).

A comparison between the effects of the loss of complexity and choice in Chapters 5 and 6 may provide a better indication of the effects of choice *per se*. In Chapter 6 the marmosets had free access between the two enclosures and showed no significant impact of the loss of this access. In contrast, in Chapter 5 the marmosets were housed in an enriched enclosure and on a few occasions were moved to smaller and less complex cages. The effects of these environmental changes were significantly negative. These differences between the studies may suggest that the choice between the enclosures had positive effects on the welfare of the marmosets in Chapter 6. However, the effects of choice *per se* are not clear as yet and further research on this issue is required. At any rate, although it has been previously found that too much choice may not be desirable for humans (Savage et al., 1979; Iyengar & Lepper, 2000), it is unlikely that captive nonhumans will suffer from too much choice as choices will always be fewer compared to those in natural environments.

10.4 CONTROL

It is obvious that the natural habitat of marmosets is complex and that wild marmosets experience a large amount of choice in their daily life, but do they control their environment? After all, they cannot switch the sun on and off, and they do not press levers in order to earn food, so what do we really mean when we say that wild animals have control over their environment? Snowdon and Savage (1989) argued that "animals must be able to act on the environment and consequences must result from their actions" (p. 81). Wild animals are free to act on environmental changes and it is possible that this freedom demonstrates their ability to exercise control over their environment. Barnes (1981, p. 410) suggested that "the extent to which the environment enables a person to successfully achieve plans and goals determines the person's level of satisfaction with himself or herself and with the environment". Barnes described the emotional reactions of human beings to their interaction with the environment; however, this argument may also be appropriate when describing the interactions of nonhuman animals with their environment. Thus, natural habitats provide the animals with more freedom to fulfil their motivations (i.e. they may control their own actions) and therefore they may be more satisfied than captive animals, which lack this freedom.

Many scientists have argued that captive animals should be provided with opportunities to control their environment (e.g. Bayne, 1989a; Chamove & Anderson, 1989; Line et al., 1990a; Scott, 1991; Buchanan-Smith, 1997a). Nevertheless, little research has been done on the effects of control over positive stimuli on welfare. Furthermore, as mentioned in Chapter 2, studies in which the authors argued that they allowed animals to exert some control are very different from each other. Skinner

(1996) suggested that when the same term refers to very different constructs, findings may appear inconsistent or even contradictory when in fact it is the definitions that are inconsistent. This is the case in control studies and thus it is necessary to provide an appropriate definition for the term ‘control’ and especially to discriminate between the various levels and types of control that may be given to captive animals.

Sambrook and Buchanan-Smith (1997) defined control as the likelihood of an event occurring depending on an animal’s behaviour. They also provided grades of controllability in novel objects (p. 212):

1) Fixed- animal can move only with respect to object (e.g. swinging on bars).
2) Moveable- animal and object free to move with respect to each other and enclosure (e.g. throwing or pushing objects, transfer between animals).
3) Malleable- action applied to point on object results in effect at same location (e.g. squeezing rubber ball, bouncing on tree limbs).
4) Analogue- action applied at one point generates analogue effect at another (e.g. use of levers).
5) Digital- no analogue relationship between cause and effect (e.g. most electronic mechanisms).

According to these authors, the grades are ordered in terms of increasing sophistication of cause and effect relationships. Therefore, the higher grades are unnatural and may be undesirable in captive environments by those who support the natural approach to environmental enrichment. On the other hand, if animals provided with enrichment graded in any of these categories are consequently considered to have control, then almost all captive animals exert some level of control over their environment. However, the effectiveness of this controllability is questionable. Those who support the behavioural engineering approach to environmental enrichment would argue that it is more effective to provide captive animals with higher levels of controllability, even by using artificial techniques to enable this control (Markowitz, 1982; Barber & Kuhar, 2006). This last approach appears to be more useful in laboratories which, in contrast to zoos, have more freedom to provide any kind of enrichment, even very artificial, and usually are not able to provide the animals with naturalistic environments. Zoos, on the other hand, are more restricted in enclosure design as they are obliged to stick to more ecologically relevant stimulation and natural behaviours, due to their responsibility for public education and conservation (Kreger et al., 1998; Young, 2003). The contribution of this approach to the welfare of the animals is debatable.

Sambrook and Buchanan-Smith (1997) graded levels of control by the action that was necessary in order to exert control. I would like to suggest a classification of degrees of control dependent on the consequences of the animal’s behaviour and its implications for the animal itself. In other words, control would be classified by the degree to which the animal’s behaviour changes its environment, and the effects of this change on the animal. By performing various behaviours in different situations (see grades of controllability above, Sambrook & Buchanan-Smith, 1997) animals may cause changes in different aspects of their environment. These changes may be described as levels of control that the animal has over its environment (see Table 10.7).

Table 10.7: Degrees of control that an animal may exert over its environment

Type of control	**Description**	**Examples from literature**
Attaining food	The animal earns food by exerting work	Markowitz, 1982; Swaisgood et al., 2005
Changing location of a particular object	The animal is able to move objects within the environment	Bayne, 1989a
Changing characteristics of a particular object	The animal is able to change structure of objects or able to produce sounds from a particular object	Yanofsky & Markowitz, 1978; Sheferly et al., 1993; Sambrook & Buchanan-Smith, 1996; Brent & Stone, 1998; Vick et al., 2000; Ross et al., 2000; Tarou et al., 2002, 2004; Videan et al., 2005
Changing aspects of part of the environment	By changing the structure of objects the animal change parts of the environment (e.g. disperse pieces of paper or cardboard on the floor)	Fujita, 1987, 2001; Shefferly et al., 1993; Brent & Stone, 1998; Videan et al., 2005; Chapter 8 this thesis
Changing general characteristics of the environment	The animal change general characteristics of the entire environment (e.g. illumination, thermal conditions, music)	Goodrick, 1970; Joffe, 1973; Kavanau, 1964, 1978; Savory & Duncan, 1982; Jones & Nicol, 1998; Taylor et al., 2001; Chapters 7 & 9 this thesis
Changing location	The animal is able to move between separate enclosures and hence control its physical and/or social environment	Rumbaugh et al., 1989; Chapter 6 this thesis

The above classification suggests that almost any type of enrichment provides the animals with some degree of control; however this degree depends on the quantity and the quality of the environmental change that the animal causes by its behaviour. The greater change the animal's behaviour causes, the greater the degree of control that the animal has. It is essential to emphasize that Table 10.7 is not entirely graded. For example, attaining food is not necessarily less sophisticated in terms of control than changing characteristics of the environment, and changing locations is not necessarily more sophisticated than changing environmental features. These first and last grades in the table are arguably not necessarily related to control. Some scientists consider that attaining food through work is a type of control that the animals gain over the environment (e.g. Mineka et al., 1986; Line et al., 1990a; Roma et al., 2006).

However, according the definition of Sambrook and Buchanan-Smith (1997), this behaviour could not be described as controllability as by performing it, animals reduce the likelihood of getting food compared to the option of getting free food (i.e. work reduces time for eating free food). The last example in Table 10.7 is also questionable. By changing its own location, the animal's behaviour does not cause any change in the environment, but for the animal itself the whole environment has been changed. In the present thesis such an option was given to the marmosets in Chapter 6 where they were allowed free access between two different enclosures. In the present thesis I used the term choice to describe this specific contingency; alternatively one could have argued that the marmosets had control over their own location and their companions. This case demonstrates again the confusion between choice and control and the difficulty of drawing clear distinction between the two terms.

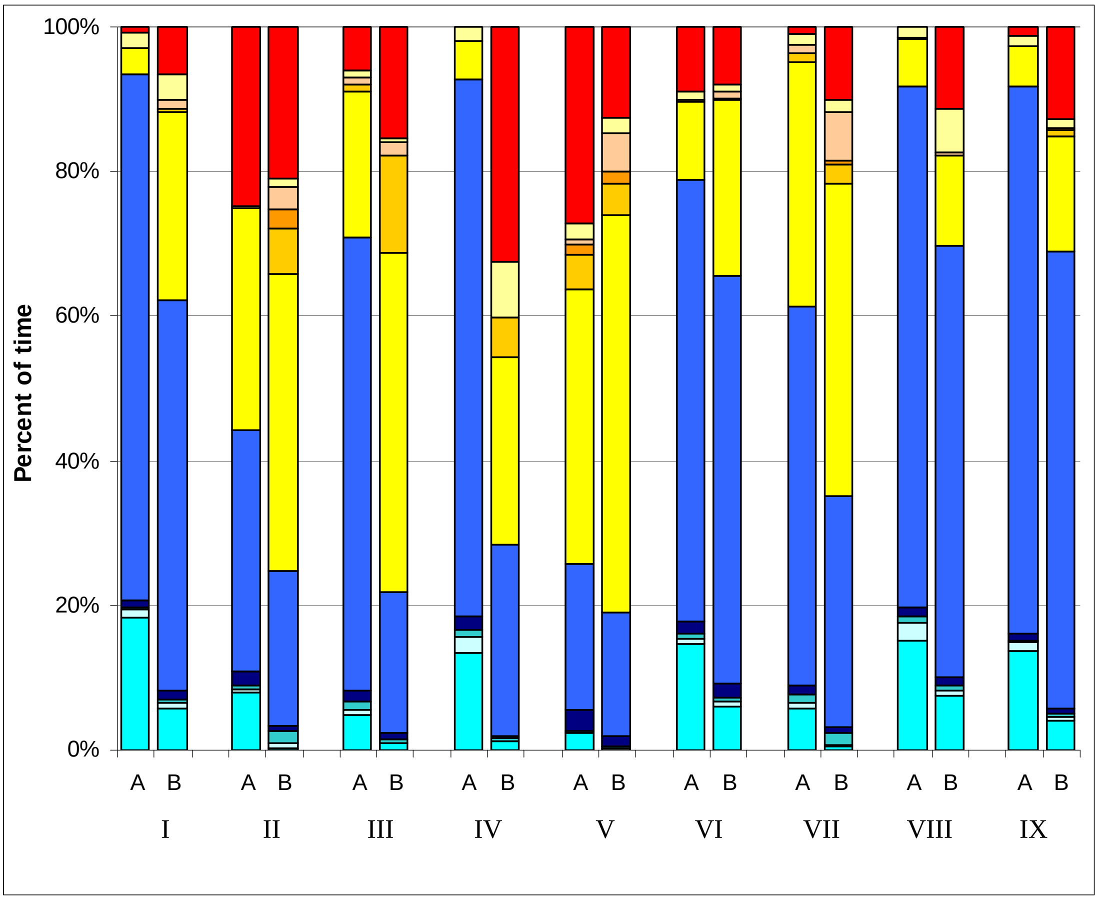
In Chapters 7, 8 and 9, the marmosets could change different characteristics of their environment by touching a touch sensitive button. In Chapters 7 and 9, the marmosets controlled the level of illumination in their cage, which may be considered to be a general characteristic of the environment (the intensity of the light changed the whole of the lower part of the cage). In Chapter 8, the marmosets controlled the projection of coloured lights into their cage. This could be considered to be a lesser degree of control as it involves changing aspects of only part of the environment (coloured lights were projected on one wall only). The behaviour of the marmosets was affected similarly by these two different control opportunities. However, the marmosets showed a significant reduction over time in their reaction to the controllability when the consequence of their behaviour was the projection of coloured lights and not when it was an increased light intensity. This variation between the two studies may suggest that when marmosets could control a more general aspect of their environment, this contingency was more significant to them.

10.5 THE EFFECTIVENESS OF THE 'THREE CS'

The effects of complexity, choice and control were investigated in various studies and situations. The results of these studies are summarised in Figure 10.6, which shows changes in levels of desirable and undesirable behaviours between the Baseline phase and following the manipulation in each of the studies. Table 10.2 (p. 340) describes the main characteristics of each study.

The findings of the present thesis underline the significance of each of the 'Three Cs'. The enhancement of complexity, choice opportunities and controllability all resulted in decreases in levels of undesirable behaviours, increases in levels of desirable behaviours and an overall improvement in the welfare of the marmosets. These results validate previous recommendations (see above) together with national legislation and international guidelines (IPS, 1993; Council of Europe, 2004; Home Office, 2005) regarding the importance of complexity, choice and control for captive primates.

Figure 10.6: Comparison between the various studies of the thesis in relation to changes in desirable and undesirable behaviours (A- Baseline phase; B- Enriched phase)



Desirable	**behaviours**	**Undesirable**	**behaviours**
■	Inactive rest	■	Inactive alert
■	Allogroom	■	Scratch
■	Social play	■	Tree gouge
■	Solitary play	■	Scent mark
■	Explore	■	Agitated locomotion
■	Calm locomotion		

In addition, in contrast to expectations, based on previous research (e.g. Brady, 1958; Hanson et al., 1976; Zimmerman & Koene, 1998) no significant negative effects of loss of complexity, choice or control were found (with the exception of the study in Chapter 5). Therefore, it is beneficial for captive marmosets to be exposed to complex environments and choice opportunities and to exert some control over their environment even if these enhancements have to be occasional. A comparison between all studies reveals several interesting findings, differences in the reactions of the marmosets to each of the ‘Three Cs’ and age differences in these reactions.

The level of the cage (Chapter 4, Study I) affected only scratching behaviour, which is considered to be stress related. Other recorded behaviours were not affected, but it is noted that all cages at both levels were relatively small and provided relatively poor housing conditions for the marmosets. In contrast, the size of the cage (Chapter 4, Study II) had an influence mainly on locomotion and inactivity patterns. It is likely that the marmosets had more activity options in the double cages, but the housing conditions were not different enough from those in the single cages to influence other behaviours. The exposure to more complex enclosures (Chapters 5 and 6) as expected resulted in increases in levels of exploratory behaviour (Berlyne, 1960; Dember & Warm, 1979; Hughes, 1997). No changes in levels of exploratory behaviour were seen in response to enhanced levels of control (Chapter 7, 8 and 9). However, if behaviours which were related to the device were included in general exploratory behaviour, exploration increases (although not to levels of exploration in outdoor cages). Finally, exposure to complex outdoor enclosures and the freedom to choose between these enriched enclosures and the home cages had the greatest effects on the behaviour of both young and adult marmosets. However, as mentioned before, it is impossible to separate between the effects of complexity and choice in this study (Chapter 6).

Differences between the responses of young and adult marmosets were also found, especially in relation to controllability (Chapters 7 and 8). Young marmosets were affected by the manipulations (controllability and increase in light intensity/exposure to visual stimulus) much more than adults. In addition, youngsters manipulated the apparatus more than adults. These results are in agreement with previous studies on callitrichids (Menzel & Menzel, 1979; Box, 1984a; Millar et al., 1988; Molzen & French, 1989; Majolo et al., 2003). However, when the novel object was food, adults dominated access to it (Box & Smith, 1995). In contrast, when adults were housed in pairs the influence of controllability on their behaviour was greater compared with family group-housed adults (see Chapter 9). In addition, no such age differences were found when the marmosets were exposed to the outdoor enclosures. These distinctions emphasize the point that different housing enhancements have dissimilar effects on the behaviour of the marmosets, and affect adults and youngsters differently.

Chapter 1 outlined the goals of environmental enrichment. The first goal was to prevent or reduce the performance of abnormal behaviours. Abnormal unnatural behaviours, such as stereotypies, were seen at such low frequencies that precluded statistical analyses. In several studies, levels of scent marking, scratching, tree gouging and agitated locomotion were reduced in the enriched phases. These behaviours are considered to be undesirable and abnormal when performed in high frequencies and/or out of context. The second goal was to increase the range of desirable, species typical behavioural patterns. Few novel behavioural patterns were performed in reaction to most of the manipulations in the present thesis. However, when the marmosets were allowed access to outdoor enclosures they performed more natural behaviours such as prey catching and sunbathing (i.e. resting in a ‘sprawl position’ on a sunlit branch, Stevenson & Rylands, 1988). In addition, in all studies, the marmosets showed more relaxed locomotion and inactivity patterns which were apparently more natural. The third goal was to increase the normal distribution of behaviour patterns. Figure 10.1 shows that the activity budget of the marmosets was closer to the activity budget of their wild conspecifics in the enriched conditions. To sum up, all three goals were fulfilled, that is to say, complexity, choice and control were shown to be important elements in enhancing the lives of captive marmosets.

10.6 FINAL CONCLUSIONS AND RECOMMENDATIONS

The study of animal welfare

Whilst it may not be possible to conclude from the available data the normal ranges of locomotion, inactivity and scent marking for captive common marmosets, it has been useful to provide details on the range recorded in different situations and contexts. It is strongly recommended that future researchers distinguish between different categories of locomotion and inactivity, and where possible follow consistent behavioural definitions and methodology to allow valid comparisons to be made. This would bring behavioural data in line with some of the body weight, growth rate and physiological parameters for which a range is available in the literature (e.g. Hearn et al., 1975; Abbott & Hearn, 1978; Poole & Evans, 1982; Ross, 1991; Araŭjo et al., 2000; Rensing & Oerke, 2005), and improve the accurate interpretation of welfare.

The ‘Three Cs’

It is impossible to rank the ‘Three Cs’ in terms of importance as they are so inter-related. Complexity affords greater choices, and more choice allows a greater degree of control. It is recommended that enclosures, furnishings, feeding and other husbandry or positive reinforcement training routines are designed to be complex, afford choice, and provide opportunities that increase the likelihood of an event occurring based upon the behaviour of the animal. It is also strongly recommended that the social conditions and the age of the individuals are considered before providing enrichment, as the various types of environmental enhancements have dissimilar effects in different conditions.

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