Chapter 1

Introduction

Captive environments are often impoverished when compared to the richness of natural habitats and so can usually be found lacking in terms of choice, complexity, and change. Therefore, the welfare of animals kept in captive environments may be compromised. In an attempt to maintain a general welfare standard for captive animals, the National Health and Medical Research Council (NHMRC) oversees the use and care of captive animals in Australia. Animal facilities that hold non-human primates are required to maintain welfare standards according to the codes of practice published by the NHMRC. These regulations typically encompass the general needs of the animals, which include housing, food, disease prevention, and veterinary care.

To further improve captive animal welfare, environmental enrichment is used as a means to enhance impoverished, non-stimulating environments. For the purposes of the present study, environmental enrichment was defined as any stimuli, such as objects, sights, sounds, smells, and manipulanda, that promote species-appropriate behaviours and activities. Environmental enrichment is used to emulate natural environments within captive environments so captive animals are provided with the surroundings and stimulation considered likely to promote species typical behavioural repertoires.

Environmental enrichment can be considered under various categories including structural, objects, social, and food and foraging enrichment. These types of enrichment may be used to better approximate wild activity budgets for captive animals, since there are often discrepancies between captive and wild activity budgets (Little & Sommer, 2002), especially in regard to foraging (Molzen & French, 1989). In general, wild Callitrichids, marmosets and tamarins, forage throughout the day and spend up to 60% of their daily time budget actively foraging (Poole, 1990). Common marmosets feed on spatially clustered exudate sources (Maier, Alonso, & Langguth, 1982; Scanlon, Chalmers, & Monteiro da Cruz, 1989) and fruits and insects that are dispersed

throughout their habitat (Rylands & de Faria, 1993). Little information exists about captive marmoset time budgets. However, since marmosets are often fed in predictably located, centralized food bowls, it is likely that their foraging time is markedly reduced.

Food and foraging enrichment can be employed to increase the time spent foraging and can stimulate foraging behaviours that are similar to those observed in wild conspecifics (Molzen & French, 1989). Thus, food and foraging enrichment provides opportunities for captive animals to exhibit natural behaviours and can alter the activity budgets of captive animals so that they better emulate the budgets of their wild counterparts. In addition, food and foraging enrichments are used widely because they are relatively inexpensive and involve feeding which is an integral part of husbandry procedures that are already in place in captive animal facilities (Beirise & Reinhardt, 1992; M. Heath & Libretto, 1993; Reinhardt, 1993a, 2001; Reinhardt & Garza-Schmidt, 2000). Food bowls have been shown to increase the space use of captive common marmosets (Buchanan-Smith, Shand, & Morris, 2002). Foraging devices, such as puzzle feeders, may be more ecologically relevant than food bowls and therefore may have more beneficial qualities. The benefits of the foraging devices may be indicated by behavioural changes such as increased activity as well as increased use of the space in which the devices are present. The current project examines the issues involved with attempting to improve the welfare of captive common marmosets, *Callithrix jacchus,* through the use of food and foraging devices and their effects on space use.

1.1 Animal Welfare Issues

Animal welfare is a broad topic dealing with the well-being of captive animals. Defining animal welfare sparks vigorous debate because it inherently involves values and ethics concerning the quality of an animal's life and whether or not animals suffer (Appleby & Sandøe, 2002; Hurnik, 1988; Sandøe, Nielsen, Christensen, & Sorensen, 1999). Bradshaw (1990) has argued that it is better to err on the side of caution by considering an animal's feelings, since if animals happen to *not* have subjective experiences, we will not have lost anything by considering them.

Animal welfare draws on perspectives from many different disciplines: behaviour, psychology, ethology, pathology, and philosophy (A. F. Fraser, 1989; Mench, 1993). Welfare considerations may vary according to the reasons for which animals are being kept. Such reasons may include biomedical research, food production, zoos, and behavioural research. Since animal welfare involves a multi-disciplinary approach and is based on ethical and value-based judgements, it is unlikely that it can be adequately summarised by a single definition (Mench, 1993). Therefore, definitions of animal welfare vary depending on the context to which the definition pertains.

Animal welfare addresses the ways in which animals may suffer in captivity, and can be defined in terms of individual factors: an animal's ability to cope with its environment (Broom, 1988, 1991), its psychological needs and processes (Duncan & Petherick, 1991) including contentment and comfort (Appleby & Sandøe, 2002; D. Fraser, 1993), and its physiological needs (Hurnik, 1988; Moberg, 1987) which may have an impact on reproduction (Sandøe et al., 1999). Duncan and Petherick (1991) contend that an animal's welfare depends solely on its cognitive needs and that satisfaction of cognitive needs will lead to the satisfaction of other physical needs. However, rather than defining animal welfare solely on one factor and contending that satisfaction of that factor leads to the satisfaction of all others, it may be appropriate to view animal welfare as a combination of many factors. A.F. Fraser (1989) discusses animal welfare in light of five factors: 1) ethical use of the animal, 2) reasonable standards of husbandry and production, 3) control of suffering for improved well-being, 4) provision of veterinary care, and 5) ecological management. A.F. Fraser (1989) maintains that assessment of these factors leads to the overall objective of relieving suffering.

The UK's Farm Animal Welfare Council (FAWC) has also developed five factors, the *Five Freedoms*. The Five Freedoms were originally developed for farm animals. Nevertheless, these guidelines have relevance to the welfare of all captive animals. The Five Freedoms are: 1) freedom from hunger, thirst, and malnutrition, 2) freedom from discomfort, 3) freedom from pain, injury, or disease, 4) freedom to express normal behaviour, and 5) freedom from fear and distress (Farm Animal Welfare Council, 1992). The FAWC factors describe more what *not* to do than what to do, and

all factors outlined by A.F. Fraser (1989) and the FAWC need to be translated to more specific conditions, different species and individual subjects.

Three-level hierarchies of animal needs have been proposed (Buchanan-Smith, 1994; Curtis, 1987; Hurnik, 1988; Hurnik & Lehman, 1988; Snowdon & Savage, 1989), with their highest levels being contingent on the use of environmental enrichment. A useful example of such a hierarchy comes from Curtis (1987) who adapted his hierarchy for agricultural animals' needs from Maslow's (1970) hierarchy for human needs. All hierarchies proposed follow the same basic progression (Table 1.1). The "life-sustaining" or "physiologic" needs consist of the minimal requirements to keep an animal alive. Failure to satisfy these needs will result in death. Curtis (1987) states these life-sustaining needs are the most well understood of animal needs, as can be seen in current governmental regulations (National Health and Medical Research Council, 1997; National Research Council, 1996). Buchanan-Smith (1994) and Snowdon and Savage (1989) take their first level, "veterinary-medical" needs, one step further and include good physical health and freedom from disease. Therefore, these are not just requirements to sustain life, but requirements to keep an animal free from illness. This level still does not involve a social or psychological component.

The second level classifications vary the most of the three levels. The "health-sustaining" classification of Hurnik (1988) and Hurnik and Lehman (1988) is similar to the "veterinary-medical" classification of the previous authors' Level 1 in that failure to satisfy the health-sustaining needs leads to illness. Hurnik (1988) and Hurnik and Lehman (1988) include among their health-sustaining needs food that satisfies all nutritional requirements, fresh air, and "temperature within a narrower range than that necessary merely to sustain life for a very short time." Curtis (1987) classifies this second level as "safety" needs which include physical security and freedom from fear and anxiety, while biological processes, such as reproduction, determine the next level for Buchanan-Smith (1994) and Snowdon and Savage (1989). Their "biological" classification is determined by an animal successfully reproducing and raising offspring that can also successfully reproduce. For successful reproduction to occur, there needs to be a social environment in which parental skills can be acquired and demonstrated appropriately (Buchanan-Smith, 1994; Snowdon & Savage, 1989). No clear reasoning is

provided for why reproductive success should be used as the major criterion for this second level. Perhaps, the authors believe that an environment that allows an animal to reproduce successfully is an environment in which an animal's biological needs are met. However, this idea does not suggest the means by which reproductive success could be reached.

There is general agreement on the top level in the hierarchy of needs. "Behavioural," "comfort-sustaining," and "behavioural-ecological" classifications all revolve around providing a species-appropriate environment. This naturalistic environment should facilitate the acquisition and retention of behavioural skills that would be necessary if that animal was in its natural habitat, thus stimulating psychological well-being. The intention is not to reintroduce all captive animals to the wild, but to equip them with skills that would allow them to cope with their natural environment if they were ever released (Buchanan-Smith, 1994; Snowdon & Savage, 1989). Failure to satisfy these needs tends to result in atypical behaviour, such as self-injuries and stereotypies.

Environmental enrichment is used to reach this behavioural pinnacle of the hierarchy of needs. Since enrichment is used to emulate the natural environment within the captive environment and provide the stimulation for species-appropriate behaviours, enrichment is an integral part of the behavioural needs of captive animals. Some of the physical needs of captive animals may be understood, but the behavioural needs of captive animals are the least understood (Curtis, 1987; Novak & Drewsen, 1989). Therefore, welfare and enrichment studies, such as the current project, intend to add to the available information about the behavioural needs of captive non-human primates.

Table 1.1: Hierarchies of animals' needs as described by five reviews in the authors' terms.

SOURCE	FIRST LEVEL	SECOND LEVEL	THIRD LEVEL
Curtis (1987)[*]	*Physiologic Needs* -adequate nutrition and a tolerable thermal environment -well understood	*Safety Needs* -physical security and freedom from fear and anxiety -less understood	*Behavioural Needs* -an environment that permits the animal to perform its natural behaviour repertoire -least understood
Hurnik (1988) Hurnik and Lehman (1988)	*Life-Sustaining Needs* -proper abiotic factors: space, pressure, temperature, sufficient oxygen, toxin-free air, some water and food -the failure to satisfy these needs leads to death -more critical needs	*Health-Sustaining Needs* -food that satisfies all nutritional requirements, fresh air, "temperature within a narrower range than that necessary to merely sustain life" (preferred temperature ranges) -failure to satisfy these needs leads to illness - less critical needs	*Comfort-Sustaining Needs* -appropriate environmental complexity, avoidance of aversive stimulation, social contact -failure to satisfy these needs leads to abnormal behaviour—injuries to itself or others -may be able to get away with short-term failure of these needs, but long-term failure leads to adverse consequences -least critical needs
Snowdon and Savage (1989) Buchanan-Smith (1994)	*Veterinary-Medical Criterion* -good physical health and freedom from disease for basic physical well-being -all captive environments that meet US government standards should meet this criterion - does not require a social or psychological component	*Biological Criterion* -reproductive success with viable offspring that are reared successfully by the parent -this is a continuous cycle—the offspring should also successfully reproduce -thus there is a requirement for an adequate social environment in which parental care skills can be acquired	*Behavioural-Ecological Criterion* -an environment where behavioural skills can be acquired and retained to adequately cope with the species' natural environment if the animals were ever to be released to the wild - authors claim this results in good psychological well-being

*Curtis' (1987) hierarchy was developed for agricultural animals from Maslow's (1970) human needs hierarchy

1.2 Measuring Animal Welfare

Assessment of animal welfare using the presence of physiological or behavioural indicators or preference and motivation testing is difficult since different animals have different individual experiences and natural histories that can affect how they respond to their surroundings (Mench & Mason, 1997). Many different physiological indicators are used to assess animal welfare. Cortisol concentrations are often used as an indicator of stress; if an animal exhibits increased cortisol concentrations under a certain experimental condition, then that condition is incompatible with good welfare (Barnett & Hemsworth, 1990; Boinski, Swing, Gross, & Davis, 1999; Crockett, Bowers, Sackett, & Bowden, 1993; Schapiro, Bloomsmith, Kessel, & Shively, 1993). Health has been proposed as an indicator of welfare, especially in production animals (Curtis, 1987; Hughes & Curtis, 1997). Suppression of the immune system (Moberg, 1987), reduced reproduction (Heger, Merker, & Neubert, 1986), and presence of disease (Broom, 1988) have all been used to indicate poor welfare. However, animals can be physically but not psychologically healthy.

Behavioural measures are also used as indicators of welfare (Box & Rohrhuber, 1993; A. S. Clarke, Juno, & Maple, 1982), sometimes in combination with hormonal measurements (Boinski et al., 1999; Schapiro et al., 1993). An increase or decrease in certain behaviours can be classified as beneficial to the animal. In particular, stereotypic behaviours have been used as indicators of poor welfare (Boccia, 1989a, 1989b; Boccia & Hijazi, 1998; A. S. Clarke et al., 1982; Maestripieri, Schino, Aureli, & Troisi, 1992; Novak, Kinsey, Jorgensen, & Hazen, 1998). Stereotypies are abnormal behaviour patterns that are repetitive, relatively invariant, and seem to have no apparent function. Examples include rocking, pacing (in rhesus macaques Novak et al., 1998) or self-injurious behaviour such as biting and hair plucking (in rhesus macaques Bayne, Hurst, & Dexter, 1992). Regurgitation/reingestion in gorilla (Akers & Schildkraut, 1985; Goerke, Fleming, & Creel, 1987) and head bobbing in female cotton-top tamarins, a Callirichid primate, have also been noted (Box & Rohrhuber, 1993). The Boyd Group (2002) contends that common marmosets housed in groups in enriched environments rarely exhibit stereotypic behaviours. A survey of North American zoos indicated that

6% of the New World monkeys housed in the responding zoos exhibited stereotypic behaviours in comparison to 40% of apes (Bollen & Novak, 2000).

Self-directed behaviours, such as scratching or grooming, can indicate compromised welfare when they become stereotypical or when their frequency becomes excessive and irrelevant to the surrounding circumstances (Broom, 1986, 1991; Maestripieri et al., 1992). Scratching has also been shown to be a reliable measure of stress in common marmosets (Cilia & Piper, 1997; Johnson et al., 1996). Tustin, Williams, and Brady (1996) noted that their Japanese macaque subjects hair plucked their inner thighs until they were almost bald. Common marmosets show a behavioural and physiological stress response when cage mates are separated (Norcross & Newman, 1999), as noted by a two-fold increase in self-grooming in isolated adult marmosets (Rothe, 1970). A decrease in these self-directed behaviours would indicate an improvement in welfare (Cilia & Piper, 1997; Maestripieri et al., 1992; Schapiro, Suarez, Porter, & Bloomsmith, 1996).

The presence and frequency of species-typical behaviours in captive animals that are part of the behavioural repertoire and activity budget of wild counterparts indicates improved welfare (Buchanan-Smith, 1994). However, activity budgets of captive animals may not truly reflect those of their wild counterparts (Little & Sommer, 2002; Molzen & French, 1989). Little and Sommer documented that the London Zoo's Hanuman langurs, on average, groomed more and locomoted less than wild troops in Jodhpur, India.

Activity and foraging are discrepant areas of captive and wild activity budgets. Captive non-human primates, such as cotton-top tamarins and common marmosets (McKenzie, Chamove, & Feistner, 1986), chimpanzees (Bloomsmith & Lambeth, 1995), and orang-utans (Tripp, 1985) have been considered inactive. In addition, captive common marmosets weigh more than wild common marmosets which was related to diet and inactivity (Araújo et al., 2000). There also are often marked differences in wild versus captive animal foraging. Captive animals are often fed in predictable, easily accessible food bowls (Molzen & French, 1989) when their wild counterparts forage for extended periods and the location of food resources is unpredictable (Kleiman et al., 1986). As a result, captive animals have a low foraging effort that still results in a high

foraging efficiency. However, their wild counterparts have a high foraging effort with a low foraging efficiency. As a consequence of this discrepancy, captive animals spend less time foraging and eating as compared to their wild counterparts and possibly have more time in the day to perform other, unnatural behaviours (Anderson & Chamove, 1984). Therefore, if natural activities that induce species-typical behaviours and actions can be provided, the welfare of captive animals improves in that regard as well as through the secondary effect of limiting the amount of spare time that could potentially be filled with abnormal behaviours.

Another system of measuring animal welfare involves preference testing (Broom, 1988, 1991; Dawkins, 1980; Webster, 1994). Preference testing gives an animal the power to choose between two or more different options, such as environmental conditions or food choices, and select which is the preferred condition relative to the others, thus giving the animal some control over its environment (D. Fraser & Matthews, 1997). Preference testing is contingent upon the animal caregivers modifying the animals' management accordingly. Preference testing is based on the assumption that allowing an animal to choose its preference permits the animal to control its own pleasure instead of being subject to value-based judgements humans make on its behalf (Duncan & Fraser, 1997). Preference testing has been used to assess the relative value of various housing conditions, such as branch cluster preference (Chamove & Goldsborough, 2004) and flooring for marmosets (Hardy, Windle, Baker, & Ridley, 2004), common marmoset food preference (Petto & Devin, 1988), and food bowl height preference in common marmosets (Buchanan-Smith et al., 2002; Hannaford, 1996).

An underlying problem with these factors, measures, and indicators used to assess animal welfare is that they remain open to interpretation for each species and each individual animal (Barnett & Hemsworth, 1990). Even the suggested physiological and behavioural welfare indicators are not straightforward gauges of good or bad welfare. For instance, a decrease in self-grooming could be beneficial to an animal who stereotypically over-grooms its pelage while a decrease in self-grooming could be detrimental to an animal who is not maintaining its coat properly (Barnett & Hemsworth, 1990; Mench, 1993). Similarly, individual non-human primate subjects can

respond differently to the same condition (Box, 1975). Hienz (2000) noted that wooden log interactions varied among the study's baboons subjects. Four subjects increased their log use over the 104-day exposure period, while two decreased their log use. Chimpanzees had marked interindividual differences in novel food acceptance and consumption (Visalberghi, Yamakoshi, Hirata, & Matsuzawa, 2002). Individual chimpanzee responses ranged from neophobia to completely accepting the novel foods.

In addition, there are limits to the amount of change intended or expected through any experimental procedure. An experimenter may intend to increase activity in a sedentary animal, but not to an extent that would indicate distress or stereotypical behaviour. Likewise, a decrease in self-grooming may be advantageous, but self-grooming should not decrease to an extent that would indicate an apathy for coat maintenance. To resolve the dubious problem of how to measure animal welfare, a variety of measures should used, because a single measure can be too variable (Broom, 1988; Crockett, 1998; International Primatology Society, 1993; Novak & Suomi, 1988).

Understanding welfare in domestic animals is more developed as it includes species-specific guidelines available in government regulations. However, welfare is less understood for captive exotic animals, such as common marmosets, as can be seen in legislation. Government regulations are used as standards for the use and care of captive animals in many countries, such as Australia, United Kingdom (UK), Canada, and the United States of America (USA). Similar to the varied definitions and indicators of animal welfare, legislation also varies. Some countries' codes of practice include species-specific information, while others have general 'non-human primate' information. Likewise, some policies have provisions for environmental enrichment implementation, while others do not refer to environmental enrichment.

1.3 Legislation

Various legislative bodies in individual countries oversee the use and care of captive animals on a local and/or national level. In these countries, animal facilities that hold non-human primates are required to maintain welfare standards according to the

codes of practice published by the respective legislative bodies. The regulations typically encompass the general needs of the animals, which include housing, food, disease prevention, and veterinary care. For the same species, the regulations can vary widely between countries or are very vague in their recommendations as explored below (Poole, 1995).

In Australia, the maintenance of captive animals used for research is regulated by the *Australian code of practice for the care and use of animals for scientific purposes* (1997) which is published by the NHMRC, the main funding body for biomedical research in Australia. In addition, the NHMRC has guidelines for the use of non-human primates, *Policy on the care and use of non-human primates for scientific purposes*, to be used in conjunction with the *Code of Practice* (National Health and Medical Research Council, 2003).

Australia's NHMRC *Code of Practice* regulates the management of all non-human vertebrate animals used for scientific purposes including dogs, rats, birds, and non-human primates. The *Code of Practice's* guidelines are written broadly to encompass all the species included in the *Code*. Statements such as these, '4.1.14: Animals must be provided with environmental conditions which suit their behavioural and biological needs' and '4.4.15: Air exchange, temperature, humidity, light and noise should be maintained within limits compatible with the health and well-being of the animals,' are open to interpretation and offer no specific regulations tailored for taxonomic category of animal, such as primates or rats, much less an individual *Family* or species. Only one statement offers some specific information: Clause 4.7 does state that marmosets are susceptible to cold (NHMRC, 1997). Even the more-specialized *Non-human primate policy* (2003) does not offer specific information about maintaining captive primate colonies. However, it does state that an emphasis must be placed on enrichment of the physical environment with items such as toys, foraging devices, and novel furniture.

The Australian *Code* and *Policy* seem to be lacking when compared with the codes for the United Kingdom, Canada, and the United States of America. The United Kingdom, through two codes of practice, provides more progressive and comprehensive guidelines than Australia, especially concerning non-human primates. The UK's *Code*

of practice for the housing and care of animals used in scientific procedures (Home Office, 1989) includes regulations for environmental and physical factors categorized by type of animal, including Old and New World Primates. Enrichment of the environment is not discussed in these guidelines, but is in the *Code of practice for the housing of animals in designated breeding and supplying establishments* (Home Office, 1995). This code was created specifically for the welfare of animals in breeding facilities, since breeding animals are typically maintained for longer periods than animals used for scientific procedures. Some research facilities maintain colonies for the duration of the animals' lives, similar to breeding facilities, but do not subject the animals to invasive experimental procedures, in contrast to most medical research facilities. The UK code for breeding facilities stresses the need to satisfy the behavioural and psychological needs of animals that are resident in the long term and suggests environmental enrichment is a way to meet those needs. The code provides regulations for various *Genuses*. In particular, this code describes marmosets' (*Callithrix*) needs relating to their arboreal nature and behavioural expressions, such as the provision of wooden cage furniture so that the marmosets can gnaw and scent mark their surroundings.

The Canadian Council on Animal Care (CCAC), while not providing detailed procedures by *Genus* similar to the UK, does present an overarching analysis of the behavioural needs of non-human primates. Since behavioural needs have been described as the least understood animal need (Curtis, 1987), the CCAC *Guide to the care and use of experimental animals* (1993) has demonstrated its progressiveness by broaching this subject. The CCAC *Guide* stresses the need to provide behavioural enrichment, social peers, appropriate food gathering activities and control of the surrounding environment.

The Animal and Plant Health Inspection Service (APHIS), a division of the United States Department of Agriculture (USDA), enforces non-human primate welfare standards in the US through the *Specifications for the humane handling, care, treatment, and transportation of nonhuman primates* (APHIS & USDA, 1991, Updated 2001). The USDA includes a disclaimer stating, "these minimum specifications must be applied in accordance with the customary and generally accepted professional and husbandry practices considered appropriate for each species, and necessary to promote their psychological well-being" (APHIS & USDA, 1991, Updated 2001). Consequently,

the US *Specifications* are not as specific as the UK guidelines for environmental factors such as temperature and lighting, which the UK describes on a taxonomic *Family* level.

The APHIS/USDA has published an additional report, the *Final report on environmental enhancement to promote the psychological well-being of nonhuman primates* (1999). This report indicates there is a need for clarification of the minimum criteria stated in the US *Specifications*, especially in the area of environmental enhancement to promote psychological well-being. It appears that the USDA sought to amend this shortcoming by providing a literature review and analysis within the US *Final Report*. In itself, the literature review does not provide information on the specific needs of various primate species. However, it provides references to the appropriate articles in which those specific needs are investigated.

Except for the USDA *Final Report*, individual country guidelines generally focus on the issues of environmental and physical factors, mostly without relating these issues to the psychological well-being of the captive animals. In addition to the USDA, the International Primatology Society (IPS) has drafted the *International guidelines for the acquisition, care and breeding of nonhuman primates* (1993) with the direct aim of ensuring the physical environment and care for non-human primates meets their behavioural and welfare needs. In particular, environmental enrichment is highlighted as a means of improving animal welfare, but the enrichments suggested are still not species-specific.

1.4 Environmental Enrichment

Captive environments are often impoverished and so can usually be found lacking in terms of choice, complexity, and change when compared with an animal's natural environment. Environmental enrichment is a means of improving the impoverished, non-stimulating captive environments, thus enhancing animal welfare. Similar to animal welfare, environmental enrichment has no universal definition or any widely accepted guidelines that delineate its effect, design, or implementation. Mellen and MacPhee (2001) suggest there is no single definition for environmental enrichment

for all species since each species has different needs. Therefore, environmental enrichment should be re-defined for each species.

Environmental enrichment is often described in terms of its intended purposes: inducing species-typical behaviours (Beilharz, 1994; Melfi & Feistner, 2002; Platt & Novak, 1997; Sainsbury, Mew, Purton, Eaton, & Cooper, 1990); reducing abnormal activity (Platt & Novak, 1997); improving the impoverished captive environment (Chamove, 1989); improving biological functioning (Newberry, 1995); providing species-appropriate opportunities and experiences (Mellen & MacPhee, 2001; Platt & Novak, 1997), and apparatus manipulation (Melfi & Feistner, 2002). These intended purposes can be achieved by providing natural surroundings (Kuczaj et al., 2002; Melfi & Feistner, 2002; Newberry, 1995), choices (Mellen & MacPhee, 2001), and arousing stimuli (Platt & Novak, 1997).

The benefits of environmental enrichment are measured in various ways. The main goal of environmental enrichment is to improve welfare. Therefore, assessment of enrichment coincides with the measures used to assess animal welfare. If the presence or use of an enrichment device results in the reduction of stereotypical or self-directed behaviours, that enrichment device has beneficial qualities for the subjects. Similarly, if an enrichment device increases activity in a sedentary, inactive subject, the subject's welfare has improved by the device's inclusion in the environment. A behavioural change in the direction of its presence and frequency within the activity budget of wild counterparts indicates improved welfare (Buchanan-Smith, 1994).

The presence of certain behaviours while certain devices are accessible may indicate a lack of beneficial qualities in the devices. For example, huddling and allogrooming are passive social behaviours. Huddling involves cage mates resting next to each other with physical contact (Box, 1975) while allogrooming is social grooming of a conspecific (Stevenson & Poole, 1976). The presence of these behaviours while a device is intermittently available does not directly indicate a decrease in welfare. More likely, the presence of these passive behaviours and lack of interaction with the device indicates that it is not enriching to the subjects. For example, if a foraging device is present 20 minutes per day, but the subjects do not use the device and instead allogroom or huddle, this device is most likely not enriching. Majolo, Buchanan-Smith, and Bell

(2003) noted that their female common marmoset pairs did not allogrooming in the presence of enrichment devices. Thus, allogrooming may be incompatible with optimal use of objects or devices that are intended improve an animal's welfare.

For the purposes of the present study, environmental enrichment was defined as any stimuli, such as objects, sights, sounds, smells, and manipulanda, that promote species-appropriate behaviours consistent with their natural behavioural repertoire. When applying the concepts of environmental enrichment, the individual's history and species' natural history should be considered, since these affect the ways in which an animal responds to its surroundings (Mench & Mason, 1997). In addition, Kuczaj et al. (2002) found that variable presentations of objects evoked more contact with the objects than when the objects were presented continuously over extended periods of time.

Attempts at environmental enrichment generally arise from the best of intentions, but scientists are often misguided in their use of enrichment because of the lack of rigour in three areas: 1) Enrichments are not systematically tested. 2) Devices, ideas, or methods are deemed 'enrichment' before they have been tested to see if they have any beneficial qualities. 3) Researchers provide basic furniture and other physical additions under the pretence that these are 'enrichments' even though physical additions, such as perches or platforms, should probably be considered environmental necessities and standard elements of the standard housing and husbandry procedures.

There is a need for systematic enrichment testing (Crockett, 1998; Morgan, Line, & Markowitz, 1998; Newberry, 1995; Scott, 1991). Galef (1999), also a strong advocate of systematic testing, contests enrichment programs based on good intentions and professional judgement might be counterproductive and therefore not meet the obligation to improve welfare. Also, many studies offer information about a suggested enrichment method, but fail to provide quantitative data (Adams, Adair, Olsen, & Fritz, 1992; Burt, A. I. A. T., & Plant, 1990; M. Heath & Libretto, 1993; Moazed & Wolff, 1988; Watson, Houston, & Macallum, 1989; Williams & Kelley, 1998) or basic statistical analysis (Hamilton, 1991; Hienz et al., 2000; O'Neill, 1988; Tustin et al., 1996). Others merely review the enrichment methods currently being used. These reviews often include studies without quantitative data or statistical analysis (Chamove, 1989; Fajzi, Reinhardt, & Smith, 1989; Reinhardt, 1993b; Scott, 1991). Statistical

analysis can determine a significant difference between two conditions, whereas data that have not been analysed statistically can be discussed only in terms of trends. Accordingly, Young (2003) contends that statistical analysis offers credibility to scientific results.

Enrichment reviews and studies without statistical analysis can be used as a starting point for future research and husbandry practices. However, the information they offer should not be directly implemented for a captive animal without prior assessment and evaluation of the species' natural history and the animal's individual history. Therefore, caution is advised when introducing new devices to naive subjects, especially if the devices have not been previously systematically tested for that species.

In addition, items or procedures can be suspected of having enriching qualities, but they cannot be deemed enriching until they have been shown to have benefits for the study animals (Crockett, 1998; Heyman, 2003; Newberry, 1995). Defining and measuring 'enriching benefits' is a difficult issue. Not all enrichment is uniformly enriching (Mellen & MacPhee, 2001), and so it seems unfortunate that researchers label objects 'enriching' even after a study has established that they have minimally enriching qualities (Hamilton, 1991).

As means of measuring welfare improve, those devices, ideas, or methods that have been labelled as 'enrichments' should be regularly renewed and reassessed. Furthermore, those that have been deemed to provide 'basic needs' should perhaps be considered a fundamental part of the requirements for maintaining captive animals. The objectives of environmental enrichment are to assist in meeting the "behavioural-ecological" needs of animals. It seems unfortunate that even after 20 years of focused research since the 1985 revision of the US Animal Welfare Act, those methods, objects, or social structures that we know to be part of the animal's ecology and are beneficial to the animals, are still being considered enrichment. As scientific understanding progresses, these 'enrichments' should be considered 'basic needs' and part of the requirements for maintaining captive animals. Therefore, since it is known that social primates benefit from conspecific interaction (Reinhardt, Houser, Eisele, & Champoux, 1987), pairing social animals together when they are typically housed individually should not be considered enrichment. Instead, it should be classified as meeting the

basic needs of the animal. Housing social animals individually should be considered substandard.

Environmental enrichment can be considered under various categories including structural, objects, social, and food and foraging enrichment. Each type of enrichment encompasses species-appropriate behavioural components. Structural enrichment entails the physical aspects of the cage or enclosure, including nesting materials (Brent, 1992), flooring (Hardy et al., 2004), swings (Dexter & Bayne, 1994), perches (Ely, Freer, Windle, & Ridley, 1998; Neveu & Deputte, 1999; Reinhardt, 1991), and branches (Reinhardt, 1987; Reinhardt & Smith, 1988). Providing rotational access to larger exercise or activity cages (Lynch & Baker, 1998) or rooms (King & Norwood, 1989) has been used as enrichment, and has reduced stereotypical hair plucking in Japanese macaques (Tustin et al., 1996). Stereotypical behaviours including pacing, rocking, and repetitive swaying, were also reduced in individually housed cynomolgus monkeys while the monkeys were in the activity cage, but these behaviours reappeared upon return to the home cage (Bryant, Rupniak, & Iverson, 1988). Permanently changing enclosures from cages to more naturalistic environments has been well-documented (Chamove & Rohrhuber, 1989; Chang, Forthman, & Maple, 1999; Hutchins, Hancocks, & Crockett, 1984) and can reduce abnormal behaviours for between three months (Little & Sommer, 2002) and 5.5 months (A. S. Clarke et al., 1982). Meanwhile, moving common marmosets from a semi-natural greenhouse environment to cages was associated with reduced behavioural repertoires with fewer exhibited behaviours, most notably, reduced social behaviours (Schoenfeld, 1989).

Objects that can be incorporated into the physical environment, include toys (Adams et al., 1992; Boinski et al., 1999; Hamilton, 1991; O'Neill, 1988; Renner, Feiner, Orr, & Delaney, 2000), video (Platt & Novak, 1997), or radio (Jones, 2002). Habituation frequently occurs with non-responsive, inanimate objects (Menzel & Juno, 1982; Renner et al., 2000). However, animals often interact with objects with a responsive quality (Sambrook & Buchanan-Smith, 1996) such as a rattling maraca versus an empty maraca (Vick, Anderson, & Young, 2000).

Socializing with conspecifics can provide stimulation and security (Canadian Council on Animal Care, 1993) and has been deemed enrichment. Social enrichment

has included not only interactions with conspecifics, but also interactions with human care-givers. Pairing individually housed adult rhesus monkeys with a recently weaned infant reduced stereotypical behaviours in the adult (Reinhardt et al., 1987). However, as previously noted, providing conspecific interaction should not be considered 'enrichment.' It should be considered a basic need for a social animal. The present definition of social enrichment may be exemplified by giving animals the opportunity to watch others (Buchanan-Smith, 1994). Watching or interacting with other conspecific groups is an aspect of the natural environment for wild non-human primates such as red-bellied tamarins (Buchanan-Smith, 1991) and common marmosets (Lacher, da Fonseca, Alves, & Magalhaes-Castro, 1981; Lazaro-Perea, Snowdon, & Arruda, 1999). In captivity, the creation of a spy hole between two cotton-top tamarin families' enclosures allowed one family group to observe another family (Moore, Cleland, & McGrew, 1991). However, Moore et al.'s (1991) study did not test the enriching qualities of this procedure. Instead, this study assessed age-related use of the spy hole, so the enriching qualities of this procedure will have to be determined in a future study.

Food and foraging enrichment are used widely because they are relatively inexpensive and involve feeding which is an integral part of husbandry procedures in every captive animal facility (Beirise & Reinhardt, 1992; M. Heath & Libretto, 1993; Reinhardt, 1993a, 2001; Reinhardt & Garza-Schmidt, 2000). Captive common marmosets weigh more than their wild counterparts (Araújo et al., 2000), possibly because their standard rations are predictably fed in an easily consumed form (Newberry, 1993) typically in a bowl (Poole, Hubrecht, & Kirkwood, 1999). Newberry (1993; 1995) maintains that feeding in this manner results in minimal searching activity so time becomes available for other, possibly stereotypical, activities.

Food and foraging enrichment devices increase the time spent foraging by captive Callitrichid monkeys by requiring movement or some work to obtain the food they contain, and they stimulate foraging behaviours that are similar to those observed in wild conspecifics (Molzen & French, 1989). Foraging enrichment has been achieved by introducing foods in various ways: embedded in straw or grass (Chamove, Anderson, Morgan-Jones, & Jones, 1982; McKenzie et al., 1986), unfamiliar foods or unpredictable variety (Box & Smith, 1995; Glick-Bauer, 1997; M. Heath & Libretto,

1993), foraging devices such as puzzle feeders (Crockett, Bellanca, Heffernan, Ronan, & Bonn, 2001; de Rosa, Vitale, & Puopolo, 2003; S. Heath, Shimoji, Tumanguil, & Crockett, 1992; Murchison, 1994; Novak et al., 1998), Kong® toys (Crockett, Bielitzki, Carey, & Velez, 1989), foraging boxes filled with biscuit ration (Murchison, 1995), biscuit ration and alfalfa (Boinski et al., 1999), or hay (M. Heath & Libretto, 1993), raisin boards (Moazed & Wolff, 1988), food frozen in ice cubes (Fritz & Howell, 1993), randomly-rewarding food dispensers (Voelkl, Huber, & Dungl, 2001), extractive devices (Vick et al., 2000), liquid dispensers (Bramblett & Bramblett, 1988), and gum feeders (McGrew, Brennan, & Russell, 1986).

Puzzle feeders and foraging devices require multiple manipulative steps to be completed before food is obtained from them. Examples of such steps include having to move food through three pipes before it can be obtained at a collection point or sifting through a substrate to obtain hidden food. Puzzle feeders are more effective in reducing whole body stereotypy, including pacing and rocking, in rhesus monkeys than treats alone, which implies that their benefits are not just nutritional (Novak et al., 1998). When offered a choice between a cage containing a puzzle feeder and a cage containing the usual food dishes, three families of captive common marmosets spent more time eating from the puzzle feeder when less hungry than when hungry (de Rosa et al., 2003) and explored the puzzle feeder more than the food bowls regardless of variations in motivation to feed. The efficacy of this same puzzle feeder in combination with a gum feeder was also tested on singly-housed and paired common marmosets (Roberts, Roytburd, & Newman, 1999). Some habituation occurred at the end of the three-hour exposure. However, frequency of stereotyped pacing and time spent sitting decreased in the presence of both feeders, regardless of housing condition. Likewise, abnormal behaviour, such as stereotypic movement and grooming, in brown capuchins decreased more with the introduction of a foraging box than with the introduction of a plastic "toy" (Boinski et al., 1999).

Foraging devices have also been used to induce natural foraging behaviours in animals undergoing reintroduction programmes. In an attempt to stimulate extractive foraging skills in captive golden lion tamarins (GLTs) that are part of an activity budget resembling that of free-ranging GLTs, Molzen and French (1989) introduced a

suspended feeding station filled with litter and raisins. This approach reduced foraging yield and increased foraging effort. Kleiman et al. (1986) implemented a training program for reintroduction candidates to wean them from locating cut foods in a predictable location to searching for randomly and spatially distributed and/or hidden food. The authors used traditional, stationary food bowls, randomly re-located food bowls, and "pseudo-naturalistic puzzle boxes" containing hidden food to graduate their subjects to more naturalistic feeding strategies. As the challenge increased from bowl to puzzle boxes, the number of visits to food sites (*foraging effort*) increased, while amount of food taken overall (*foraging efficiency*) decreased. Castro et al. (1998) surveyed the techniques previously used to improve reintroduction candidates' foraging. Castro et al. (1998) determined that the Golden Lion Tamarin Conservation Project's (GLTCP) method of providing foraging trays post-introduction did not significantly improve GLT survival after reintroduction. However, there were many individual confounding factors: sex, age, and individual histories.

1.5 Behavioural Needs of Common Marmosets

Common marmosets, *Callithrix jacchus*, are small, social New World primates from Brazil. Typically, the natural family composition of common marmosets consists of a dominant breeding pair and its resulting offspring (Stevenson & Rylands, 1988). Only one female breeds at any one time and all family members assist in infant-rearing (J. E. Clarke, 1994; Stevenson & Rylands, 1988). Common marmosets have a high fecundity with an interbirth interval of approximately 5 months, and twinning is common (Stevenson & Rylands, 1988). Intragroup aggression is also common between males (J. E. Clarke, 1994). Due to capacity limitations, high fecundity, and intragroup aggression, captive marmosets are often separated into isosexual parent/offspring or sibling groupings. Common marmosets should not be isolated, since separation of cage mates stimulates a physiological and behavioural stress response (Norcross & Newman, 1999).

Marmosets communicate with a varied vocal repertoire (Epple, 1968; Snowdon, 1993; Stevenson & Poole, 1976; Stevenson & Rylands, 1988). Phee, tsik, chatter, and chirp vocalisations are measured in the present study. Phee calls are long distance contact calls (Epple, 1968; Stevenson & Rylands, 1988). Tsik calls are a mobbing call and are also exhibited as a reaction to novel objects (Epple, 1968). Chattering vocalisations are often emitted in aggressive social contacts (Epple, 1968). Chirping is an amicable vocalisation given in close visual and bodily contact and is often elicited in response to a favourable food item (Stevenson & Rylands, 1988).

Common marmosets are omnivorous, particularly exudativore-insectivores, feeding on a varied diet, including gum exudates, insects, vegetables, fruits, eggs, small birds, and lizards (J. E. Clarke, 1994; Rylands & de Faria, 1993; Stevenson & Rylands, 1988). Wild C. jacchus use their specialised canines to gouge into the bark of trees to induce the flow of exudates, gums or saps, carbohydrate-rich food sources (Rylands & de Faria, 1993). A link between gouging and scent marking behaviours has been seen in Callithrix jacchus (Lacher et al., 1981; Rylands, 1985). Common marmosets often gouge a substrate and then scent mark the gouge site by rubbing their ano-genital or sternal regions on surfaces to leave a scent (Stevenson & Rylands, 1988). This behaviour was also observed in the University of New England (UNE) marmoset colony. Scent markings of female common marmosets may permit individual identification (Smith, Tomlinson, Mlotkiewicz, & Abbott, 2001). UNE colony marmosets were also observed scent marking their recently replenished food bowls and food that had fallen from the bowls. For these reasons, a relationship was suspected between gouging, scent marking, and food sites within the UNE marmoset colony.

Lacher et al. (1981) suspected a relationship between scent marking/gouging and exudate feeding sites. Scent marking has been associated with newly opened gouging sites (Lacher et al., 1981), territory marking (Epple, 1970), and deterring conspecifics from using a previously marked area (Sutcliffe & Poole, 1978). Rylands (1985) contends that gouging is a visual sign for scent marking locations which then facilitates sociosexual communication. Gouging has also been noted in captivity on wood substrates regardless of the lack of gum from the substrate (Lacher et al., 1981).

In general, wild Callitrichids, marmosets and tamarins, forage throughout the day and spend up to 60% of their daily time budget actively foraging (Poole, 1990). Marmosets spend more than 30% of their daily time budget engaging in exudate feeding (Maier et al., 1982). Foraging for animal prey ranges from 24 to 30% of their daily activities (Stevenson & Rylands, 1988). Wild *C. jacchus* concentrate their gum exploitation efforts on spatially clumped core areas of their home range where gum-producing tree densities are higher (Maier et al., 1982; Scanlon et al., 1989). Gum exploitation may be negatively related to the availability of fruits (Rylands & de Faria, 1993). Highly frugivorous marmosets, *C. kuhli* and *C. humeralifer*, have two to five times larger home ranges than the exudativorous *C. jacchus* (Rylands & de Faria, 1993), implying a more dispersed feeding pattern for highly frugivorous marmosets.

Unfortunately, only limited information exists about the activity budgets of captive Callitrichids. Stevenson and Poole (1976) documented that captive adult common marmoset pairs spent 26% of their active hours moving, 7% allogrooming, 48% stationary (includes 11% stationary contact, 10% stationary within 30cm of one another), 11% spent feeding, and 8% in the nest box. McKenzie et al. (1986) documented that captive common marmosets spent 1% of their time on bare floors. Overall, providing readily accessible, unrestricted food in a predictable location at fixed times of day greatly reduces the time spent foraging in captive animals (Molzen & French, 1989).

In captivity, fruit typically comprises the main staple of the common marmoset diet, along with pre-prepared biscuit rations or monkey cake. This food is generally not distributed in ways that elicit natural foraging patterns. Wild common marmosets are able to adapt to varying terrains, habitats, and food availabilities (Ferrari, 1993; Rylands & de Faria, 1993), so captive common marmosets may also be able to adapt to varying feeding strategies. *C. jacchus* may retain a clustered feeding strategy because of the gum-based dietary niche they occupy in nature but may still thrive when subject to a dispersed feeding strategy because of their ability to exploit fruit. Hence, depending on the type of food resources and how they are distributed (i.e. clustered or dispersed) captive common marmosets may exhibit both clustered and dispersed feeding patterns. Food distribution may affect competition: Sterck, Watts, and van Schaik (1997) and

Strier (2000) contend that a clustered food distribution increases competition within a group while a dispersed food distribution decreases competition because the animals are required to scramble to scattered food locations.

In the UNE marmoset colony, one bowl of food is offered per cage of two marmosets. The bowl is offered in the same location, mid-height in their home cages, and at roughly the same time of day, noon. Although food is provided in one location per cage, food competition is not typically seen between adult cage mates. In addition, the UNE marmosets have rotating free access, via a runway system, to an exercise room that is four times larger than their home cages. However, increasing space has been documented to not, in itself, improve welfare. In Chamove and Rohrhuber's (1989) study, common marmosets subjects were given access from their indoor cages to a much larger outdoor open area, but all subjects avoided areas with little cover. As a result, their use of the available space was restricted. Providing dense cover in the outdoor area increased its use as well as increased the behaviour repertoires exhibited by the marmosets when outdoors. Subsequently, the authors claim that any space provided in the name of enrichment or improvement needs to be "useable" space.

The exercise room space at the UNE marmoset colony has been designed to be useable, as it is furnished similarly to the home cage with a proportionally larger number of furnishings, such as perches, platforms, nest boxes, tubes, tunnels, tyres, and hanging objects. Most importantly, the marmosets will voluntarily enter this room and utilize the furniture and different areas, but then choose to stay for extended periods in their home cages. There are two possible reasons for this: 1) The home cages contain the marmosets' sleeping sites, even though nest boxes are available in exercise room and home cages. 2) The marmosets were also originally housed only in their home rooms from birth to the August 2001 addition of the runways that allowed rotating free access to the exercise rooms. Buchanan-Smith (1991) noted that wild red-bellied tamarins used areas of their home range more if they included a nesting site. Common marmosets also use core areas of their habitats, which Scanlon et al. (1989) have noted also contain a higher density of gum-producing trees than other areas of the habitat. It appears that perhaps because of a property as simple as familiarity, the home rooms are more appealing to the UNE marmosets than the exercise rooms.

Operant conditioning has been used to train pandas (Bloomsmith et al., 2003) and chimpanzees (Bloomsmith, Stone, & Laule, 1998) to move on command from one enclosure to another, but training does not address the behavioural and environmental needs of the animal (Hutchins et al., 1984). Therefore, rather than train the marmosets to tolerate an inadequate environment, the challenge was to find a motivating enrichment device that made the exercise room space more useable, so that the subjects would take advantage of the exercise room space more.

Space use of habitats in non-human primates has been documented in mountain monkeys (Kaplin & Moermond, 2000), white-faced sakis (Vié, Richard-Hanson, & Fournier-Chambrillon, 2001), mountain gorillas (Watts, 1998), GLTs (Dietz, Peres, & Pinder, 1997), and common marmosets (Hubrecht, 1985; Scanlon et al., 1989). In nature, *C. kuhli* feed at heights between 8 to 15 m above the forest floor (Rylands, 1989) while tamarin species (the other member of *Callitrichidae*), such as moustached tamarins, feed above 10 m (Rylands, 1987) and GLTs feed above 12 m (Rylands, 1989). Wild *Callithrix* marmosets feed at heights of 0 to 15 m above the forest floor (Rylands, 1987). Common marmosets inhabit areas below 12 m and frequently visit areas below 1 m above the ground (Stevenson & Rylands, 1988) and come to the ground briefly for quick foraging forays (Sussman & Kinzey, 1984) or to cross the forest floor (Stevenson & Rylands, 1988).

Other studies have also examined non-human primate space use within captive environments. Captive orang-utans spent more time in the upper canopy of their enclosure, which included many tree limbs, than in the lower canopy which included fewer perches (Hebert & Bard, 2000). This was the anticipated result, as the flooded-floor design of the indoor enclosure was constructed to encourage the orang-utans to display their arboreal nature and inhabit the areas above the enclosure's floor (Hebert & Bard, 2000). Reinhardt (1992) found that higher-ranking rhesus macaques predominantly use high-level structures more while low-ranking macaques used the lower-level structures. Overall, individuals were positioned on elevated structures 89.8% of the time and the floor 8.6% of the time even though the floor area was three times larger than the area comprised by the elevated structures. In addition, adult

animals tended to use fixed elevated structures, while young animals utilised moving structures (Reinhardt, 1992).

In captivity, red-bellied tamarins (Buchanan-Smith, 1991) and common marmosets (McKenzie et al., 1986) briefly descend to the floor. However, McKenzie et al. (1986) determined that a barren floor could become a useable space for captive common marmosets if it was covered with woodchips or shredded paper. As a result, by adding these substrates, activity within enclosures can be increased, and the marmosets' floor use increased from 1% to 10% of the observation sessions. The increased floor use was maintained for 2.5 months while the floors were covered, indicating bare floors are aversive to common marmosets. These authors also noted that if the marmosets were startled while on the floor, they would leap to higher elevations. The risk of predation may deter arboreal monkeys from descending to the ground (Prescott & Buchanan-Smith, 2002). Thus, McKenzie et al. (1986) further contend that captive marmosets' frequency of floor visits could roughly serve as an inverse measure of stress.

Common marmosets have shown a preference for the upper versus lower part of the cage (Ely et al., 1998). This preference was related to the size of the cage: The preference for the upper part of the cage increased as cage size increased. In addition, when familiar human observers sat on the floor, the marmosets' spatial preference shifted and the marmosets increased their use of the lower parts of the cage. In keeping with these reports, Kitchen and Martin (1996) found that time spent on the cage floor decreased in common marmosets when the cage height was doubled from 82 cm to 195 cm. However, when the overall cage complexity was increased by adding more branches and perches, subjects increased time spent in the lower half of the cage and the floor. Therefore, common marmosets prefer the upper versus lower parts of cages (Ely et al., 1998), but will take advantage of lower areas if made sufficiently useable with branches and perches (Kitchen & Martin, 1996). In addition, common marmosets are also quicker to explore objects higher in the cage and explore these objects for longer periods than objects located lower in the cage (Majolo et al., 2003).

It has been noted that captive common marmosets also prefer to feed from bowls (Buchanan-Smith et al., 2002; Hannaford, 1996) or foraging boxes (Morrissey, 1994) located higher within the cage rather than from a location lower in the cage. In

Hannaford's study, two food bowls were placed at a different combination of height (high, middle, low) and cage side (left and right) for one week. The test subjects were a family of seven marmosets that typically received their food in a bowl located at the middle height level. Once given the choice of height and cage side, the marmosets ate more food from the higher bowl and visited it more. Preference then decreased with descending height, and there was no preference for the left or right side bowl (Hannaford, 1996).

Buchanan-Smith et al. (2002) performed a similar experiment with six common marmoset pairs (2 male-male; 2 female-female; 2 male-female pairs) housed in a 2-tier caging system. These authors tested three different food bowl conditions, a food bowl was placed either on the highest shelf in each cage, on the cage floor, as per standard husbandry practice, or in both locations. The marmosets visited more and spent more time with the high bowl in comparison to the low bowl, and their use of the cage shifted depending on where the bowls were located. When the bowl was located in the top of the cage the marmosets used the top half 91.2% of the time and bottom half 8.8%. When the bowl was located in the bottom half, time in the lower half increased (top: 71.5%, bottom: 28.5), and when bowls were located in both positions, the percentage of time in each half was intermediate to the other two conditions (top: 79.9%, bottom: 20.1%).

Using boxes filled with litter and hidden raisins, Morrissey (1994) found the dominant breeding pair in a 10-member family of common marmosets fed from the foraging box at 150 cm above ground level while the other group members foraged from the ground level foraging box. Snowdon and Savage (1989) also cursorily reported, and did not provide quantitative data, that their cotton-top tamarins were hesitant to approach food bowls positioned near the cage floor when carrying infants. They also suggest that this hesitation disappeared when the food dishes were raised to at least 1 m above floor level, and they noted a marked improvement in infant-rearing success because of this intervention.

Most research on space use within enclosures for non-human primates has examined occupants' preferences for infrastructure at different heights within a cage or feeding height preference. Little research has been reported on altering space use with enrichment devices. In addition to the marmosets preferring the upper versus the lower

part of the cage, Ely et al. (1998) showed that the addition of a platform projecting from the outside of the cage, a "veranda," shifted the cage use of common marmosets. The use of the veranda was 10 times greater than expected by its volume alone, possibly due to the veranda providing better surveillance of the room.

Bayne et al. (1992) and Bayne, Strange, and Dexter (1994) performed two similar cage side preference studies with rhesus macaques. In both studies, cage side preference was first determined for eight rhesus macaques before enrichment devices were tested. The devices were placed on the less preferred cage side to determine their enrichment value. Neither the non-nutritive devices (Bayne et al., 1992) or the nutritive devices (Bayne et al., 1994) were successful in changing the cage side preferences of all subjects. There were mixed results in both studies. In both studies, only four subjects changed their cage side preference to the transiently enriched side. In the non-nutritive enrichment study, the side preference was not necessarily altered in the presence of the enrichment devices whereas the four subjects in the 1994 study switched their cage side preference in the presence of the nutritive enrichment. These enrichment interventions also had mixed behavioural effects, indicating that the use of these enrichment devices does not suggest that the interventions were strongly attractive, possibly because they lacked ecological relevance to the subjects.

In conclusion, marmosets have shown a preference for upper parts of a cage versus lower parts (Ely et al., 1998) as well as food bowls (Buchanan-Smith et al., 2002; Hannaford, 1996) and objects located higher within the cage than in the lower parts of the cage (Majolo et al., 2003; Morrissey, 1994). Environmental enrichment such as structural perches (Kitchen & Martin, 1996) or verandas (Ely et al., 1998) has made the available space more useable, resulting in increased use of space by the subjects. Food bowls placed low within the cage increased the use of the lower cage areas (Buchanan-Smith et al., 2002).

Food bowls are centralized, unchallenging sources of food that result in high foraging efficiency, but low effort. Foraging devices require more skill to obtain the same amount of food. Foraging devices are more ecologically relevant to common marmosets because they resemble their natural foraging strategies of searching for hidden or embedded food (Rylands & de Faria, 1993). Puzzle feeders also lower

foraging efficiency and increase foraging effort (Kleiman et al., 1986). As a result, it would be expected that foraging devices, more than food bowls, would promote species-typical behaviours. In addition, presentation of foraging devices in a captive environment may increase the useability of the environment, more so than food bowls.

The present study utilized devices that are ecologically relevant to the subjects in a familiar room. The female marmoset subjects do voluntarily enter the exercise room and utilize the different areas, but since they choose to spend significantly more time in the home cages, the exercise room space may not be as useable as the home rooms. Since foraging enrichment is relatively inexpensive, easily implemented by a variety of captive animal facilities, and addresses the marked difference between captive and wild conspecific time budgets, foraging feeders were used in the present study. The female subjects used in the current study, in general, did not exhibit abnormal behaviours or stereotypies. Intermittently, the marmosets had been observed to have missing hair from their tails. In particular, this pattern of hair loss was observed if a subject had to be isolated or after the subject had travelled to the colony. Therefore, the present study aimed to determine if the feeders had beneficial qualities indicated by behavioural adjustments, such as decreased self-directed behaviours and increased activity, and space use measures. The present study intended to answer the following questions:

1) Does foraging enrichment alter space use in common marmosets?
    a. Between the home cage and exercise room?
    b. Within the exercise room?
2) Does foraging enrichment have long-term effects on time spent in the exercise room?
3) Do marmosets interact with feeders more than a food bowl?
4) Does clustered food distribution have different effects on marmoset behaviour compared to dispersed food distribution?

CHAPTER 2

METHODS

2.1 Introduction

This chapter describes the general husbandry methods used to maintain the University of New England marmoset colony as well as the methodological procedures used in the experiments described in Chapter 3. Procedures were undertaken in accordance with the *Australian code of practice for the care and use of animals for scientific purposes* (1997) and the *Policy on the care and use of non-human primates for scientific purposes* (2003) and were approved by the UNE Animal Ethics Committee (AEC 03/050).

2.2 Subjects

The UNE colony consisted of 15 common marmosets, *Callithrix jacchus*, (11 females, 4 males) at the start of the experiments of which 8 adult females, ranging from 8-12 years old (mean: 9 yrs 10 months ± 2 months), were used in the experiments. The sample size was limited to 8 subjects, since the remaining 7 marmosets were already grouped into two mating pairs, their infant offspring, and one lone male. This male was housed individually because his brother and father died and no suitable companions were available for him. Six additional offspring were born to these mating pairs during the current study. Of these, four survived (Figure 2.1). All colony members were born in captivity and were not used for experiments before arriving at UNE if they were born elsewhere. All subjects were housed in Animal House B at the University of New England Animal House Complex, Armidale, NSW, Australia.

The six founding members of the UNE colony were bred from Foundation 41 in Sydney, Australia, and were obtained in 1992 at 6 months of age. Although the six original members had not had invasive procedures performed on them before they came to UNE, they originated from a Sydney facility in which other marmosets were undergoing biomedical research procedures. These six founding marmosets were bred to establish the UNE colony. Once the new colony reached holding capacity and juveniles began to reach sexual maturity, family members were maintained within the same room and separated into same sex groupings of parent/offspring or siblings. Then Trinity, Kai, and Aziz came from the Monash Animal Service at Monash University, Victoria, Australia, in 2002 to augment the colony. Trinity was paired with Delta, an existing colony member, while Aziz and Kai were paired together for breeding.

All the marmosets were familiar with human contact, as they were handled regularly at UNE. At no time have invasive procedures been performed on any members of the colony.
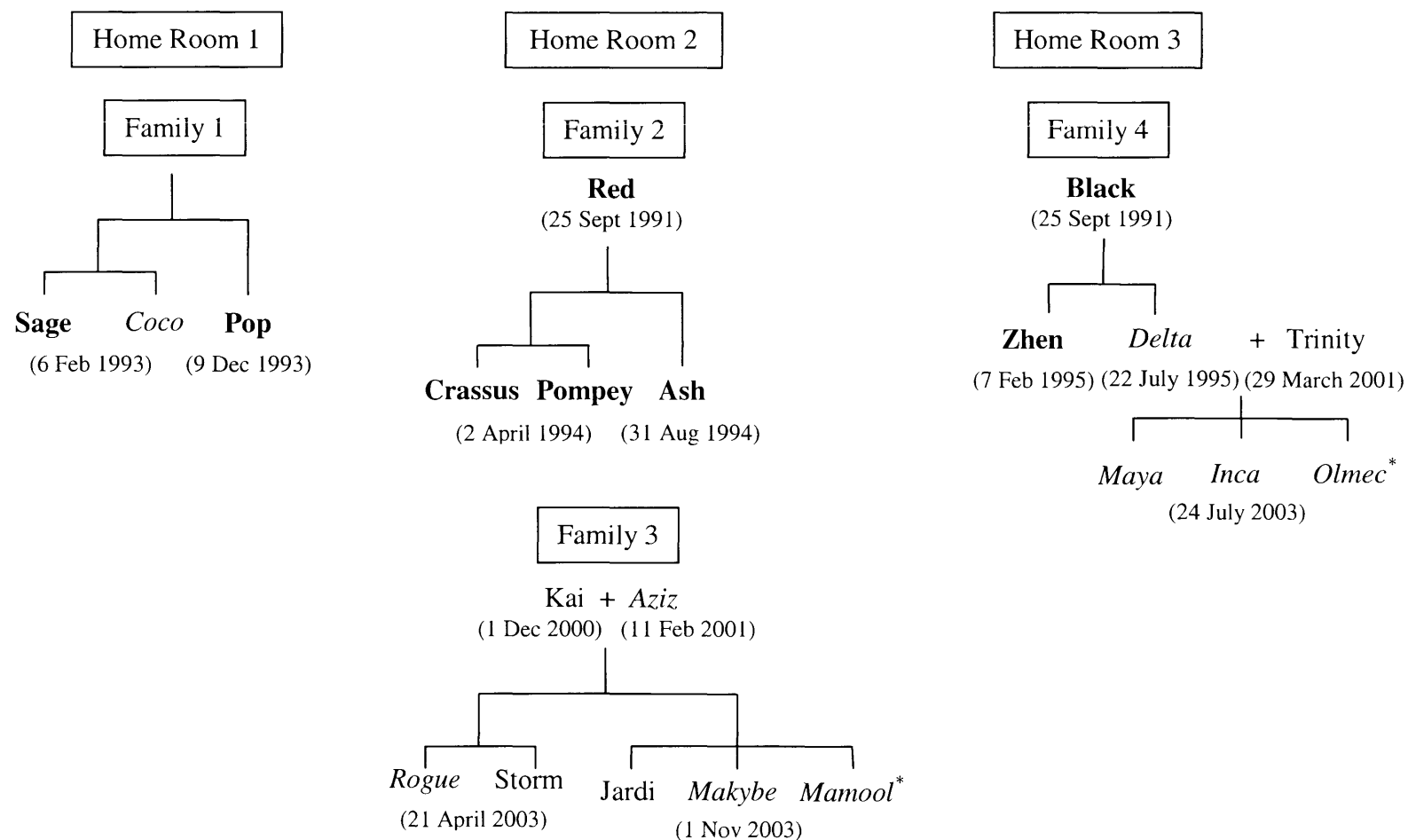
```
┌─────────────┐            ┌─────────────┐                    ┌─────────────┐
│ Home Room 1 │            │ Home Room 2 │                    │ Home Room 3 │
└─────────────┘            └─────────────┘                    └─────────────┘

  ┌──────────┐               ┌──────────┐                       ┌──────────┐
  │ Family 1 │               │ Family 2 │                       │ Family 4 │
  └──────────┘               └──────────┘                       └──────────┘

                                 Red                               Black
                             (25 Sept 1991)                    (25 Sept 1991)

Sage    Coco    Pop          Crassus  Pompey  Ash          Zhen      Delta      +  Trinity
(6 Feb 1993)  (9 Dec 1993)   (2 April 1994)  (31 Aug 1994) (7 Feb 1995) (22 July 1995) (29 March 2001)

                                                                Maya    Inca    Olmec*
                                                                     (24 July 2003)

                              ┌──────────┐
                              │ Family 3 │
                              └──────────┘

                              Kai  +  Aziz
                          (1 Dec 2000)  (11 Feb 2001)

                    Rogue   Storm   Jardi   Makybe   Mamool*
                    (21 April 2003)          (1 Nov 2003)
```

Figure 2.1: Family groupings in each Home Room of the UNE marmoset colony during the current study, June-December 2003. Names in regular font are those of females. *Italicized* names are those of males. Study subjects' names appear in **bold** font. Birthdates are in parentheses. An asterisk (*) is used to identify an infant that was not supported by the mother and died within days of birth.

2.3 Housing And Husbandry

2.3.1 Housing

All marmosets were housed in pairs, bar one lone male and two mating pairs with resulting families. The UNE family groupings are not typical of common marmosets' natural family composition. Due to capacity limitations and intragroup aggression, the UNE marmosets could not stay in their complete family groups, similar to other captive facilities (J. E. Clarke, 1994). Therefore, UNE marmosets were housed in same sex parent/offspring or sibling groupings to prevent breeding and to limit agonistic interactions.

The large structurally enriched home cages (HCs) were on average $5.3m^3$ with the smallest cages at $4.4m^3$ and the largest cages at $6.1m^3$. Dimensions were at least 1.0m x 2.4m x 1.8m high. Cages were raised 0.2m off the floor of the room. Furniture per cage included one nest box (0.18m x 0.15m x 0.29m), tyre, hanging parrot mirror, hay tray and multiple perches, tubes, and platforms. Cages were swept out and hosed down three times per week.

Figure 2.2 shows the marmoset housing arrangement. Members of each family were kept within the same room, and separated into same sex groupings of parent/offspring or siblings. All marmosets in the Animal House were in auditory and olfactory contact, and members of the same room also had visual contact. Each enclosure consisted of a Home Room (HR), Exercise Room (ER), and Outdoor Cage. Home Room 2 housed two unrelated families; Home Room 3 housed one family and an unrelated female paired with the male for breeding (see Figure 2.1). A hash (#) and the number, 1, 2, 3, or 4 indicate home cages of testing pairs. Table 2.1 shows the subject, testing pair, and enclosure classifications. Sage/Pop were located in Enclosure 1, Red/Crassus and Ash/Pompey were in Enclosure 2, and Black/Zhen were in Enclosure 3.
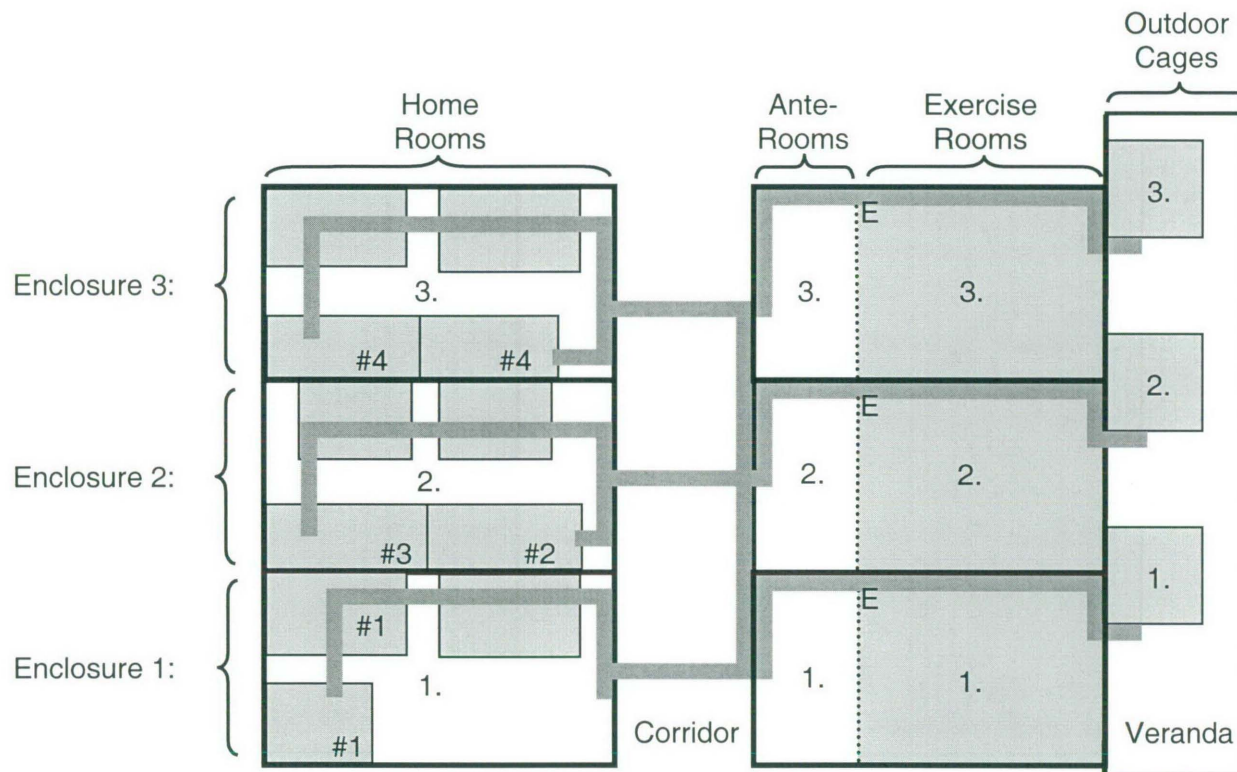
Figure 2.2: Room and cage arrangement for the UNE marmoset colony. Marmosets had access to shaded areas (▢). Marmosets from each enclosure were allowed rotational access to other rooms of the enclosure via the runway system (▭). The dotted line (┈┈) indicates the one-way mirrors used for observation. The letter "E" indicates the marmosets' entrance into each ER. A hash (#) and a number, 1, 2, 3, or 4, indicate home cages of testing pairs. Testing pairs are outlined in Table 2.1.

Table 2.1: Study subject and testing pair classification by enclosure.
Each testing pair was housed together in the same home cage, as
indicated in Figure 2.2, and both cage mates were given simultaneous
access to the ER within their respective enclosure. The division of pairs
into Testing Groups is explained in Section 2.5.

Enclosure	Testing Pair	Subject No.	Subject	Testing Group
1	#1	1	Sage	1
		2	Pop	
2	#2	3	Red	
		4	Crassus	
	#3	5	Ash	2
		6	Pompey	
3	#4	7	Black	
		8	Zhen	

Cage groups from each HR had rotating access to their respective ER via the
runway system; one cage group had access at any one time per enclosure. This network
of runs linked all marmoset rooms and could be blocked off at various points to direct
travel and prevent contact between non-cage mates. Weather permitting, typically
during the summer months, the marmosets also had access to outdoor cages located on a
covered veranda through the same rotational system. Therefore, whichever pairs had
access to the ERs also had access to the outside veranda area. The current experiments
were conducted during the winter and spring of 2003. As a result, weather and
experimental procedure allowed access to the home and exercise rooms only.

ERs 1 and 2 were 3.0m x 3.0m x 2.6m with a personnel access area (3.0m x
0.4m x 2.6m) along the veranda wall that was separated from the rest of the room by a
mesh wall. ER 3 did not have a personnel access area, so the area available to the
marmosets was the entire room (3.0m x 3.4m x 2.6m). One-way mirrors facing into the
ERs from each anteroom (1.4m x 3.0m x 2.6m) allowed the experimenter to observe the
marmosets in the ERs. ERs and home cages were similarly furnished. Furniture per ER
included one nest box (0.18m x 0.15m x 0.29m), tyre, hanging parrot mirror, hay tray,
sand box and more perches, tubes, platforms than there were in the home cages. The
quantity of each type of furnishing was equivalent across ERs. Figure 2.3 displays a
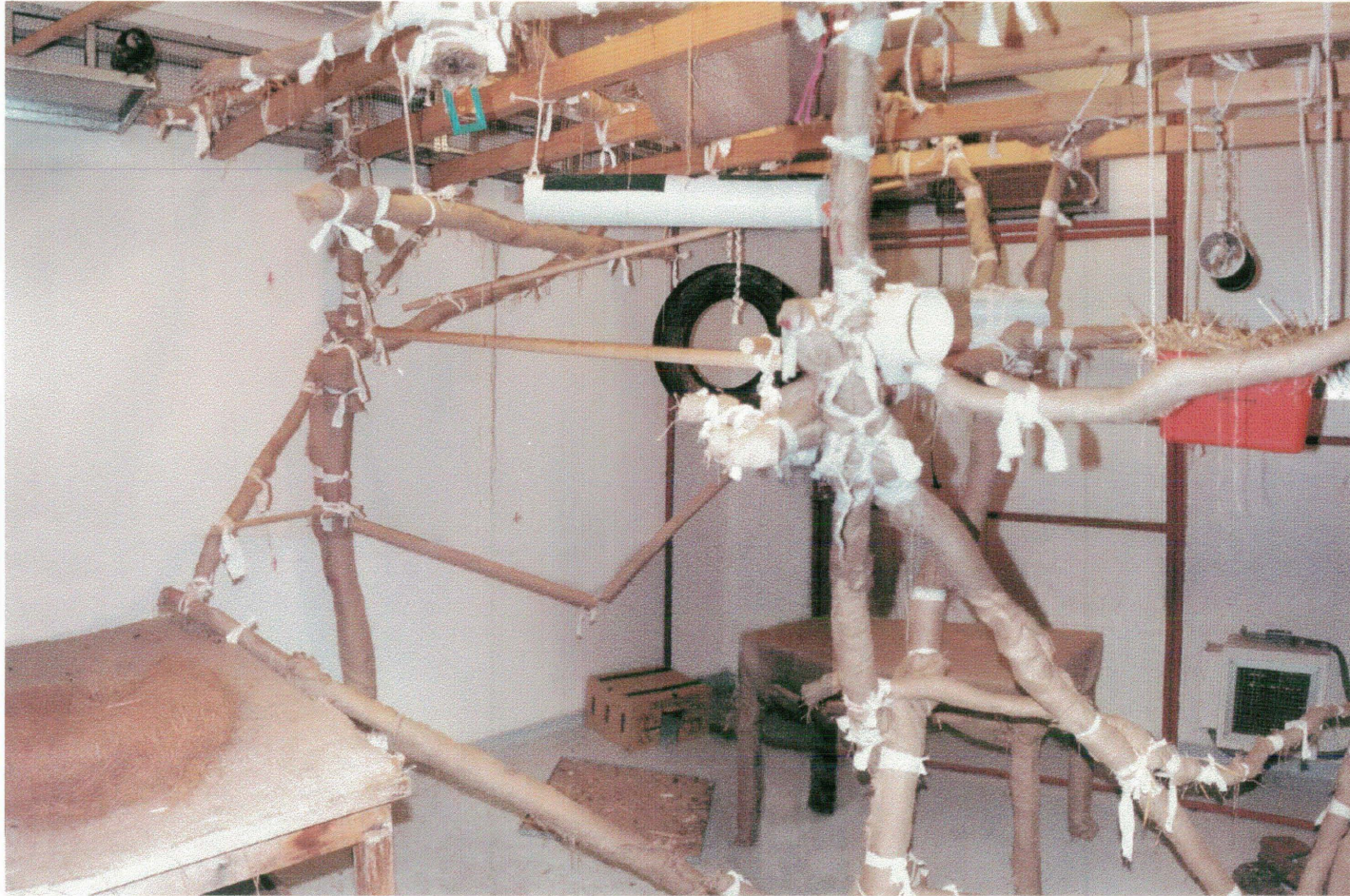photograph of ER 1.

Figure 2.3: Typical layout of Exercise Rooms as depicted by a photograph of ER 1. All ERs were furnished similarly. A marmoset is sitting at the marmoset entrance to the ER in the upper left hand corner.

2.3.2 Husbandry

The temperature in all marmoset rooms was maintained between 18 and 28 °C. Fluorescent lights for both the HRs and ERs were programmed on a 12-hour light/dark cycle. They came on at 07:30 every morning, and extinguished at 19:30 every evening. Ultraviolet light (350-390 nm) in each home room supplemented the marmosets' Vitamin D intake for 60 minutes between 13:00 and 14:00. A skylight in each home room provided natural, additional light that exposed the marmosets to varying day lengths and seasonal lighting, apart from the programmed 12-hour light/dark cycle. To assess health and maintain records, the marmosets were weighed monthly after having voluntarily entered a perspex tube, which was then weighed. Preferred foods, such as banana, were used to reward this behaviour.

The experimenter (S. Bjone) was involved in general management of the marmosets, including feeding 2-3 times per week for 4 months prior to the start of the experiment and every day during the experiment as well as general maintenance, cleaning, and marmoset husbandry. In addition to this general exposure, the experimenter habituated the marmosets to her presence by interacting with them during occasions that did not involve management and husbandry procedures.

2.3.3 Diet

As per standard husbandry procedure, the marmosets were fed varied foods in bowls once daily from 12:00-13:00. The bowls remained in the cages to allow the marmosets to free-feed throughout the day, and then the bowls were removed, cleaned, and refilled the next day. Apart from brief bowl cleaning and refilling periods, the marmosets were not food deprived since there was always food left in the bowls after each 24-hour *ad libitum* feeding, and the marmosets' weights were maintained from June-December 2003 (Table 2.2). Water was available *ad libitum* at all times in all HCs and ERs. Pentavite®, a liquid human infant dietary supplement, was soaked into wholegrain bread to provide a vitamin supplement and fed weekly.

Table 2.2: Marmoset weights for the length of the study.

Subject	Weigh Date					
	20-Jun-03	29-Jul-03	25-Aug-03	19-Sep-03	31-Oct-03	21-Nov-03
SAGE	430	442	427	421	424	408
POP	480	476	480	474	476	432
RED	389	386	406	399	389	383
CRASSUS	423	390	414	417	399	395
ASH	409	385	408	392	394	377
POMPEY	433	447	464	440	434	424
BLACK	410	383	381	391	389	392
ZHEN	457	442	468	472	470	449

Table 2.3 outlines the standard diet of the UNE colony marmosets. The diet has been similarly reported in Cross (2002), Shuster (2001), and Hook-Costigan (1997). The basic core of the diet supplied each day consisted of specially prepared monkey cake* and meatloaf**, dog pellets with no artificial colours/flavours or preservatives, and apple. Table 2.3 also outlines the Additional foods included in the daily diet as well as the recipes for the cake and meatloaf. Banana was used in experimental procedures and offered at each meal. Crickets and mealworms were offered intermittently either as rewards or during experimental procedures.

Table 2.3: Marmoset diet for the UNE colony.

Basics of diet provided every day:
> Monkey cake* and meatloaf**, dog pellets, apple.

Additional foods provided to supplement the Basics:

Monday	Wholemeal bread with vitamin supplement (Pentavite®), orange, fruit yoghurt
Tuesday	Cheese, sultanas
Wednesday	Boiled egg, vegetable such as green beans or broccoli, fruit such as grapes, peaches, or melon, depending on seasonality
Thursday	Boiled egg, sultanas, Nutri-grain™ cereal
Friday	Peanuts (unsalted, unflavoured)
Saturday	Pear
Sunday	Fruit yoghurt, peanuts (unsalted, unflavoured)

*Cake

25g uncooked rice
105g polenta
25g desiccated coconut
15g sunflower seeds
1 egg
1 mashed banana
25g skim milk powder
25g sultanas
1 rice cake
15g dicalcium phosphate
25g brown sugar

**Meatloaf

600g mincemeat
6 slices wholemeal bread
20g dicalcium phosphate
2 eggs
45g bran cereal
7g vitamin C
45g dog pellets
1 cup of water

No members of the UNE colony exhibited any nutritional defects, such as marmoset wasting syndrome (Diniz & de Costa, 1995).

2.4 Apparatus

2.4.1 Motion Sensor Camera

The motion sensor camera was a Logitech® QuickCam® Pro 4000 internet camera with supported Image Studio software run by a Toshiba Satellite laptop computer with a Windows® XP operating system, 5.6 GB memory, Pentium® III 500 MHz processor, and 192 RAM (Figure 2.4). This camera was capable of video capture resolution up to 640 x 480 pixels and still image capture resolution up to 1280 x 960 pixels with a frame rate of 30 frames per second. The software catalogued the motion sensor photographs by date and time in hours: minutes: seconds.

Figure 2.4: Photograph of Toshiba laptop and Logitech® QuickCam® Pro 4000 internet camera.

2.4.2 Food Bowls

Eight identical glazed ceramic dog bowls (550ml volume, 5.5cm deep x 11cm diameter) were used as food bowls. All food bowls were rotated and cleaned daily with

Sunlight dishwashing liquid, so that no one bowl was consistently marked with a particular scent.

2.4.3 Cluster Feeder

The cluster feeder consisted of one PVC plastic board (45cm wide x 35cm tall x 2.2cm thick) with 12 2.5cm diameter holes drilled 2cm deep into the plastic (Figure 2.5). Each hole was covered with an engraving plastic PVC disc (5cm diameter, 2.5mm thick) that swung freely, returned to a vertical resting position, and had a counter sink screw (with a 3mm diameter nut) for a handle. A 13cm x 42cm x 0.55mm-thick galvanized sheet metal platform, covered in hessian was attached to the bottom of the feeder, and allowed the subjects to perch at the feeder. In addition, a 13cm band of 25mm weldmesh was mounted around the top and sides of the cluster feeder, so that every direction and hole was accessible, by either reaching and/or climbing. The feeder was hung with four ropes tied to furniture within the ER.
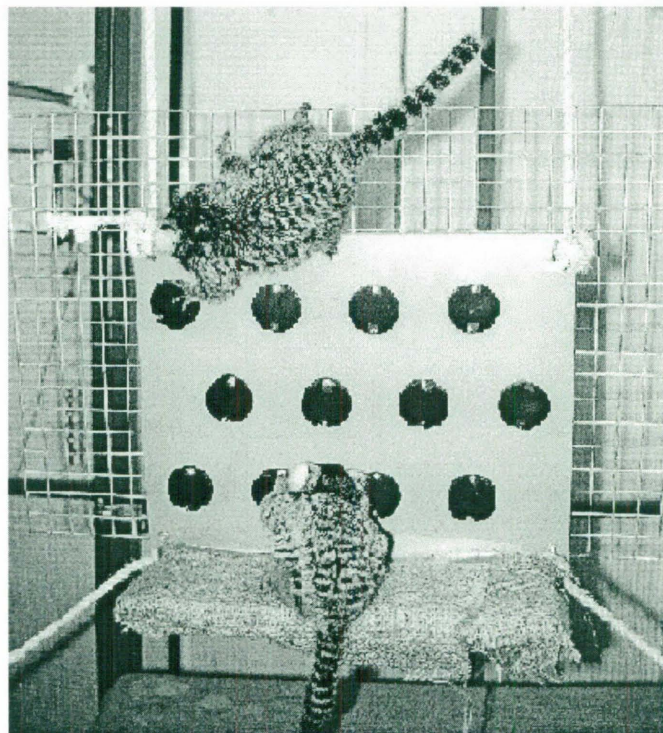
Figure 2.5: Two cage mates using the cluster feeder.

2.4.4 Dispersed Feeders

The dispersed feeders were scaled-down versions of the cluster feeder (10cm wide x 13cm tall x 2cm thick) made of 19mm solid pinewood with two metal braces on the back to allow for hanging (Figure 2.6). These dispersed feeders consisted of one hole similar to that found in the cluster feeder (2.5cm diameter hole, 2cm deep) covered by the same disc arrangement as used in the cluster feeder.
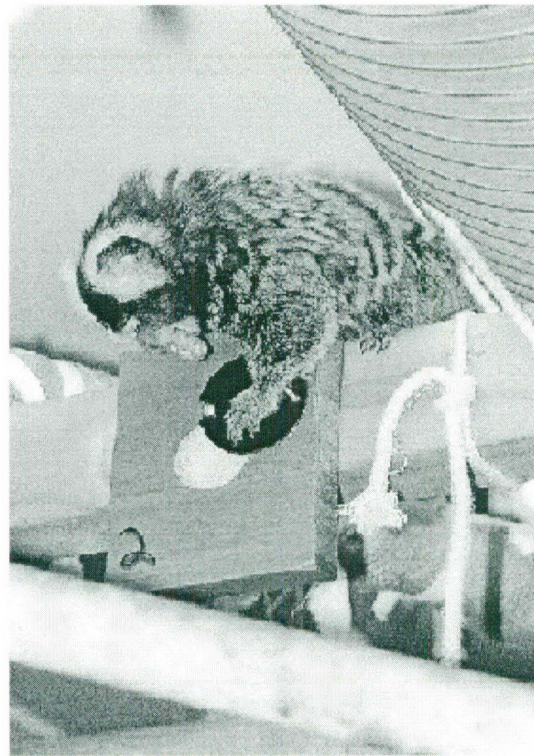
Figure 2.6: Photograph of marmoset subject using a dispersed feeder.

2.5 General Methodology

Separation of cage mates stimulates a physiological and behavioural stress response in common marmosets (Norcross & Newman, 1999). Therefore, cage mates were not separated during the study. Two testing pairs were located in the same enclosure (Figure 2.2, Table 2.1). Both pairs could not have simultaneous free access to ER 2, and ER access needed to be continuous for the current testing pair for the length of an experimental condition. For these reasons, the four testing pairs were divided into two Testing Groups (TGs). Testing Group #1 (TG1) consisted of Pairs #1 and #2. Testing Group #2 (TG2) consisted of Pairs #3 and #4 (Table 2.1). Experimental testing alternated between TGs to accommodate this arrangement.

2.5.1 Outline of Experimental Conditions

Marmoset pairs were observed in their respective ERs during three non-experimental conditions and four experimental conditions. Non-experimental conditions consisted of Empty Room 1, Empty Room 2, and Empty Room 3. Experimental conditions consisted of 1) Food Bowl Introduction, 2) Changing Bowl Position, 3) Cluster Feeder Introduction, and 4) Dispersed Feeders Introduction. The conditions were tested in the following order for all subjects:

1) Empty Room 1 condition
2) Food Bowl Introduction (Bowl condition)
3) Changing Bowl Position (CBP condition)
4) Empty Room 2 condition
5) Cluster Feeder Introduction (CF condition)
6) Empty Room 3 condition
7) Dispersed Feeders Introduction (DF condition).

Testing the conditions alternated between the two testing groups (Table 2.4). Empty Room 1 condition was first tested for both TGs so that the data could be analysed

in order to develop the future conditions' protocols. The remaining conditions were grouped into clusters that were tested successively: Bowl/Changing Bowl Position, Empty Room 2/Cluster Feeder, and Empty Room 3/Dispersed Feeders conditions. In between each of these clusters was a two-day interim period, *Access Change*. During this period, runway access to the ERs was given to testing pairs in the alternate TG to accustomise the subjects to the recent ER access change. The ERs were also swept and faeces removed before the alternate TG was allowed access.

Table 2.4: Experimental conditions presentation order. A member of Pair #3 (TG2) injured her tail during the Changing Bowl Position condition; therefore, testing for that pair stopped, but continued for Pair #4 (TG2). Both Bowl conditions were then presented to TG1 before Pair #3 was retested, which allowed 14 days for the tail to heal.

Experimental Conditions Presentation Order		Number of Days Per Condition
TG1	Empty Room 1	8
	Access Change	2
TG2	Empty Room 1	8
Break to analyse data and develop following conditions' protocols		
TG2	Bowl	4
	Changing Bowl Position	4
	Access Change	2
TG1	Bowl	4
	Changing Bowl Position	4
	Access Change	2
Pair #3 (TG2) Retest	Bowl	4
	Changing Bowl Position	4
	Access Change	2
TG1	Empty Room 2	2
	Cluster Feeder	4
	Access Change	2
TG2	Empty Room 2	2
	Cluster Feeder	4
	Access Change	2
TG1	Empty Room 3	2
	Dispersed Feeders	4
	Access Change	2
TG2	Empty Room 3	2
	Dispersed Feeders	4
	Total Days:	78

To avoid the interventions becoming predictable, the marmosets were not tested at the same time each day. Instead, all testing was done within ranges of time, because presentation variability has been documented as a beneficial aspect of enrichment (Kuczaj et al., 2002). Testing sessions were completed in the morning between 08:45 and 11:15 while afternoon sessions were completed between 14:00 and 16:30. These time ranges accommodated the general maintenance and husbandry practices of the Animal House. As a result, it was easy to restrict access to the Animal House to anyone but the Experimenter during those times.

No additions or modifications were made to the ERs during the Empty Room conditions; the ERs were maintained as they were originally kept. The Empty Room conditions, in addition to the time spacing between conditions, were used as intermediate checks to see if the sequence of testing conditions produced an order effect (i.e. to ensure that the results did not simply reflect ongoing changes in the animals' responses). During the Empty Room 1 condition, subjects were observed during two 30-minute testing sessions, one in the morning and one in the afternoon, for eight days, totalling 16 sessions. This was done to create a solid platform of data under the Empty Room 1 condition, which would help determine which aspects of the room should be investigated in the future conditions.

The protocol for subsequent conditions was altered after evaluation of the Empty Room 1 condition protocol. The subsequent conditions had 20-minute testing sessions. The Empty Room 1 condition data were adjusted (by multiplying each value by two-thirds) to reflect 20-minute not 30-minute sessions to make them comparable to the rest of the conditions. The number of testing sessions also changed. The number of testing days for the Empty Room conditions was reduced after the Empty Room 1 condition from eight days to two days. The time spent in the ER during the first two days of the Empty Room 1 condition did not differ from the time spent in the ER during the third to eighth testing days of the Empty Room 1 condition. Therefore, Empty Room 2 and 3 conditions consisted of four testing sessions during two days, two morning and two afternoon sessions.

All four experimental conditions were monitored during six testing sessions that occurred over four days, three morning and three afternoon sessions. Morning and

afternoon testing sessions were spread throughout the four testing days to provide a level of variability similar to the use of testing time ranges. The first day had two testing sessions (one morning, one afternoon), the second day had one afternoon session, the third day had two testing sessions (one morning, one afternoon), and the fourth testing day had one morning session. Session times remained within the time ranges previously outlined.

The ER was divided into sections to denote the locations of each apparatus within the ER during each condition. Each ER was divided into three vertical divisions (High, Middle, Low) and three horizontal divisions starting from the marmoset's room entrance to the back of the ER (Divisions 1, 2, 3). Figure 2.7 is a three-dimensional illustration of the ER. The horizontal and vertical divisions resulted in nine room sections: H1, H2, H3, M1, M2, M3, L1, L2, and L3 (Table 2.5).
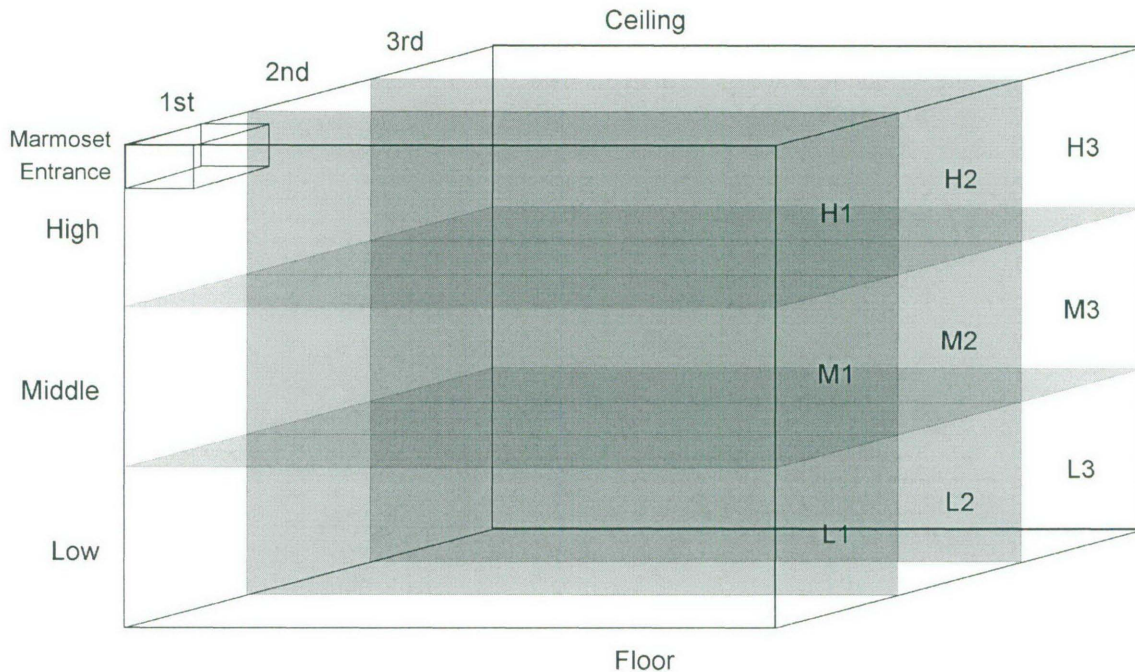
Figure 2.7: Three-dimensional diagram of ER with vertical and horizontal divisions. The ER was divided into vertical thirds (High Middle, Low) and horizontal thirds (1, 2, 3). These vertical and horizontal divisions resulted in room Sections H1, H2, H3, M1, M2, M3, L1, L2 and L3.

Table 2.5: Room divisions and resulting sections. An asterisk (*) denotes the room section that includes the marmoset's room entrance. The caret (^) indicates the farthest section away from the marmoset's room entrance.

DIVISION	#1	#2	#3
High (H)	H1*	H2	H3
Middle (M)	M1	M2	M3
Low (L)	L1	L2	L3^

2.5.1.1 Food Bowl Introduction

In the Bowl condition, a food bowl was introduced into the ER. This was a change for the marmosets since they typically were fed in their homes cages. One food bowl was placed in its customary position in the home cage: mid-height in cage near entrance from runways. The other bowl was placed in the ER at a similar height (mid-room) and position (near the room entrance) as the HC bowl. The ER food bowl was placed in Section M1, bowl Position 1 (Figures 2.7 and 2.8). Each bowl contained a full feed of Basics and Additional foods listed in Table 2.3 so that the subjects could eat fully from any one bowl (Table 2.6). Table 2.6 lists the apparatus food contents and locations. As per the regular husbandry practices outlined in Section 2.3.3, food bowls were left in the HCs and ERs throughout the day and were cleaned and replenished during the next day's feeding time.

The first food bowls placed in the HC and ER were positioned the day before the start of testing, so that on the first testing day, the subjects had access to the food for the entire day from the moment they entered the ER. All bowls were weighed before and after feeding to measure the amount of food removed (either consumed or dropped) as an indication of preference for feeding in the HC versus the ER and to ensure that the marmosets were maintaining a satisfactory dietary intake.

The Bowl condition was the control for the other three experimental conditions, since they built upon the Bowl condition procedures.

Table 2.6: Apparatus food contents and locations. The letter "B" indicates the Basic foods while the letter "A" indicates the Additional foods as outlined in Table 2.3. Room sections M1 and M3 are depicted in Figure 2.7. The HC bowl stayed stationery in its customary position within the home cage. Placement of the ER food bowl is diagrammed in Figure 2.8. Dispersed feeder locations are listed in Table 2.8.

	APPARATUS FOOD CONTENTS			LOCATION OF APPARATUS	
Condition	HC Bowl	ER Bowl	Feeder(s)	ER Bowl (see also Figure 2.8)	Feeder
Bowl	B + A	B + A		M1	-
CBP	B + A	B + A		M1, M3	-
CF	B	B	A	M1	M3
DF	B	B	A	M1	See Table 2.8

2.5.1.2 Changing Bowl Position

In the CBP condition, the location of the ER food bowl was rotated through four different positions located at the same height level in the ER, approximately 1m above the floor, to determine if bowl position in the ER had an effect on behaviour. All bowl positions were in the Middle division of the ER. The food bowl was positioned approximately 0.75m from each corner of the room. The positions were numbered 1-4 starting from the corner closest to the marmoset entrance to the room and working clockwise (Figure 2.8). Positions 1 and 2 were in horizontal room Division 1, while Positions 3 and 4 were in horizontal room Division 3 (Figure 2.8). Bowl position per day and pair was determined using a Latin Square (Table 2.7). As in the Bowl condition, all bowls contained a full feed of the Basics and Additional foods (Table 2.6) and were weighed before and after feeding.

Figure 2.8: Aerial view of ER's Middle division and bowl positions during the CBP condition. The letter 'E' indicates the marmoset entrance into the ER. P1, P2, P3, and P4 indicate the locations of the bowl positions 1, 2, 3, and 4. Room Divisions 1, 2, and 3 are the horizontal divisions of the ER as diagrammed in Figure 2.7.
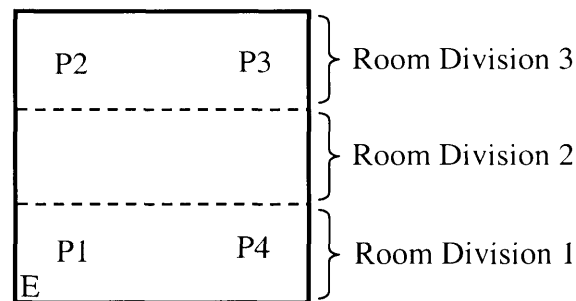
P2 P3	} Room Division 3
	} Room Division 2
P1 P4 E	} Room Division 1

Table 2.7: Latin square of bowl positions. Each testing pair underwent one testing day with the food bowl in each of the four positions. Position 1 was the location of the bowl during the Bowl condition.

Pair	Day			
	1st	2nd	3rd	4th
1 Sage/Pop	1	2	3	4
2 Red/Crassus	2	3	4	1
3 Ash/Pompey	3	4	1	2
4 Black/Zhen	4	1	2	3

2.5.1.3 Cluster Feeder Introduction

Before the marmosets were tested with the cluster feeder, it was first determined that all marmosets were cognitively and physically capable of manipulating the feeder discs and completing the task that would be presented to them in the feeder experiments: i.e. to swing a disc to the left or right to uncover a food reward. Before introducing any feeder (cluster or dispersed), training sessions were performed with one dispersed feeder, but with the hole initially covered by a perspex disc, then the testing opaque disc. Each subject was shaped to use the feeder by being given individual access to the dispersed feeder with the perspex disc propped completely open, half-open, and

then closed. Then the subject graduated to a dispersed feeder with the opaque testing disc and was tested through the same disc stages, completely open, half-open, and then closed, until she successfully retrieved the food immediately behind the closed opaque disc in one trial. Once all subjects of the same testing group met this criterion, they progressed to the Cluster Feeder condition.

The CF condition was similar to the Bowl condition with a few changes. A food bowl was provided *ad libitum* in the ER as well as a food bowl provided in the HC for each testing pair. However, the Feeder conditions' food bowls differed from the Bowl conditions' food bowls. Since the feeders were only present during testing sessions, and the marmosets' regular husbandry procedure was to have *ad libitum* food access, the Basics (see Table 2.3) were not loaded into the feeders. In addition, the Basics provided a well-rounded nutritionally sufficient diet, but were also pre-processed and offered little to induce natural foraging behaviours. For these reasons, equal amounts of the Basics were kept in the HC and ER food bowls (Table 2.6), and they were available *ad libitum* as per regular husbandry procedure to ensure the marmosets had continuous access to sufficient food. Similar to the Bowl conditions, all bowls were weighed before and after each feeding.

The cluster feeder was loaded with the normal daily amount of Additional foods as listed in Table 2.3, which were the more ecologically relevant foods from the diet: sultanas, egg, cheese, peanuts, Nutri-grain^{TM}, fruits, vegetables, mealworms, and crickets (Table 2.6). Amount of food eaten from the feeder was difficult to assess and was not scored since the food was loaded into 12 locations versus one bowl, the softer fruits, such as banana, smeared into the holes, and food that dropped from the feeders may or may not have been retrieved later by a subject.

During the first day of testing, all 12 holes were filled with food. During the remaining three testing days, 10 holes were filled to provide a level of unpredictability, similar to that experienced by wild common marmosets when foraging (Kleiman et al., 1986). Vacant holes were randomised for each testing session. Before the start of each session, the cluster feeder was loaded with food and suspended in the ER approximately 1.3m from the floor and ceiling in Section M3. The feeder was withdrawn at the end of each session.

2.5.1.4 Dispersed Feeders Introduction

The DF condition involved the same procedure as the CF condition except that the Additional foods were placed within 12 dispersed feeders. The 12 dispersed feeders were spread throughout the nine room sections as shown in Table 2.8. The feeders were introduced at the beginning of each session and withdrawn at the end.

Table 2.8: The number of feeders located in each room section, H1, H2, H3, M1, M2, M3, L1, L2, and L3, during the DF condition.
Each vertical (H, M, L) and horizontal (1, 2, 3) room division contained four dispersed feeders.

DIVISION	#1	#2	#3	Totals
High (H)	2	1	1	4
Middle (M)	1	2	1	4
Low (L)	1	1	2	4
Totals	4	4	4	12

2.5.2 Behaviour Scoring

During testing sessions, the experimenter was located behind a one-way mirror that looked into an ER from the anteroom. Since the marmosets travelled through the anterooms to enter the ER (Figure 2.2) and the Experimenter was located in the anteroom, the Experimenter was also hidden under a hide to block visual contact. An 8mm video camera also located under the hide videorecorded any subject interactions with the food bowls during both Bowl conditions and the feeders during the Cluster and Dispersed Feeders conditions. The same behaviours were recorded during all conditions. The Experimenter continuously recorded the marmosets' behaviours within the ER using an all-occurrences sampling method with a shorthand created to expedite record keeping (Altmann, 1974). Table 2.9 outlines all behaviours recorded during the testing sessions. The notations in parentheses indicate the shorthand codes. The frequency of all behaviours was recorded, and for some behaviours, the duration of each event was also

recorded. The Experimenter started a stopwatch at the beginning of each session. The session finished when the stop watch reached 20 minutes. The time on the stopwatch was used to record the beginning and end of certain behaviours to obtain a behaviour duration. An example of five minutes of record keeping for one subject is: (P0:00) H1 H2 H3 (S/Lp 0:20 Sc Sc 1:40) Lt H2 M2 M1 (bt 2:00 2:30) (S/E 2:30 5:00). This running behavioural record for the marmoset means that Subject, P, entered the room at the start of the testing session (P0:00). She crossed through room sections, H1, H2, H3, before sitting next to a light (S/Lp) for 1 min 20 sec (0:20 – 1:40). While she was sitting next to the light, she scratched twice (S/Lp 0:20 Sc Sc 1:40). The subject then touched the light and moved into room sections H2, M2, M1 where she interacted with the bowl from 2:00 to 2:30 (Lt H2 M2 M1 (bt 2:00 2:30)). The subject then stayed in Section M1 and ate while sitting from 2:30 to 5:00 (S/E 2:30 5:00).

**Table 2.9: Definitions for behaviours recorded during testing
sessions.** A notation in parentheses indicates a shorthand code for the
behaviour it precedes. The frequency of all behaviours was recorded.
Those behaviour marked with an asterisk (*) indicate behaviours for
which the time duration of each event was also recorded.

(Subject's Initial + time) = a subject entered the ER at that time
(X + time) Exit = subject exited the ER at that time

DEGREE OF ENTRANCE IN TO THE ROOM = the number of movements into
each of the nine room section combinations (H1, H2, H3, M1, M2, M3, L1, L2,
L3) was recorded (see Figure 2.7)

Vertical Divisions
(H) High = the upper 1/3 of the room
(M) Middle = the middle 1/3 of the room
(L) Low = the lower 1/3 of the room

Horizontal Divisions (starting from the marmoset's entrance in to the room and going
towards the back of the room)
(1) First = the first 1/3 of the room
(2) Second = the second 1/3 of the room
(3) Third = the third 1/3 of the room

BOWLS/FEEDERS

(bt) Bowl Touch* = interactions with the food bowl
(ft) Feeder Touch* = interactions with a feeder
(E) Eating* = ate a food item in the ER, sometimes recorded in combination with
sitting, S/E or S/Lp/E

FOOD-RELATED BEHAVIOURS

(sm) Scent Mark = sternal, facial, or circum-genital scent mark
(g) Gouging = used teeth to gnaw/gouge a surface
(~) Chirp = favourable vocalisation often associated with food

SITTING = no body locomotion, body could pivot in the same spot

(S) Sitting overall[*]= marmoset sat down on behind, was sometimes performed in combination with the following behaviours:

(S/Lp) Sitting next to a Light[*] = a subcategory of Sitting, when a marmoset sat within one body's length from a light, did not include any eating

(S/E) Sitting while Eating[*] = a subcategory of Sitting, when a marmoset sat and ate, did not include performing this behaviour next to a light

(S/Lp/E) Sitting next to a Light while Eating[*] = a subcategory of Sitting, recorded when a marmoset sat next to a light *and* ate

SELF-DIRECTED BEHAVIOURS = those behaviours directed to the individual performing them

(G) Grooming[*] = an active engagement in hair/skin maintenance; when a marmoset used hands and/or tongue to part hair and pick at hair/skin

(G/Lp) Grooming next to a light[*] = a subcategory of Grooming, when a subject groomed itself while positioned within one body's length away from a light

(Sc) Scratching = used a foot or hand to scratch another part of the body, in comparison to grooming, this is more of a casual, ephemeral action

AFFILIATIVE BEHAVIOURS = those behaviours involving a social interaction

(U) Huddling[*] = a passive social contact, cage mates sat next to each other with body contact

(AG) Allogrooming[*] = marmosets groomed each other, huddling was recorded if allogrooming occurred

VOCALISATIONS

(^) Phee = long-distance contact call

(') Tsik[*] = mobbing call or a response to something novel

(ch) Chatter[*] = aggressive vocalisation

MISCELLANEOUS

(Lp) Light-Proximity = recorded in conjunction with other behaviours (such as grooming or sitting), when a marmoset was within a body's length from a light

(Lt) Light-Touch = stretched with, hung from, or touched a light in any way

(St) Stretching = extended body by hanging on/from furniture, other than a fluorescent light (if a subject stretched from a light, it was marked as "Lt")

Using a subject's entrance and exit times, the number of entries and the duration of each visit were calculated to create a total time spent in the ER per testing session. Movements within the room were determined by the number of times the marmosets moved into a different room section (similar to Bayne et al., 1992; Bayne et al., 1994). The number of movements into each room section was used to assess the overall room use. In addition, the three horizontal sections (1, 2, 3) were combined for each vertical division to create a total of movements for each of the vertical divisions, High, Middle, and Low.

Interactions with either of the two fluorescent lights on the ceiling of the ER were recorded because it appeared the marmosets were motivated to come into the ER so that they could interact with a light. As a result, contact made with the light and grooming or sitting next to a light were recorded.

Four different variations of Sitting behaviour were recorded. Sitting overall (SO) included any type of sitting regardless of the location or other behaviour being performed while sitting. Sitting next to a light (SL) involved sitting within one body's length from one of two fluorescent light strips on the ceiling of the ER. Sitting and Eating (SE) was recorded when a marmoset sat and ate.

SL and SE were not independent behaviours. A marmoset could have performed both behaviours concurrently resulting in the behaviour: Sitting next to a Light and Eating (SLE). To separate these behaviours, the definitions of SL and SE were clarified. SL did not include any Eating (E), and SE did not include any time spent performing this behaviour while next to a Light (L). Therefore, SE and SL were recorded as separate behaviours. The scores for SLE could be added to either SL or SE behaviours to get a grand total of SE or SL. All four sitting behaviours were recorded as events and times.

Two different types of grooming behaviours were recorded. Self-directed grooming, or autogrooming, is termed grooming within this text. Grooming a conspecific is labelled as allogrooming within this text. Similar to the sitting behaviours, grooming was sometimes performed next to a fluorescent light. Therefore, Grooming next to a Light (GL) was also recorded as a subcategory of Grooming Overall (GO), and both were recorded as times and events. The experimental subjects have been observed plucking hair from their tails when stressed, especially when isolated. However, the

experimental subjects, in general, did not have a history of excessive or abnormal scratching or grooming prior to the experiment.

2.5.3 Motion Sensor Photographs (MSPs)

A galvanised metal box was fixed to the wall of each ER to house the internet camera. The testing sessions determined the short-term effects of food bowl or feeder presence, while the MSPs helped to ascertain if the food bowls or feeders had a long-term effect during the 12-hour light cycle (07:30-19:30). The camera with motion sensor software recorded the marmosets' entries and exits to/from the ER during the 12-hour light cycle. The camera commenced taking pictures as soon as it sensed movement and while the movement continued in front of the camera. The Logitech® QuickCam® software then catalogued each picture by date and time taken in hours: minutes: seconds, so they could be analysed later by the Experimenter.

There was one motion sensor camera, so one testing pair could be photographed at any one time. During the Empty Room 1 condition, MSPs were taken for three days for each testing pair, to create a solid base of data about the marmosets' movements without any ER modifications. During the Empty Room 2 and 3 conditions, MSPs were taken for one day per testing pair. Each testing pair had MSP monitoring for two days during the experimental conditions: Bowl, CBP, CF, DF.

The marmosets moved too quickly past the camera to permit individual identification. Therefore, data collected from the MSPs were for each pair and not individual subject. The motion sensor captured all movement in front of the camera, so there were many more photographs than just those containing entries and exits. The mean total number of photographs taken per day was 905 ± 15. The Experimenter reviewed the photographs for each day using IrfanView 3.91 freeware graphic viewer. IrfanView showed the time the pictures were created as each picture was displayed. The first photograph containing a marmoset entering the ER (usually head and ear tufts) was recorded as an Entry, while the last photograph containing a marmoset leaving the ER (usually a tail) was deemed an Exit. The Experimenter then manually entered the times for all Entries and Exits into a spreadsheet. Entry time was subtracted from Exit time to

determine entry duration. Rarely, the number of entries and exits did not match up. If this occurred, the irregular entry or exit was discarded. In a total of 56 motion sensor days, only 0.65% of the entries or exits were discarded out of 5,570 total entries and exits from 60,000 MSPs overall. Total time in the ER, number of entries, and entry duration were calculated for each testing pair.

2.6 Statistical Analysis

The Statistical Package for the Social Sciences (SPSS®) was used to analyse the data. Each subject's records were averaged for each behaviour per experimental condition, creating a subject mean per 20-minute testing session for each experimental condition. Subjects did not necessarily enter the ER during every testing session. Therefore, the means per subject also included the 'zeros' from sessions in which the subjects did not enter the ER. The frequencies of behaviours were recorded and/or the total amount of time the behaviour was exhibited per 20-minute testing session (time in minutes). Since the same subjects were evaluated for each experimental condition, repeated measures ANOVA (RMA) was used to determine whether there was a significant difference between the experimental conditions for one dependent variable and Multivariate ANOVA (MANOVA) was used for more than one dependent variable (Tabachnick & Fidell, 2001). Although there were inter-individual differences in response intensity to the experimental conditions, all individual subjects and testing pairs showed similar patterns of behaviour to the experimental conditions.

The Empty Room conditions, in addition to spacing experimental conditions, were used as intermediate checks to determine whether the sequence of testing conditions produced an order effect. RMA was used to determine whether there was a significant difference in each behaviour for Empty Room conditions 1, 2, and 3. The results from each of these analyses are in Table 2.10. If the Empty Room conditions for a certain behaviour were significantly different from one another, this was marked in Table 2.10 with an asterisk (*), and was discussed further in Chapter 3. Since these conditions were checks, they served their purpose by *not* being significantly different.

Then the four experimental conditions, Bowl, Changing Bowl Position (CBP), Cluster Feeder (CF), and Dispersed Feeders (DF) were examined also using RMA. The degrees of freedom for all experimental condition analyses were (3, 21) while for analysis of motion sensor data they were (3, 9).

Sphericity was checked for all RMA using Mauchly's check as provided by SPSS®. If sphericity could not be assumed, Greenhouse-Geisser values were used and the RMA's p-value was labelled with a "G-G" (Tabachnick & Fidell, 2001). The Bowl condition was the control for all other experimental conditions. Simple contrasts using the Bowl condition as the control compared to the other three experimental conditions and Tukey's *Honestly Significant Difference* (HSD) were used to determine the significance of the differences between experimental conditions (Keppel, 1991).

Certain behaviours were exhibited infrequently and the data sets included a number of zeros so a sphericity p-value was not produced for some RMAs. In this event, Friedman rank tests were used to determine significant differences (Marascuilo & McSweeney, 1977). Significance levels were set at $\alpha=0.05$. The strength of association was represented by eta-squared, η^2, for analyses with one dependent variable and partial eta-squared, partial η^2, for analyses with more than one dependent variable (Levine & Hullett, 2002; Tabachnick & Fidell, 2001).

Table 2.10: Summary table for the statistical analyses of all behaviours during the Empty Room conditions. All behaviours were analysed with RMA, df (2, 14) unless otherwise noted. (ns) indicates the behaviour was not significantly different across the Empty Room conditions, while an asterisk (*) indicates the behaviour was significantly different. Superscript "a" (^{a}) indicates a Greenhouse-Geisser p-value was used. Superscript "b" (^{b}) indicates a Friedman rank test was used (n=8). The letter "x" indicates those behaviours that were not available options during the Empty Room conditions.

Behaviour	P-Value	Significance	Eta-Squared
Total Time IN	0.11	ns	
Entries	0.19	ns	
Total Movements	0.24	ns	
Motion Sensor Total Time IN	0.48	ns	
Motion Sensor Entries	0.95	ns	
Motion Sensor Entry Duration	0.40	ns	
High Sections	0.18	ns	
Middle Sections	0.34	ns	
Low Sections	0.28	ns	
High1 Section	0.17	ns	
High2 Section	0.20	ns	
High3 Section	0.25	ns	
Middle1 Section	0.16	ns	
Middle2 Section	0.47	ns	
Middle3 Section	0.03^a	*	η2=0.464
Low1 Section	0.27^a	ns	
Low2 Section	0.34^a	ns	
Low3 Section	0.16^b	ns	
Time spent with a Food Bowl	x		
Number of Food Bowl Interactions	x		
Amount of Food Eaten from HC and ER Bowls	x		
Time spent Eating	x		
Number of Eating bouts	x		
Time spent with a Feeder	x		
Number of Feeder Interactions	x		
Number of Gouging Events	0.86^a	ns	
Number of Scent Marking Events	0.58	ns	
Time Sitting Overall	0.09	ns	
Number of Sitting Overall Events	0.09	ns	
Time spent Sitting next to a Light	0.09	ns	
Number of Sitting next to a Light Events	0.11	ns	
Total Time spent Sitting and Eating	x		
Number of Eating while Sitting events	x		
Time spent Sitting next to a Light and Eating	x		
Sitting next to a Light and Eating Events	x		
Number of Light Interactions	0.09	ns	
Number of Stretching Events	0.39^a	ns	
Number of Scratching Events	0.01	*	η2=0.468
Time spent Grooming	0.20	ns	
Number of Grooming Events	0.01	*	η2=0.468
Time spent Grooming next to a Light	0.25^a	ns	
Number of Grooming next to a Light Events	0.01	*	η2=0.454
Total time spent Huddling	0.37^b	ns	
Number of Huddling Events	0.37^b	ns	
Total Time spent Allo-Grooming	0.37^b	ns	
Number of Allo-Grooming Events	0.37^b	ns	
Total Time spent Tsikking	0.35^a	ns	
Number of Tsikking Bouts	0.43^a	ns	
Number of Phee Bouts	0.13	ns	

CHAPTER 3

RESULTS

3.1 Introduction

Chapter 3 presents the results for this study. Data were analysed using variables described in Chapter 2. Unless otherwise noted, all behaviours are described in terms of the mean amount of time or number of times a behaviour was observed per 20-minute testing session. Error bars in figures indicate ± standard error of the mean (SEM). If, on the graphs, the error bars from two variables (displayed in bar and line graphs, for instance) crossed over and were difficult to distinguish from each other, +SEM was displayed for the upper variable (typically, the line graph), while -SEM was displayed for the bottom variable (typically, the bar graph).

The following experimental results are divided into two sections: those behaviours that were likely to increase and those behaviours likely to decrease as a result of the experimental conditions.

3.2 Behaviours Likely To Increase

3.2.1 Room Use

Room use was assessed using two data sets: data recorded during the 20-minute testing sessions and data collected from the motion sensor photographs. Using both data sets, the behaviours, number of entries into the ER and time spent in the ER, were analysed to determine the time distribution between the HR and the ER. Room use

within the ER was assessed using the number of movements into the room sections during testing sessions.

Figure 3.1 displays the time spent in the ER for all four experimental conditions. There was a significant difference in time spent in the ER between conditions ($p=0.001$, $\eta^2=0.765$). The time spent in the ER was significantly higher during both Feeder conditions than the Bowl condition (CF: $p=0.002$, $\eta^2=0.761$; DF: $p=0.001$, $\eta^2=0.837$). However, there was no significant difference between conditions in the number of entries into the ER (G-G, $p=0.303$) (Figure 3.1).
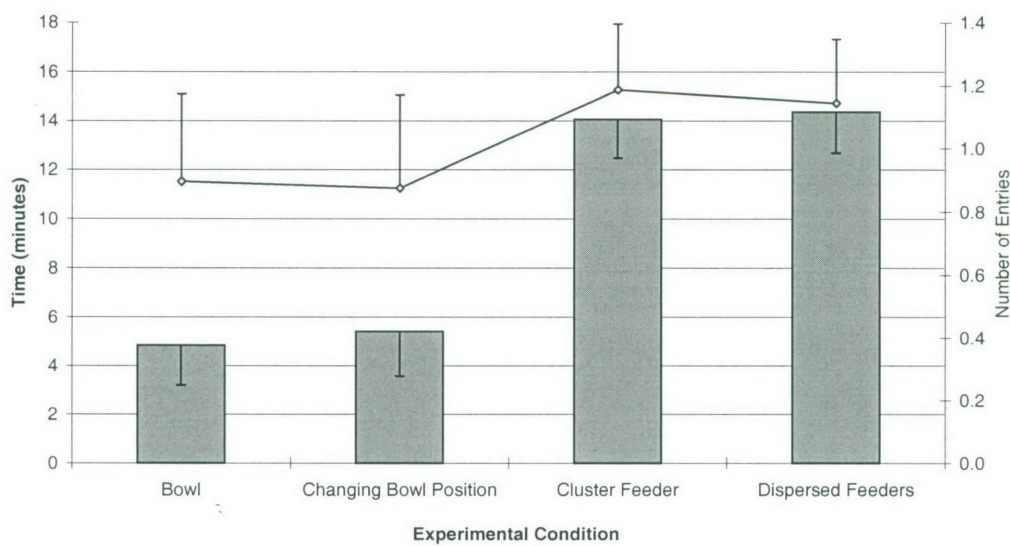
Figure 3.1: Time spent in the ER and number of entries into the ER.
Bars indicate the time spent in the ER (minutes). The line indicates the number of entries into the ER.

The motion sensor camera recorded entries and exits to/from the ER for the 12-hour light cycle. These data were collected to determine if the food bowls or feeders had a long-term effect during the 12-hour light cycle (07:30-19:30). From these data, total time spent in the ER and number of entries were determined for each day's 12-hour light cycle. The time spent in the ER per day was significantly different across conditions ($p=0.043$, $\eta^2=0.579$). Unlike the time in the ER per testing session, the time spent in the ER per day was significantly higher during the CF condition than both Bowl conditions and nearly significant to the DF condition. Therefore, the CF condition had a more long-term effect than either food bowl condition, even though the cluster feeder was present

during 20-40 minutes a day and the bowls were continuously available. Although it was not significant, on average, the marmosets spent approximately three more hours in the ER per day during the CF condition than the DF condition. The number of entries per day was not significantly different across the conditions (p=0.137) (Figure 3.2).
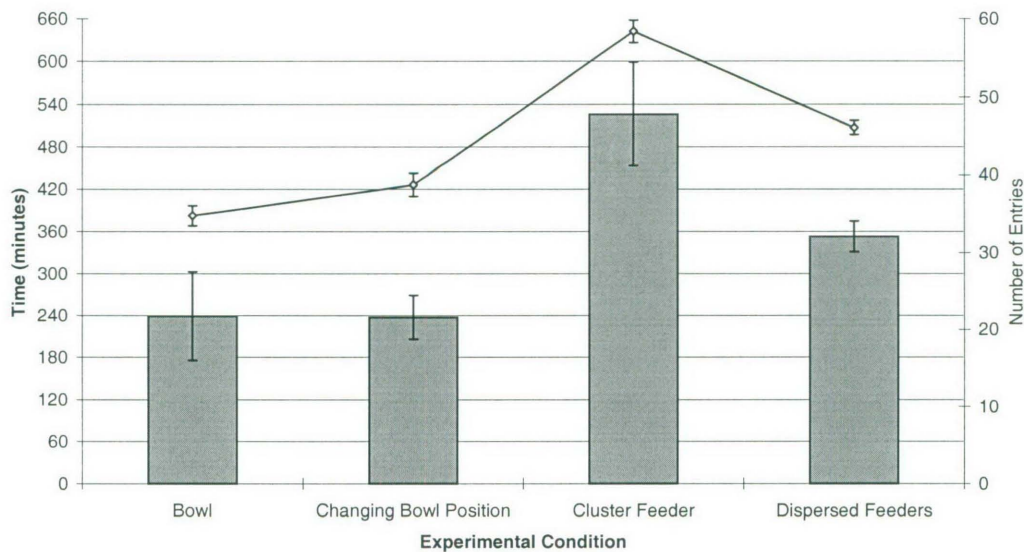
Figure 3.2: Time spent in the ER and number of entries into the ER during the 12-hour light cycle. Bars indicate the time spent in the ER per day (minutes). The line indicates the number of entries into the ER per day.

Movements within the room were determined by the number of times the marmosets moved into a different room section. Room sections are outlined in Table 2.5 and Figure 2.7. There was a significant difference in the number of total movements within the ER across the conditions (p=0.001, η^2=0.628). Significantly more movements were made during both Feeder conditions compared to the Bowl condition (Cluster: p=0.032, η^2=0.503; Dispersed: p=0.002, η^2=0.761). The DF condition involving the twelve individual dispersed feeders elicited the highest number of movements or activity compared to all other experimental conditions (Figure 3.3).
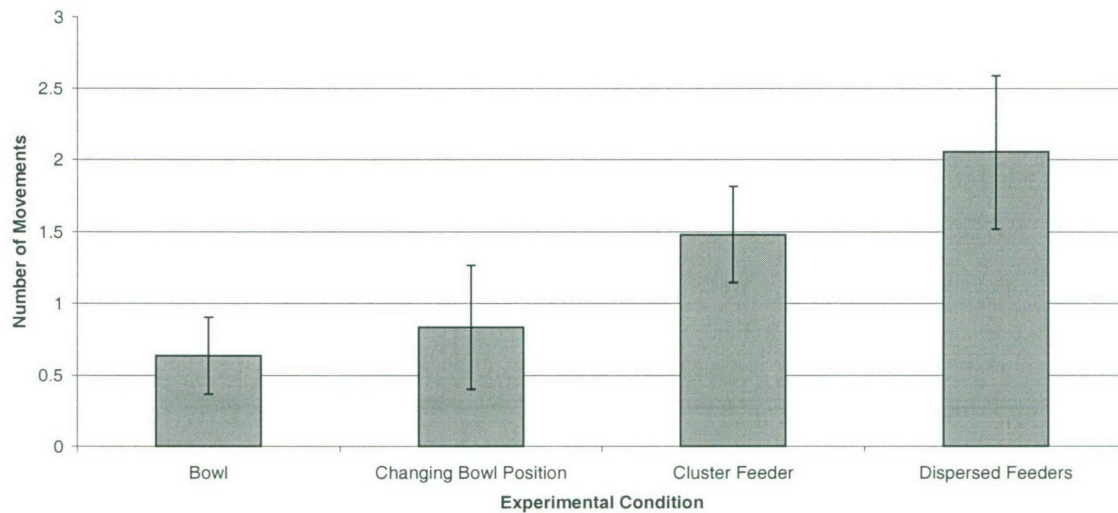
Figure 3.3: Total number of movements within the ER.

Movements into the three vertical divisions of the room, High, Middle, and Low, were also analysed. A 3x4 RMA was used to analyse the use of the High, Middle, Low room divisions across the experimental conditions. The interaction between vertical division (High, Middle, Low) and experimental condition was significant (df(6, 42), p=0.001, partial η^2=0.426), indicating there was a significant difference in number of movements into the vertical divisions across the experimental conditions. Across experimental conditions, there was a significant difference in the number of movements into the High (G-G, p=0.021, η^2=0.444), Middle (p=0.001, η^2=0.706), and Low (p=0.001, η^2=0.586) room divisions. The number of movements into the High room sections was significantly higher during the DF condition than the Bowl condition. The number of movements into the Middle room sections was significantly higher during the DF condition than all other conditions. In addition, the number of movements into the Middle room sections was significantly higher during the CF condition than the Bowl condition. The number of movements into the Low room sections was significantly higher during the DF condition than all other conditions (Figure 3.4).
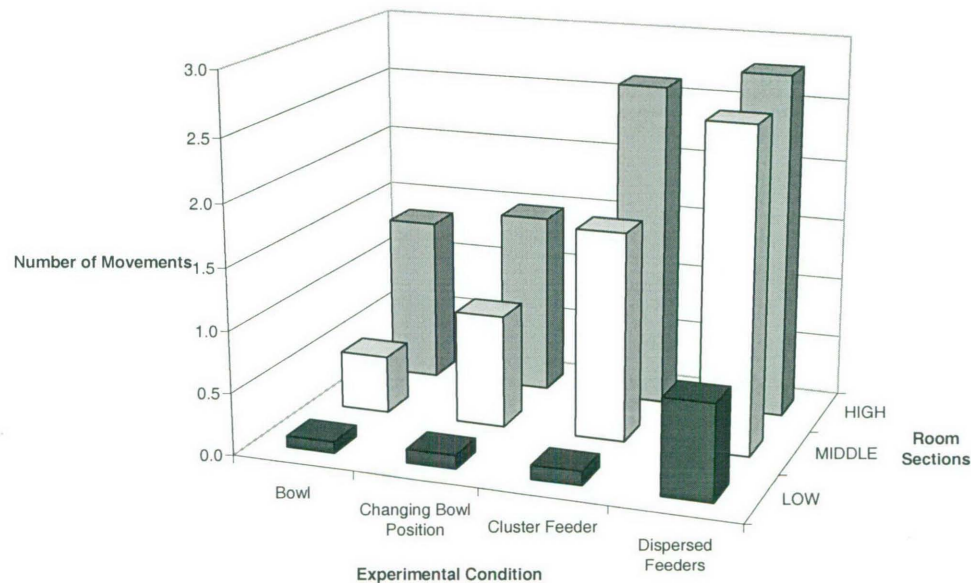
Figure 3.4: Number of movements into the High, Middle, and Low room sections of the ER per testing session.

The percentage of total entries made into each room section was calculated using the number of entries into each room section divided by the total number of entries into all room sections. The marmosets entered and exited through Section H1. Therefore, this section was biased with higher movements. The feeders and bowls were located in specific positions during different conditions (Table 2.6). When no feeder or bowl was provided in Section M3 during the Bowl condition, the subjects entered this section only 0.6% of the time. When a food bowl (CBP condition) was added to Section M3 for just half the testing sessions or a cluster feeder (CF condition) was added, the percentage of movements increased to 5.5% and 23.7%, respectively (Figure 3.5). Likewise, the Low room sections encompassed only 2.6% of the total movements during the Bowl condition, but when four dispersed feeders were placed within the Low room sections, the percentage of total movements increased to 12.6%.
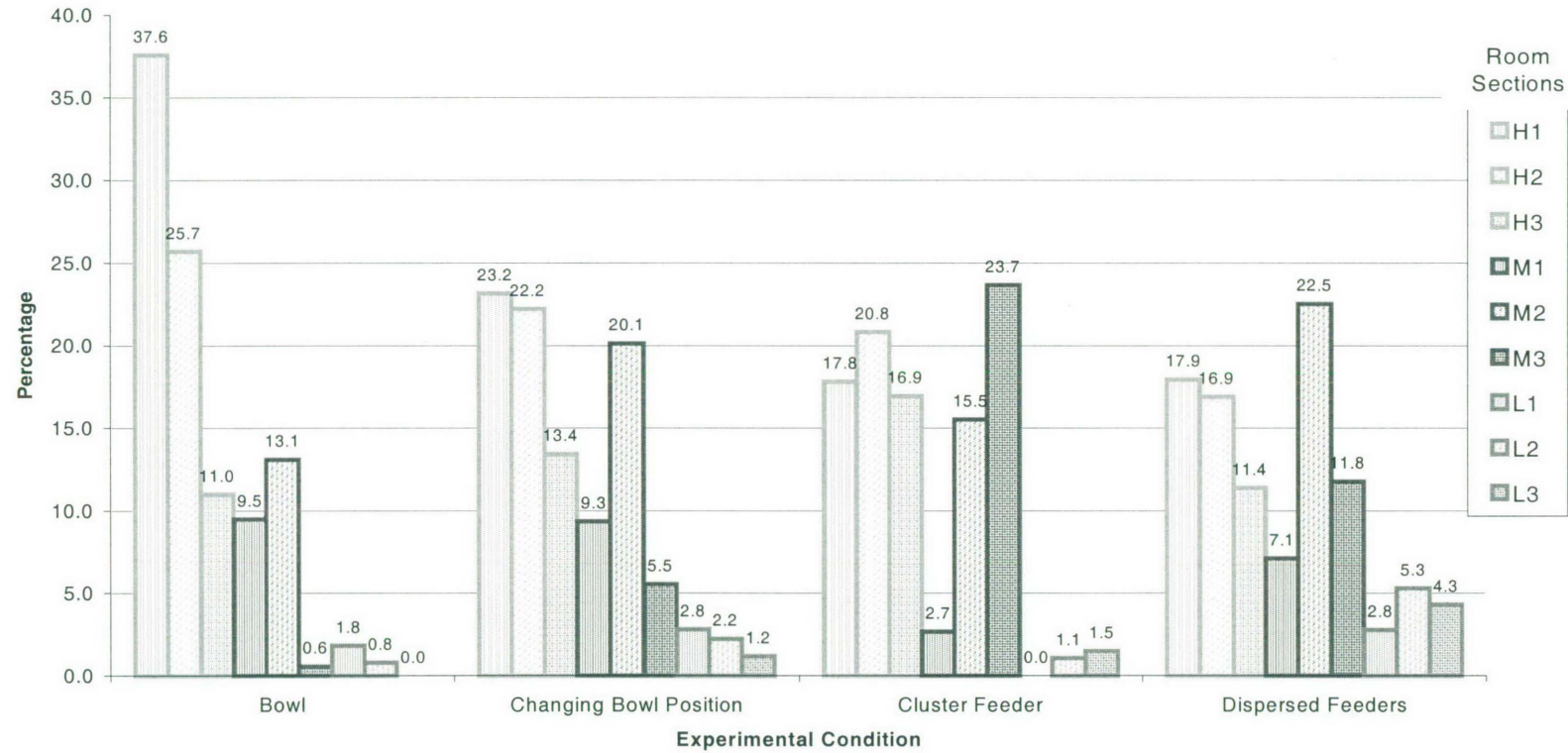
Figure 3.5: Percentages of movements into each room section. Given the choice of nine room sections to move into for each experimental condition, the marmosets chose to enter the room sections according to the labelled percentages. Therefore, during the Bowl condition, 9.5% of all section movements were made into Section M1, whereas during the CF condition, Section M1 was only entered in 2.7% of the CF condition's total movements. The food bowl was located in this section for both of those experimental conditions, which implies the food bowl lost its appeal when the cluster feeder was added to Section M3 during the CF condition.

3.2.2 Bowl And Feeder Interactions

Food bowls and feeders were presented in the ER to determine if any of these devices were successful in altering the marmosets' use of the ER. During both bowl conditions, there was a choice between a food bowl in the HC or ER. The food bowl during the Bowl condition was predictably located in the same position throughout the condition, while the food bowl during the CBP condition rotated through four different positions, one position per day. The Feeder conditions included an ER food bowl in the same predictable position as used in the Bowl condition as well as a similar bowl in the HC (the same parameters as the Bowl condition) plus a feeder type in the ER.

Even though the food bowls contained the Basics plus Additional foods during the Bowl conditions and only the Basics during the Feeder conditions, there was no significant difference in the time spent with the food bowl across the four experimental conditions (p=0.574). However, there was a significant difference in the number of bowl interactions (p=0.022, η^2=0.362). The marmosets interacted with the bowl more during the CBP condition versus all other conditions (Figure 3.6).
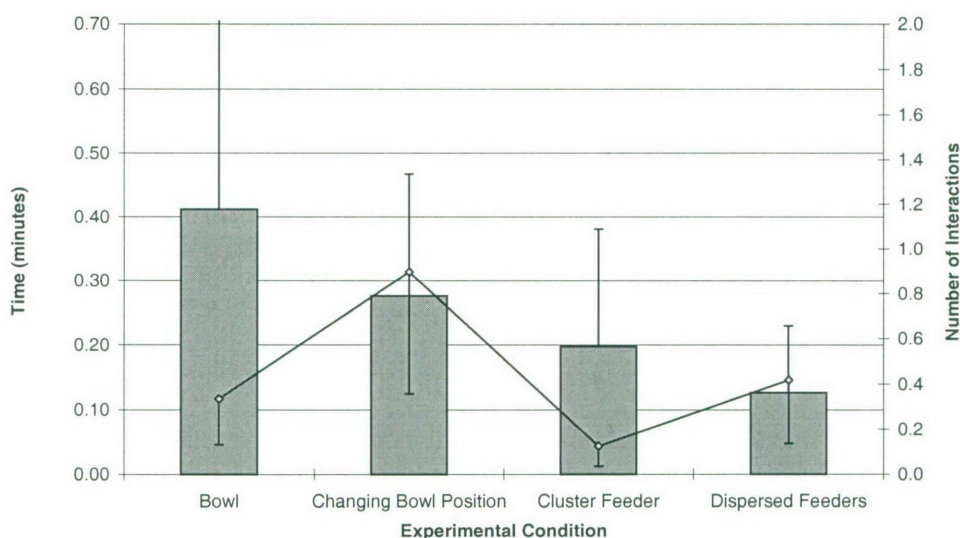
Figure 3.6: Time spent with the food bowl and the number of bowl interactions. The bars indicate time with the bowl, while the line indicates number of bowl interactions.

Food bowls were weighed before and after a day's feeding for each testing pair. A 2x4 RMA analysed the differences between weight of food eaten from the each of the HC and ER's bowls across the experimental conditions. The interaction between room and experimental condition was not significant (df (3, 9), p=0.976). The amount of food eaten from both bowls, HC and ER, was not significantly different (df (1, 3), p=0.952). Even though the Bowl conditions' food bowls contained the Basics plus Additional foods while the Feeder conditions' food bowls contained the Additional foods (Table 2.6), there was no significant difference (p=0.089) in the total amount of food eaten from both food bowls, HC and ER, across any experimental condition (Figure 3.7).
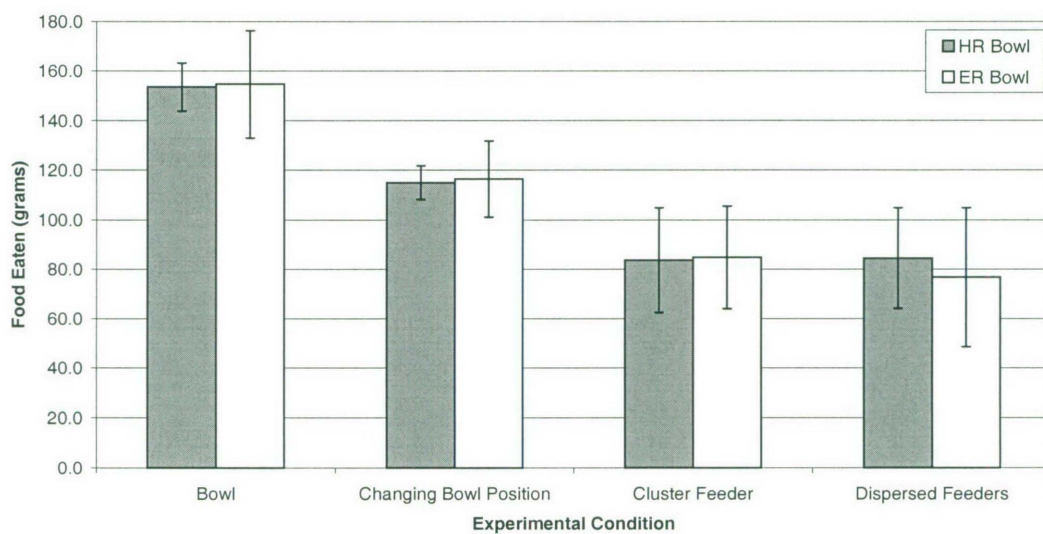
Figure 3.7: Mean amount of food eaten from the HC and ER food bowls per day.

In addition to the amount of food eaten by weight for each day, time spent eating and the number of eating bouts were recorded during each testing session. Both behaviours did significantly change across the conditions (Time: $p=0.001$, $\eta^2=0.819$; Events: $p=0.001$, $\eta^2=0.784$). Both behaviours were significantly higher during both Feeder conditions than both Bowl conditions (Figure 3.8).
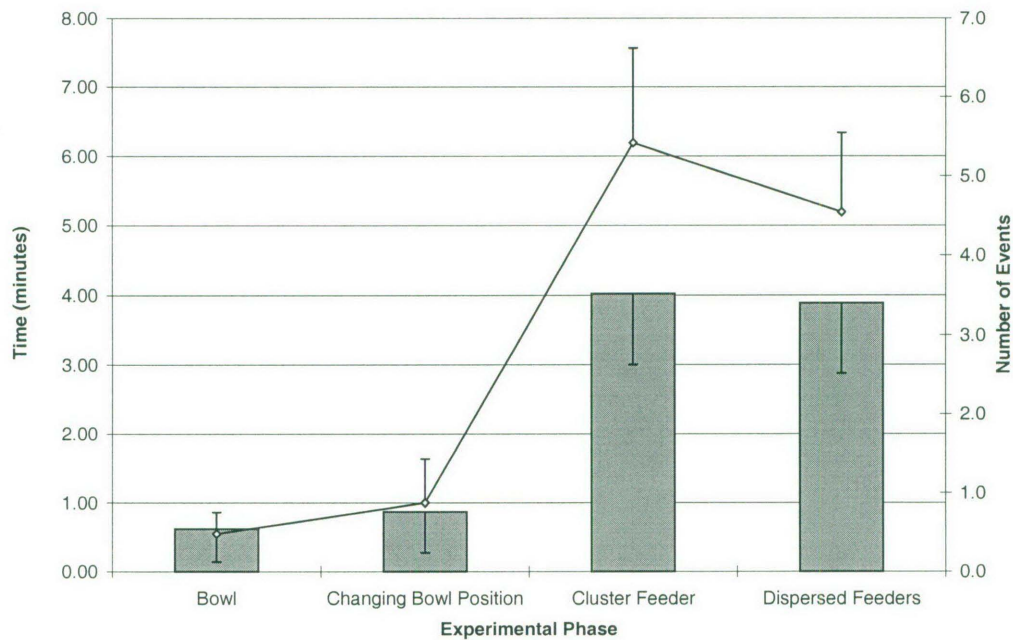
Figure 3.8: Time spent eating and number of eating events. The bars indicate time eating, while the line indicates number of eating bouts.

Feeder use was analysed using a two-tailed paired t-test. The marmosets spent significantly more time with the cluster feeder than the dispersed feeders (df=7, p=0.010) while they had significantly more feeder interactions with the dispersed feeders than the cluster feeder (df=7, p=0.003) (Figure 3.9). The twelve dispersed feeders required more interactions to obtain the same amount of food, whereas the cluster feeder maintained the marmosets' attention for fewer, but longer interactions. Therefore, the duration of interaction per feeder was longer in the CF condition.
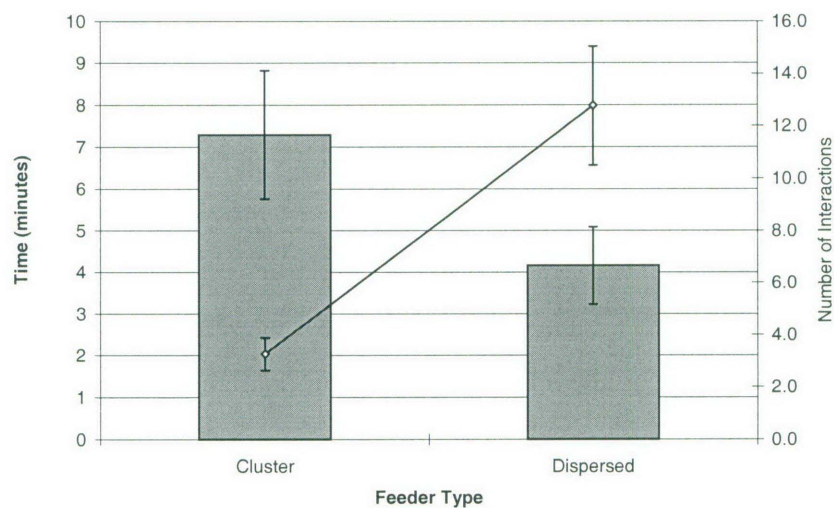
Figure 3.9: Time spent with a feeder and number of feeder interactions. The bars indicate time with a feeder, while the line indicates number of feeder interactions.

A 2x2 RMA was used to analyse the time spent with the two types of feeders versus the food bowl that was also available during the Feeder conditions. When given a choice between easily accessed food in a bowl and food from a feeder that required manipulation and/or travel, the marmosets predominantly chose to interact with the feeders more than the bowls ($p=0.001$, $\eta^2=0.824$). There was a significant interaction between the type of food device (bowl or feeder) and the experimental conditions ($p=0.015$, $\eta^2=0.597$) as well as a significant difference in the time spent with the feeders across the experimental conditions ($p=0.008$, $\eta^2=0.661$). Therefore, the marmosets spent significantly more time with the cluster feeder than the dispersed feeders and either feeder significantly more than the available food bowl (Figure 3.10).
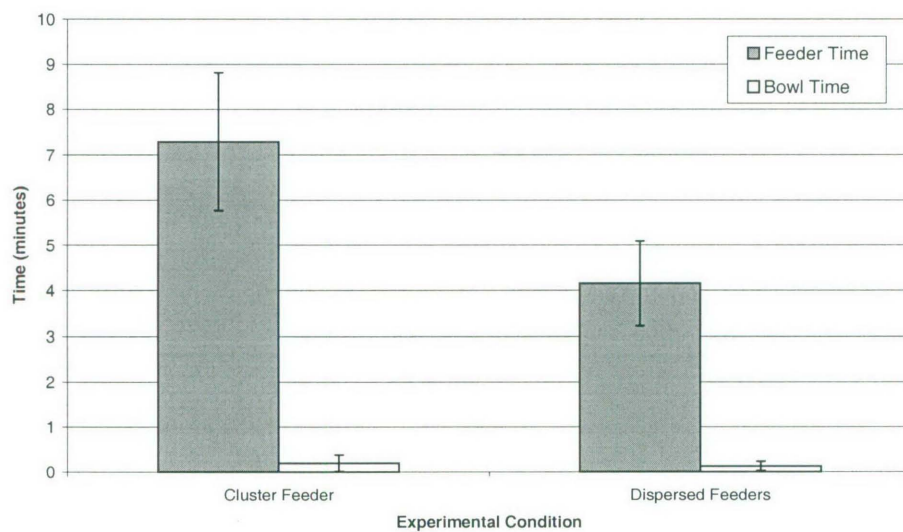
Figure 3.10: Time spent with a feeder or bowl for the Feeder conditions.

3.2.3 Food-Related Behaviours

The relationship between scent marking/gouging and food sources is unresolved. If scent marking and gouging are related to marking food locations, it would be expected that scent marking would increase from the Bowl to CF to DF condition as the number of food sites increased. Although there was an observed pattern of the UNE marmosets scent marking recently replenished food bowls, the expectation that more food locations would increase scent marking and gouging was not apparent in the data. There was no significant difference in the number of gouging events (G-G, p=0.679) or scent marking events (p=0.527) across the conditions (Figure 3.11).
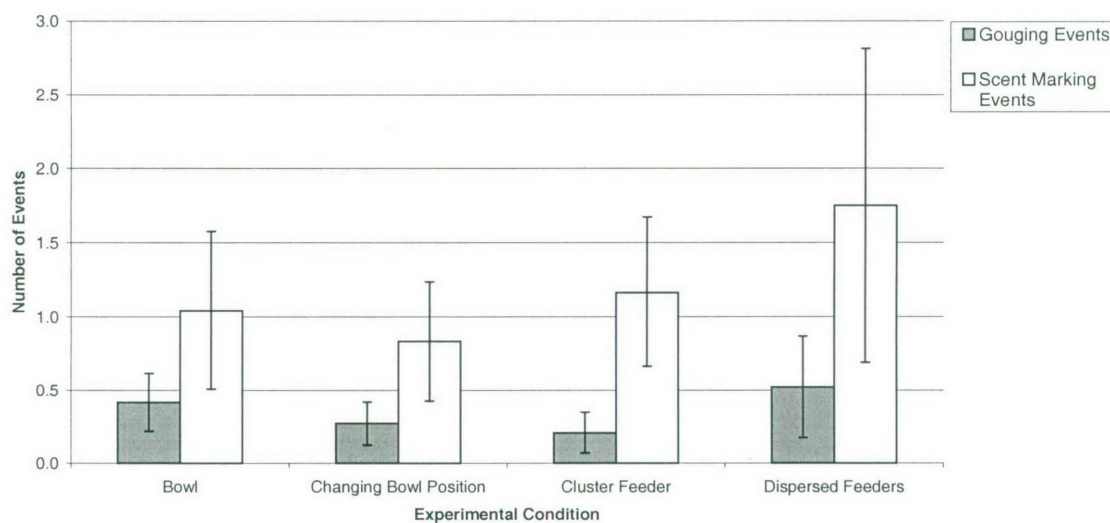
Figure 3.11: Scent marking and gouging events.

Similar to gouging and scent marking, chirping vocalisations can be associated with food. Chirps are short in duration and were recorded as events. However, this vocalisation was not performed enough to evaluate statistically. A total of six chirping events were elicited by four subjects: two during Empty Room 1 condition, one chirp event during the Bowl condition, and three chirp vocalisations during the DF condition.

3.3 Behaviours Likely To Decrease

3.3.1 Sitting and Other Inactivity Measures

Four different variations of Sitting behaviour were recorded by events and times: SO, SL, SE, and SLE. The time spent sitting overall (SO time) included SL + SE + SLE + any other uncategorized sitting combinations. SO time was not significantly different across the experimental conditions (p=0.123), but the number of SO events was significantly different (p=0.003, η^2=0.485). The number of SO events was significantly higher during both Feeder conditions than both Bowl conditions, resulting in the duration of each sitting event being shorter during the Feeder conditions.

SL time and the number of SL events did not significantly change during the testing conditions (Time: p=0.097; Events: p=0.627); however, the SL time and SL events did decrease during the CF condition and the marmosets were spending half as much SL time during the CF condition as they were during the Bowl condition.

Food was available during all experimental conditions either through the easily accessed food bowl and/or through a feeder that required some manipulative skills and/or travelling during the DF condition. The SE time and events were significantly different across the experimental conditions (Time: p=0.001, η^2=0.742; Events: G-G, p=0.001, η^2=0.780). Both SE time and events were higher during both Feeder conditions than Bowl conditions.

SLE time was significantly different (p=0.011, η^2=0.404) while SLE events showed a trend towards significance (G-G, p=0.053) across the four experimental conditions. SLE time was significantly higher during the CF condition than the Bowl condition. SLE events followed the same pattern as the SLE time. SLE events increased from Bowl to CBP to CF then dropped off during the DF condition. Figure 3.12 depicts all four sitting behaviour times with total time in the ER included for perspective while Figure 3.13 displays the sitting events.
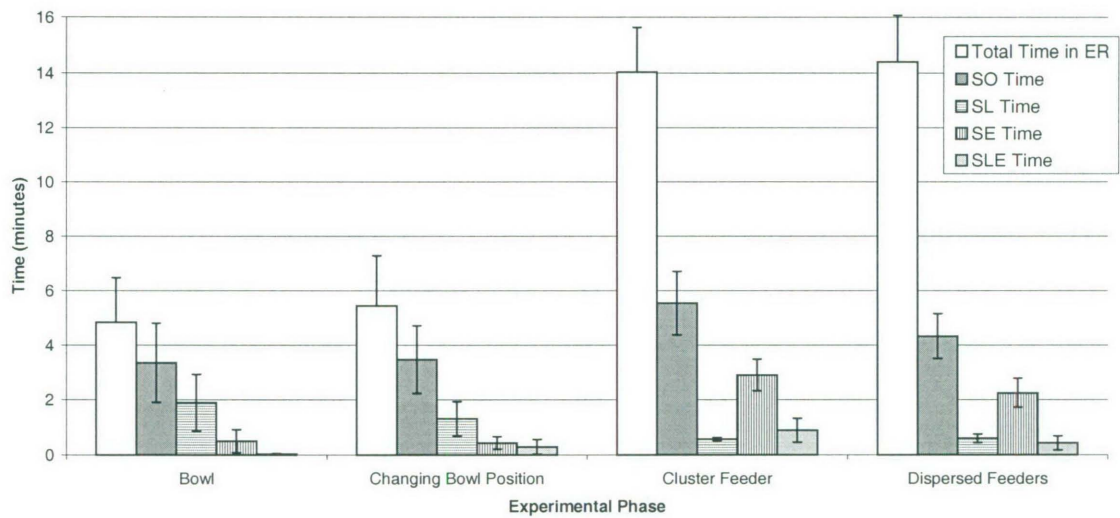
Figure 3.12: Time spent performing the four sitting behaviours: SO, SL, SE, and SLE. Total time in the ER is included as a comparison to the four sitting behaviours.
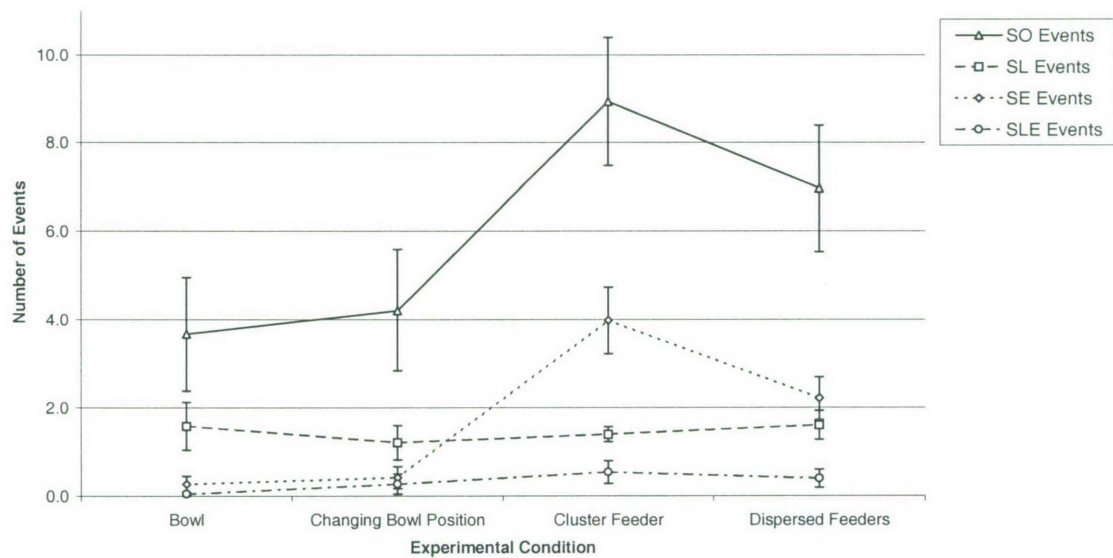

Figure 3.13: Number of events for the four sitting behaviours: SO, SL, SE, and SLE.

Figure 3.14 shows the time spent displaying the four sitting behaviours as percentages of total time in the ER. SO time was not significantly different across conditions as seen in Figure 3.12. However, the percentage of total time in the ER that was spent sitting decreased: 69.3% (Bowl), 63.8% (CBP), 39.5% (CF), 30.0% (DF). Therefore, the time spent in the room was taken up by other activities, such as feeder interactions, and not sitting, especially during the Feeder conditions. Similarly, the percentage of time in the ER spent SL decreased: 39.1% (Bowl), 24.1% (CBP), 4.1% (CF), 4.2% (DF). The percentage of time in the ER spent SE varied across the conditions: 10.3% (Bowl), 7.9% (CBP), 20.7% (CF), 15.6% (DF).

Figure 3.12 shows that SE time was significantly different across the conditions. Figure 3.14 shows that SE time constituted more of the total time in the ER during the Feeder conditions than the Bowl conditions. SE time increased from 10.3% and 7.9% of the total time in the ER during the Bowl and CBP conditions to 20.7% and 15.6% during the CF and DF conditions, respectively.
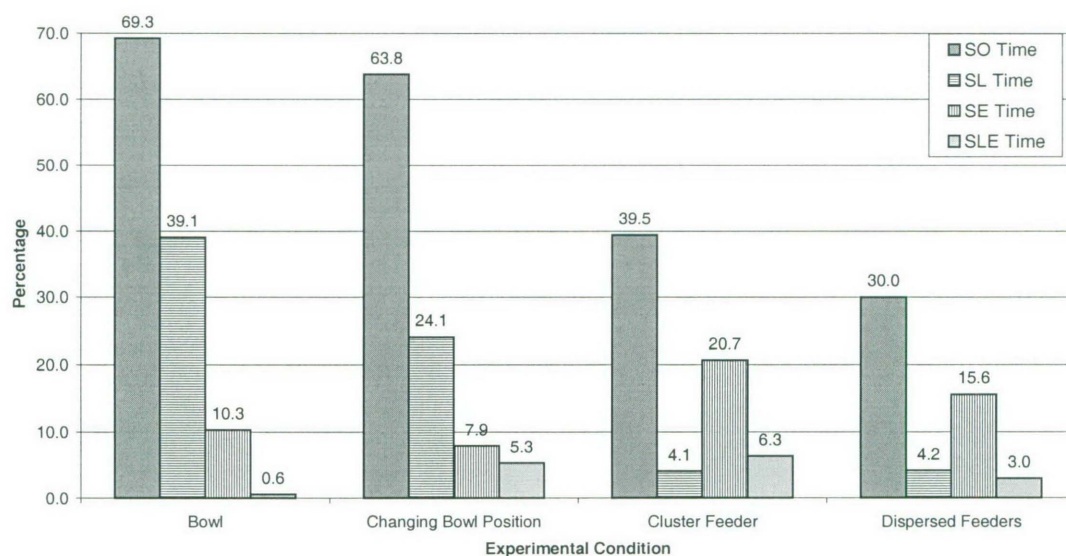

Figure 3.14: Time spent performing the four sitting behaviours as percentages of total time spent in the ER.

In addition to SL time and events, stretching from other furniture events and light interactions were recorded. Since the fluorescent lights were of some interest to the marmosets and generally, the subjects were inactive in the ER during the Empty Room conditions, a decrease in these behaviours would indicate a shift in the marmosets' activity budgets towards active manipulation of the environment, i.e. the bowls or feeders. The number of stretching events and light interactions decreased from the Bowl to Feeder conditions, but the change was not significant (Stretching: G-G, p=0.497; Light: p=0.135) (Figure 3.15). This decrease indicated that the marmosets spend their time in other ways during the Feeder conditions; the marmosets interacted with the feeders rather than interacting with a light or stretching from other furniture.
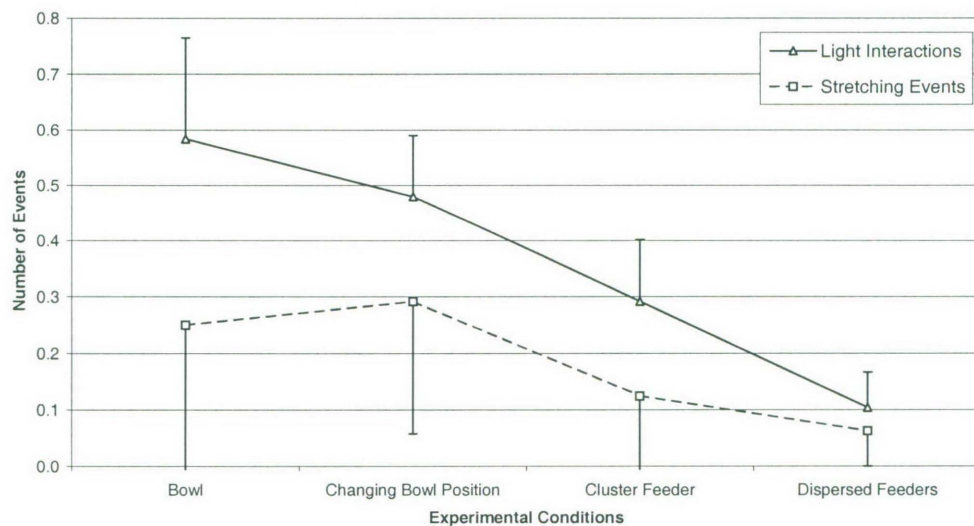

Figure 3.15: Stretching events and light interactions.

3.3.2 Self-Directed and Affiliative Behaviours

The number of scratching events was significantly different across the Empty Room conditions (p=0.012, η^2=0.468). Scratching events occurred significantly more during the Empty room 1 condition than the Empty Room 3 condition. There was no significant difference in the number of scratching events during the Bowl, CBP, CF, or DF conditions (p=0.652) (Figure 3.16). Typically, scratching occurred more during Empty Room conditions than experimental conditions. This could have been due to seasonal changes in pelage, since the experimental conditions were tested over 80 days from October 2003 to December 2003, or an experimental order effect.
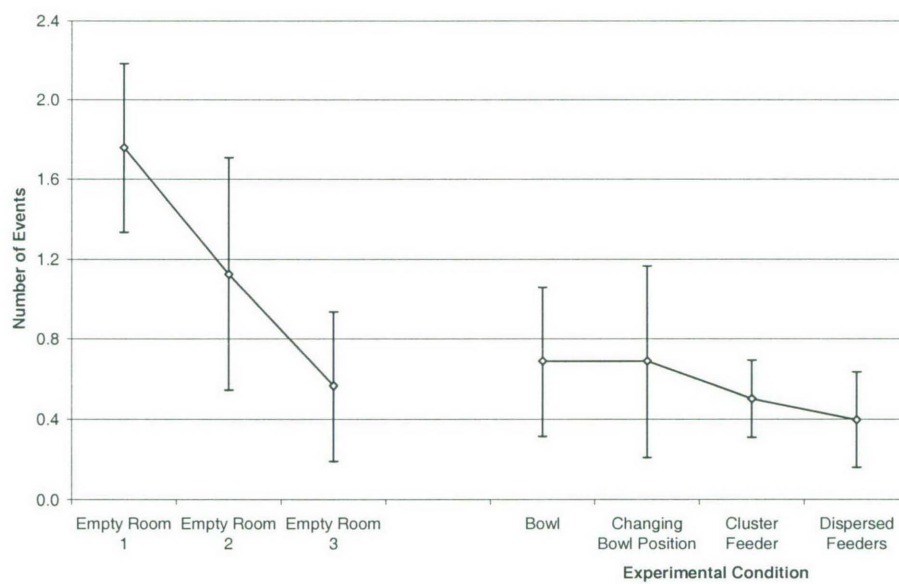

Figure 3.16: Number of scratching events. Typically, scratching occurred more during Empty Room conditions than experimental conditions.

Overall, grooming was not a regular occurrence during each testing session, and when the subjects did groom, it was not for extended periods. GO and GL events were both significantly different across the Empty Room conditions (GO: p=0.012, η^2=0.468; GL: p=0.014, η^2=0.454). Similar to scratching events, both grooming behaviour events were exhibited significantly more times during the Empty Room 1 condition than the

Empty Room 3 condition (Figure 3.17). Conversely, GO and GL times were not significantly different during the Empty Room conditions (GO: p=0.196; GL: G-G, p=0.252).
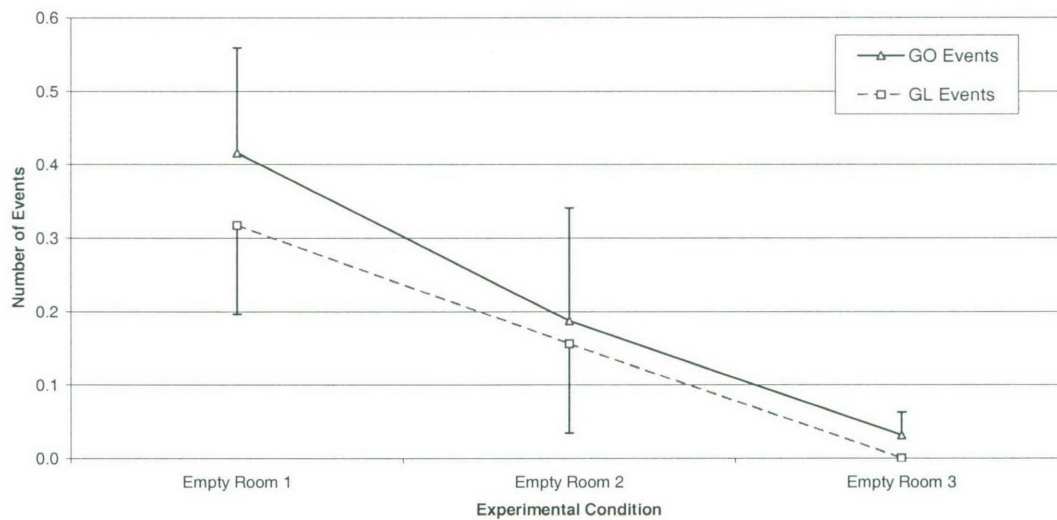

Figure 3.17: Number of GO and GL events for the Empty Room conditions.

There was no significant difference in the number of GO or GL events in the Bowl, CBP, CF, or DF conditions (GO: p=0.147; GL: G-G, p=0.135). Similarly, GO and GL time were not significantly different across experimental conditions (GO: G-G, p=0.150; GL: G-G, p=0.180) (Figure 3.18). There was a trend towards decreasing amounts of any type of grooming event from Bowl to CBP to CF.
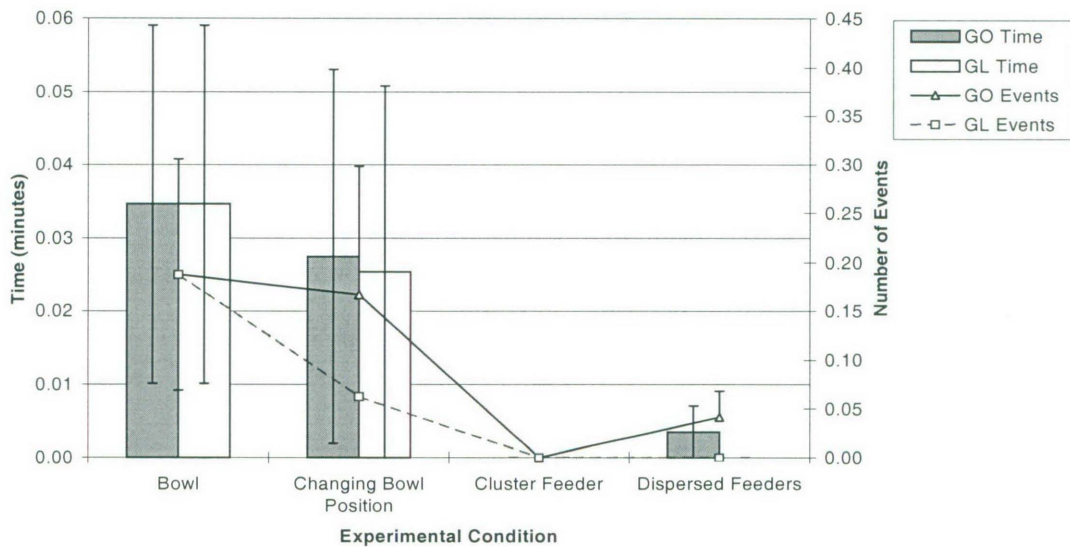
Figure 3.18: GO and GL times and events.

Huddling and allogrooming were exhibited only during the Empty Room conditions except for one marmoset pair huddled during the CF condition (Figure 3.19). It appears in this study that the marmosets were more motivated to interact with the feeders or bowls than huddle or allogroom.
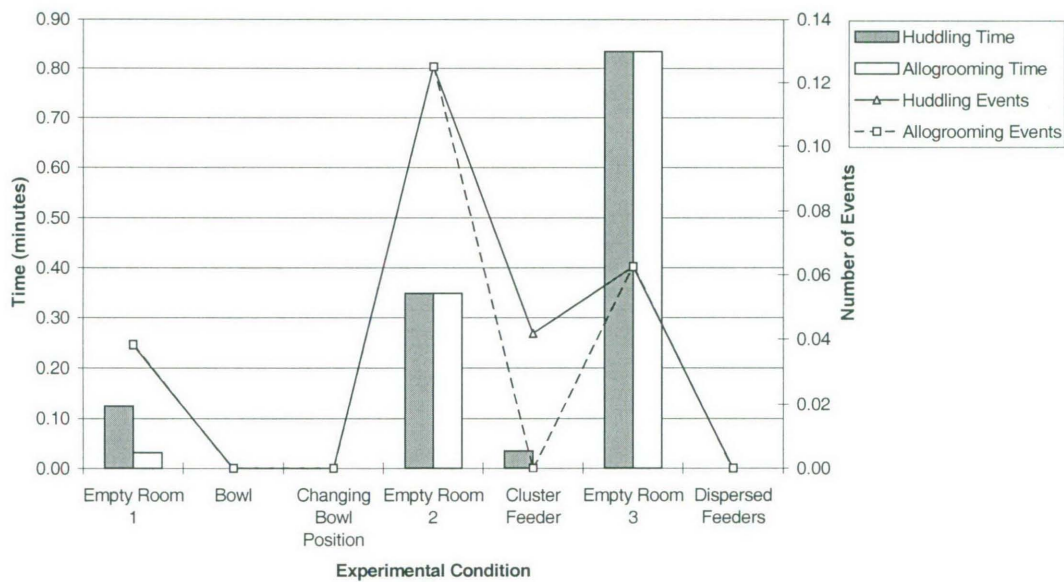

Figure 3.19: Huddling and allogrooming times and events.
Typically, when the marmosets huddled, they also allogroomed.

3.3.3 Vocalisations

In addition to the chirp vocalisation previously mentioned, three other vocalisations were recorded as events: tsik, chatter, phee. Tsik and chatter were also timed. None of these three vocalisations was emitted consistently during each testing session or condition. Therefore, Table 3.1 shows the *sums* of all vocalisation events and times exhibited by all eight subjects.

Table 3.1: Sum of vocalisation events and times exhibited by all eight marmosets during each experimental condition.

VOCALISATION	Bowl	Changing Bowl Position	Cluster Feeder	Dispersed Feeders
Time Tsik (minutes)	0	1.35	5.94	2.87
Time Chatter (minutes)	2.92	0	0	0
Tsik Events	0	2	22	38
Chatter Events	5	1	0	0
Phee Events	4	10	2	0

Extended tsikking events, with totalled times listed in Table 3.1, occurred during the CBP, CF, and DF conditions, but there was no significant difference across these conditions (G-G, p=0.396). There was a significant difference in the number of tsikking events across the conditions (G-G, p=0.026, η^2=0.418). The number of tsikking events increased from Bowl to CBP to CF to DF conditions, which could be a response to the increasing novelty of the apparatus placed in the ER. However, the only significant difference was between the DF condition and the Bowl condition (Figure 3.20).

The number of phee events did not significantly change across the experimental conditions (G-G, p=0.238) (Figure 3.20). There was a total of six chattering events during all conditions. All six were exhibited by Subject #4, Red, and were directed at the one way mirror in the ER. Since there were no chattering vocalisations directed towards any feeding apparatus, it could be claimed that neither the bowls nor either type of feeder induced any aggressive competition between cage mates.
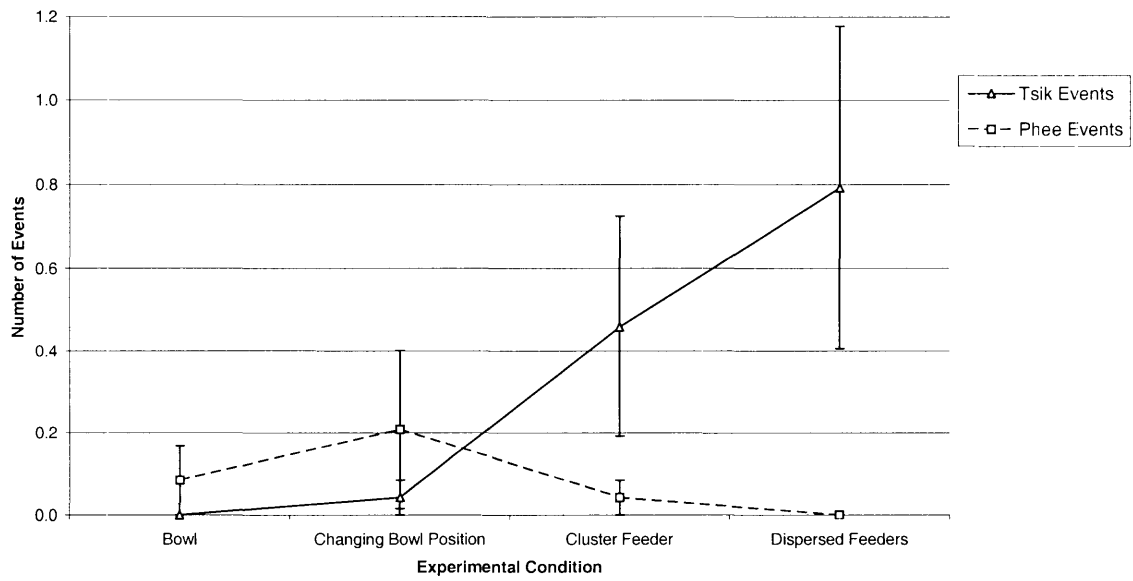
Figure 3.20: Tsik and phee events.

Chapter 4

Discussion

4.1 Introduction

The main objective of the present series of experiments was to find methods of improving the quality of life, or welfare, of captive common marmosets. Improvements can include increased activity and foraging behaviours and decreased self-directed behaviours. The present research included seven conditions: three intermediate checks of order effects (Empty Room conditions) and four experimental conditions, Bowl, Changing Bowl Position (CBP), Cluster Feeder (CF), and Dispersed Feeders (DF) conditions. Eight female common marmosets in four pairs were given free access from their respective home cages to exercise rooms in which the four experimental conditions were presented. The following questions were investigated to determine the beneficial properties of the food devices:

1) Does foraging enrichment alter space use in common marmosets?
    a. Between the home cage and exercise room?
    b. Within the exercise room?
2) Does foraging enrichment have long-term effects on time spent in the exercise room?
3) Do marmosets interact with feeders more than a food bowl?
4) Does clustered food distribution have different effects on marmoset behaviour compared to dispersed food distribution?

Throughout the present study, there were no indications that a behaviour exhibited by any subject was increasing or decreasing to an extent that indicated apathy or distress. The results indicate that both feeder types, cluster and dispersed, increased time spent in and activity within the ER as well as increased time spent eating as

compared with both Bowl conditions. This chapter presents the discussion of all experimental results and statistical analysis presented in Chapter 3.

4.2 Behaviours Likely to Increase

4.2.1 Room Use

It was hypothesised that use of the ER would increase during the presence of either feeder type in two ways: 1) the marmosets would enter the ER and stay for longer durations and 2) the use of the space within the ER would also increase. On both accounts, room use increased. The presence of the cluster feeder or dispersed feeders increased the time spent in the ER on a short-term basis (during testing sessions). The long-term effects of the feeders were assessed using the motion sensor data. The only significant increase in time spent in the ER during the 12-hour light cycle occurred during the CF condition when each marmoset pair spent on average nearly nine hours in the ER as compared with an average of approximately four hours in both Bowl conditions. Therefore, not only did the cluster feeder have a significant effect while present during testing sessions, it also had a lasting effect throughout the whole day even though the feeder was present for only 20-40 minutes in any one day. The presence of the dispersed feeders did not produce a similar significant long-term effect. However, their presence still did increase by 50% the time spent in the ER for each marmoset pair (from an average of four hours during each light cycle under both Bowl conditions to six hours under the DF condition).

Varying object presentations and thus reducing predictability, has been shown to increase object interaction in a variety of animals ranging from dolphins to macaws (Kuczaj et al., 2002). However, in the current study, altering the location of the food bowl did not increase the time spent in the ER during the testing sessions. Similar to the

short-term testing session data, changing the position of the food bowl did not increase time spent in the ER during the 12-hour light cycle.

The present study successfully increased the space use of all eight subjects using either feeder type while Bayne et al. (1992) and Bayne et al. (1994) were able to shift the cage side preference of only four of their eight rhesus macaques' using nutritive or non-nutritive enrichment devices. The devices used in the Bayne et al studies were not motivating enough to increase the use of the less preferred cage side. However, these studies may have been more indicative of issues relating to cage side rather than issues of enrichment. A future study could test these same devices on the preferred cage side to distinguish between issues evolving from the enrichment and issues relating to cage side preference.

Both of the current study's feeder types were successful in increasing the use of the space within the ER, which was assessed using the movements made into each of the nine ER room sections. Similar to Ely et al. (1998) who recorded occupancy of cage sections, room use was assessed in the present study using total movements within the room and percentage of total movements made into each individual room section. Movement within the ER was also assessed using the movements into each of the three vertical divisions. Ely et al. (1998) found that the inclusion of a protruding veranda on the outside of the cage increased use of the cage section that included the veranda. Likewise, a food bowl that changed position daily and resided in the middle section farthest from the marmoset entrance for half of the CBP testing sessions, increased the percentage of movements into this section to 5.5% from 0.6% during the Bowl condition. However, the presence of the cluster feeder in this same room section during the CF condition increased the use of that room section more than the food bowl. The movements into this section increased to 23.7% of the total movements during the CF condition, resulting in the section being visited more than any other room section during the CF condition.

The placement of the dispersed feeders was intended to evenly spread out the movements throughout each of the nine sections. If the marmosets moved equally between the nine sections, then each section would have 11% of the total movements. This was not the case in any of the four experimental conditions. Each High section

encompassed at least 11% or more of the total movements, while each Low section was consistently entered into for less than 6% of the total movements. The unpredictability of the changing food bowl position also had an effect on movements into the Low room sections. The use of the Low room sections was altered significantly only during the DF condition, which was the only condition in which feeding apparatuses were placed within these lower room sections. The movements into the Low sections increased from 2.6% of the total movements during the Bowl condition to 6.2% during the CBP condition. The percentage of movements then fell back down to 2.6% again during the CF condition, but rose to the highest during the DF condition to 12.4% of the total movements.

Captive common marmosets prefer to inhabit higher areas of their cages (Ely et al., 1998) and feed from higher rather than from lower areas (Buchanan-Smith et al., 2002; Morrissey, 1994). When the overall cage complexity increased by adding more branches and perches in Kitchen and Martin's (1996) study, foraging increased and the marmosets spent more time in the lower half of the cage and on the floor. Even though common marmosets prefer to feed from higher areas, it is still possible that they will also feed from other, lower sites within a room. As evident in the present study, marmosets will take advantage of feeding sites at multiple vertical and horizontal dimensions, and as a result, the subject's use of space increased.

Buchanan-Smith et al. (2002) maintain that placing a food bowl at the bottom of a cage did not increase overall cage use in common marmosets, because their subjects spent similar amounts of time in the top half of the cage during all three conditions. They therefore claim that attempting to increase cage use by spreading feeding sites to lower areas of the cage is not justified. Contrary to the authors' position, their data did indicate that although the marmosets spent more time in the upper half of the cage over all three conditions, the placement of the food bowl in the lower part of the cage *did* increase use of that space. Further, although it would be more ecologically appropriate to feed common marmosets in the upper parts of their enclosures, since their wild counterparts feed from trees, it is not outside the natural behavioural repertoire of these arboreal monkeys to descend to the 'forest' floor for quick foraging forays (Sussman & Kinzey, 1984) or to cross the forest floor (Stevenson & Rylands, 1988).

In the present study, the marmosets did briefly venture to the room floor to pick up dropped food, which they then took to higher elevations to eat, in ways similar to those reported for captive red-bellied tamarins (Buchanan-Smith, 1991) and other common marmosets (McKenzie et al., 1986). McKenzie et al. (1986) contend that captive marmosets' frequency of floor visits could roughly serve as an inverse measure of stress. If this were the case, the current study's findings that marmosets descended to below 1 m above the ground to manipulate dispersed feeders may indicate enhanced well-being. If the marmosets were stressed, they most likely would not have descended to the lower feeders.

Therefore, it does not seem appropriate to offer food *only* in the bottom half of the cage (as in Buchanan-Smith et al., 2002), much less only on the floor. It would make more sense to offer food in multiple locations, which include lower sites. In conclusion, placing dispersed feeders in a variety of vertical and horizontal dimensions, including lower sites, increased room use by the present study's captive common marmosets in the short-term. The cluster feeder produced a short- as well as a long-term effect, as it increased the marmosets' use of the ER during testing sessions and throughout each 12-hour light cycle.

4.2.2 Bowl and Feeder Interactions

This study concurs with previous research that shows animals often choose to feed from a device that requires more work while a food bowl that requires no work to obtain the food is concurrently available (O'Connor & Reinhardt, 1994; Reinhardt, 1994). Manipulable food devices are often more ecologically relevant than simple food bowls and they require more time and skill to obtain the food. The present study found that when given a choice between a feeder and a food bowl, marmosets consistently chose the feeders. The marmosets spent more time with the cluster feeder than with the dispersed feeders. However, the dispersed feeders also had some merit because the number of feeder interactions with them was greater than with the cluster feeder. Understandably, because there were 12 of them, the dispersed feeders required more

interactions to obtain a similar amount of food. In contrast, a single larger cluster feeder occupied the marmosets for fewer, but extended interactions. The main difference between the two types of feeders was that the dispersed feeders required more effort since the marmosets had to travel between each feeder to obtain the same amount of food they could have obtained from the cluster feeder without any locomotion. Therefore, the dispersed feeders increased foraging effort more than the cluster feeder for the same foraging efficiency.

Time spent in the ER during each day as seen in the motion sensor photographs indicates that the marmosets were most influenced by the clustered food distribution (CF condition), since after having encountered the cluster feeder in this room, they spent significantly more time in the room during this condition. Likewise, during testing sessions, the marmosets spent more time with the clustered food distribution than with the dispersed feeders. Possibly, the marmosets preferred this type of food distribution because 1) it more closely resembled the cluster foraging employed by their wild counterparts for gum exudates (De Castro, Araújo, Alho, & Dias Filho, 2000), 2) they did not want to make the physical effort to travel to 12 different food locations to obtain the same amount of food, or 3) they did not want to travel to all the areas where the twelve dispersed feeders were located. It is unlikely that the marmosets did not see all 12 dispersed feeders and therefore, did not know there were more feeders to visit, since the dispersed feeders were placed in set locations throughout the DF condition's six testing sessions and all feeders were visited at some point by each animal. Given that the UNE marmosets have been fed from single food bowls for years, the sole cluster feeder may have been a gradual step up from the regular husbandry practice of bowl feeding, whereas the dispersed feeders located at various heights may have been more of a challenge.

The dispersed feeders may have also had an effect on the amount of food eaten from the food bowls and the time spent eating during testing sessions. There was no significant difference in the amount of food eaten from each food bowl available to them, in the HC and ER. However, the amount of food eaten from the ER bowl was slightly higher than that eaten from the HC bowl during all conditions except the DF condition. In this condition, the amount of food eaten from the ER bowl was less than

that from the HC bowl. The amount of time spent eating was also slightly less during the DF condition, even though the mean amount of time spent in the ER was actually slightly higher during the DF versus CF conditions.

Therefore, the cluster feeder and its clustered food distribution were more effective than the dispersed feeders in increasing the time spent in the ER. The cluster feeder was used more than the dispersed feeders, and the marmosets spent more time eating during the CF condition. However, the dispersed feeders should not be discredited completely since they too significantly increased time spent in the ER and time spent eating relative to either Bowl condition. In addition, the dispersed feeders introduced the possible advantages of scattered locations that required locomotion and thus increased room use, activity, and foraging effort. Consequently, each feeder may merit the label 'enrichment' and caregivers of primate colonies should assess the benefit of each feeder type in relation to their animals.

4.2.3 Food-Related Behaviours

A correlation has been noted between scent marking and gouging in that marmosets gouge spots and then scent mark them with urine (Lacher et al., 1981; Rylands, 1985), but whether this relationship is also related to food had been debated in the literature. Lacher et al. (1981) documented a relationship between scent marking and gouging of exudate sources in adult *C. penicillata* marmosets only. Juveniles collected exudates from previously opened gouge sites, but did not gouge spots themselves nor scent mark any sites, even though captive juveniles do scent mark and gouge (pers. observation). More likely, sexually-mature adult marmosets scent mark for sociosexual communication reasons and not to mark food resources (Epple, 1970; Rylands, 1985). Since different family groups visit the same exudate tree, these gouging/scent marking sites would be detected by many individuals (Rylands, 1985).

Although there was an observed pattern of the UNE marmosets scent marking recently replenished food bowls, the expectation that more food locations would increase scent marking and gouging was not apparent in the data. The data indicate a

slight increase in scent marking and gouging during the DF condition when there were 12 individual food locations, but the increase was not significant. This lack of relationship between scent marking/gouging and food locations is similar to reports by Rylands (1985) and Stevenson and Rylands (1988).

Chirp vocalisations have a less ambiguous relationship with food. Stevenson and Rylands (1988) and Epple (1968) all contend that chirping is emitted in relation to discovery of food as well as other contexts all indicating comfort and satisfaction. Unfortunately, in the current study, chirping occurred rarely. Therefore, chirping could not be used to indicate a favoured feeding system.

4.3 Behaviours Likely to Decrease

4.3.1 Sitting and Other Inactivity Measures

Captive common marmosets weigh more (Araújo et al., 2000) and are considered less active than their wild counterparts (Bloomsmith & Lambeth, 1995; Chamove et al., 1982; McKenzie et al., 1986; Novak & Suomi, 1988; Tripp, 1985). The present study was designed to decrease sedentary activities without inducing excessive activity that might reflect stereotypical behaviour. Total movements within the room were used as a measure of general activity (similar to Wilson, 1982). The presence of a feeder (either cluster or dispersed) increased the marmosets' activity within the ER, as there were significantly more movements within the ER during both Feeder conditions in comparison to both Bowl conditions. As expected, the condition during which the most travel was required to obtain similar amounts of food, the DF condition, had the highest number of movements.

Sitting was used to measure inactivity. While time spent sitting overall did not decrease significantly during the Feeder conditions, this behaviour encompassed a decreasing portion of the total time in the ER from Bowl to CBP to CF to DF

conditions. This indicates the time spent in the ER was shifted from sitting to more active endeavours, such as feeder manipulation. The *type* of sitting also changed. This is probably more relevant than time spent sitting overall since there were different behavioural opportunities during the Feeder conditions (i.e. eating). A shift occurred in the sitting behaviour from sitting next to a light during the Bowl conditions to sitting and eating during the Feeder conditions. Both sitting next to a light and sitting and eating include a degree of inactivity, because the subjects were not physically moving about the ER. However, sitting and eating also includes an active behaviour, eating, while Sitting next to a light is entirely passive. The marmosets consistently sat down while eating during the Bowl, CBP, and CF condition. During these conditions, time spent sitting and eating was essentially equivalent to the time spent eating. However, during the DF condition, this equilibrium shifted so that the marmosets were not always sitting while eating. Therefore, the subjects were 'eating on the run,' and the DF condition added a locomotory element to eating.

The number of light interactions and stretching from other furniture events were also used to indicate a level of inactivity. As the number of movements within the ER increased during both Feeder conditions, both stretching and light interactions decreased. The decrease in both if these behaviours indicates that stretching and interacting with the light are of less importance to the marmosets when feeders are present.

4.3.2 Self-Directed and Affiliative Behaviours

A number of potentially undesirable behaviours were reduced through the experimental procedure. Similar to Majolo et al. (2003), the affiliative behaviours, huddling and allogrooming, were not observed during any experimental condition, except for one huddling event by one testing pair during the CF condition.

Scratching has been shown to be a reliable measure of stress (Cilia & Piper, 1997; Johnson et al., 1996). Scratching is differentiated from grooming in its quick, ephemeral action while grooming is an active engagement in hair/skin maintenance. The

number of scratching events was lowest during the DF condition and highest during the Bowl conditions, implying that the marmosets chose to spend their time travelling between and interacting with the dispersed feeders when they were available. Neither Bowl condition maintained the subjects' attention enough to reduce scratching.

Overall, grooming was not a regular occurrence during any testing session. The number of events and the time spent grooming overall and grooming next to a light were highest during the Bowl conditions and lowest during the Feeder conditions. Particularly of note is the lack of any grooming during the CF condition. Schapiro et al. (1996) also documented a decrease in grooming when food devices were present.

It was expected that an increase in activity within the ER during the DF condition would result in a decrease in other, sedentary behaviours. However, grooming was not present during the CF condition and was present during the DF condition, although minimally. The marmosets were more active during the DF condition as compared to the CF condition, but the marmosets spent less time with the dispersed feeders than the cluster feeder. This combination of increased activity, but decreased time with the dispersed feeders during the DF condition, allowed the marmosets an opportunity to groom.

As previously noted in the sitting next to a light and light interaction behaviours, the appeal of the fluorescent lights dwindled when either type of feeder was presented. This loss of appeal was also apparent in the grooming next to a light times and events behaviours. Grooming next to a light was present only during the Bowl conditions and nearly encompassed all grooming overall time, whereas grooming next to a light was not present at all during the Feeder conditions.

The marmosets were more motivated to interact with a bowl or feeder than huddle or allogroom as indicated by the presence of those behaviours during the Empty Room conditions and only one huddling event during the CF condition. Both feeder types were more effective than either Bowl condition in reducing the self-directed behaviours, scratching and grooming, in particular grooming next to a light. Meanwhile, engagement with the cluster feeder reduced grooming and scratching more than the dispersed feeders

4.3.3 Vocalisations

A reduction in chatter, tsik, and phee vocalisations was expected when the feeders were present due to the contexts in which these vocalisations are exhibited. Chattering is an aggressive social vocalisation, tsiks are used as a mobbing call which summons other marmosets to the area as well as a response to a novel object, and phee calls are long-distance contact calls (Epple, 1968; Stevenson & Rylands, 1988). These contact calls are a sort of marmoset 'roll-call' used to determine the location of conspecifics. The different food devices did not invoke any cage mate competition as indicated by the lack of chattering vocalisations. All six chattering events were exhibited by only one marmoset and were in response to her reflection in the one-way mirror. So chattering was not directed towards any feeding apparatus.

The increase in tsikking events and the time spent tsikking from the Bowl conditions to the CF condition, but not the DF condition, can be partially explained by the differential novelty of the feeder types. The marmosets did not have experience with the cluster feeder before it was presented during the CF condition. On the other hand, the marmosets previously had brief experience with a single dispersed feeder to ensure they were capable of manipulating the feeder disc and obtaining food. Therefore, when the dispersed feeders were presented during the DF condition, they were less novel than the cluster feeder, and time spent tsikking decreased from CF to DF conditions. However, there was no significant increase in the number of tsikking events from the CF to DF conditions. In extreme alarm, all marmosets within the animal house will tsik for extended periods. Such a group tsikking episode did not occur during any experimental condition. There is also little evidence of cage mates tsikking within the same testing session. Of a total of 38 tsikking events exhibited by all eight subjects during the DF condition, only four events occurred within the same testing session in which the cage mate also tsikked.

No timed tsikking events occurred in a testing session in which the cage mate also had a time tsikking event. Tsikking, as a mobbing call in a state of alarm, is intended to draw family members to the place of alarm. Since few tsikking events by both cage mates occurred within the same testing session, it is unlikely that the

marmosets were instigating a mobbing episode on the dispersed feeders. Possibly, the tsikking events may have been due to mild arousal caused by the location of feeders in multiple vertical and horizontal dimensions. Therefore, the increase in tsikking events from the CF to DF conditions may be a response to the location of a dispersed feeder and not to the feeder itself.

Marmosets phee call more during separation (Shepherd & French, 1999) and as sensory information about mates (visual, olfactory, physical contact) decreases (Schrader & Todt, 1993). The data for all eight subjects during each experimental condition included a total of two phee vocalisations during the CF condition and none during the DF condition compared to four and ten during the Bowl and CBP conditions, respectively. The lack of phee vocalisations during the Feeder conditions has two possible explanations: 1) The marmosets were less concerned with communicating with other marmosets and the feeders occupied their time or 2) a subject did not have to contact her cage mate since the cage mate was also present in the ER due to a feeder's presence (as proposed by Shepherd & French, 1999). However, phee calls are used to not only communicate with cage mates but with other members of the family within the same HR or non-related marmosets in other HRs. Therefore, a cage mate could be present while the subject is phee calling to other marmosets within the Animal House. More likely, the small number of phee calls indicates a decreased inclination to communicate while the feeders were present.

In conclusion, the feeders, more than the food bowls, maintained the attention of the subjects. As a result, there were fewer phee call communications during the Feeder conditions. The cluster feeder's novelty and the locations of the dispersed feeders did stimulate tsikking in some subjects, but did not provoke a severe alarm response which would have been indicated by simultaneous tsikking events from both cage mates and other marmosets within the entire colony. The lack of chattering in response to a feeding apparatus during any experimental condition indicates that the feeders and food bowls did not induce cage mate competition.

4.4 Impacts

Animals are maintained in captivity for many reasons, including public education, species conservation, or research. These captive environments are often impoverished and lacking in choice, complexity, and change when compared with an animal's natural environment. The current study's feeders increased choice within the Exercise Rooms. The marmosets were given the choice of whether to enter the exercise room, whether to manipulate a feeder, bowl, or no experimental apparatus, which covered holes to select (cluster feeder) and where to interact with a feeder (dispersed feeders). The current study has determined that two types of feeders have improved the welfare of eight female common marmosets by increasing their space use, activity, and the time spent acquiring and eating food. Many captive animal facilities maintain common marmosets in isosexual groupings (J. E. Clarke, 1994). Therefore, the use of either feeder would be a viable option to improve the welfare of female marmosets and possibly other captive animals in zoological parks, reintroduction programmes, or research facilities.

4.4.1 Zoological Parks

The intention of zoos is to educate the public about many different species' natural behaviour, ecology, and conservation issues. The general public would not typically be able to see the variety of species that is exhibited in zoos, in their natural habitats in a human lifetime. Through zoos, the general public can experience a myriad of species not native to their own countries. It would be contradictory to this educational objective if zoological parks exhibited animals that displayed abnormal behaviours (Akers & Schildkraut, 1985; Shepherdson, Carlstead, Mellen, & Seidensticker, 1993), had limited behavioural repertoires (Morgan et al., 1998), or were sedentary which is commonly and anthropomorphically described as 'boredom' (Wemelsfelder, 1993). Therefore, animals that display their natural behaviour repertoires are more educational (Maple & Finlay, 1989), and the exhibits hold the public's attention (Newberry, 1995). Tripp (1985) noted that zoo visitors were more interested in and rated an orang-utan

exhibit more favourably when the orang-utans were provided with manipulable and scattered edible items than when the orang-utans were in a non-enriched exhibit.

Like the UNE marmosets, animals in zoo environments may not take advantage of all the space provided to them, and as a result, may not be visible to the public. It is also a waste of resources if larger spaces are made available, but not used. An animal that cannot be seen by the public is an animal that is not educating the public as effectively as if it were viewed performing its natural behavioural repertoire. As has been previously noted, increased available space in itself does not automatically result in an improvement of welfare. The space needs to be useable. The present study's foraging devices made a quantitatively large space qualitatively viable for the study subjects. Further, this same concept could be implemented in zoos to improve the useability of a larger space and thus encourage animals to take advantage of the space available to them. For example, the cluster feeder could be placed in a specific location to encourage the animals to use a specific area more. Alternatively, dispersed feeders could be used to encourage the animals to generally use all areas of their enclosure more, not just one specific area. Moreover, the animals would be more active and more visible while exhibiting natural foraging behaviours. Shepherdson, Brownback, and James (1989) noted that use of a mealworm dispenser increased activity in meerkats and the animals were more visible to the visiting public for a larger portion of the day. Therefore, as the animals are being enriched, so is the viewing public (Young, 2003).

Potentially, either feeder could be present throughout the day as the sole source of food. Use of both feeders could be alternated, since both feeders have different advantages. Using feeders as the only source of food would be possible only if each relevant subject was able to manipulate the feeder and obtain an adequate intake. Also, feeders may be more time consuming for human care-givers, because they are more difficult to clean than a bowl and the amount of food eaten by the animals would be easier to measure if the food were in a centralized location (i.e. a food bowl). However, it is inappropriate to choose the least time-consuming feeding method for the caregivers when this method may consequently mean the animals and viewing public will receive less benefit. In addition, Young (2003) maintains that care-givers are empowered by constructing enrichment for their charges. As a result, it is not just the animals are

enriched, but the caregivers too by implementing relevant enrichment and observing its use.

4.4.2 Conservation, Breeding, and Reintroduction Programmes

Conservation, breeding, and reintroduction programmes strive to preserve viable populations of endangered species (Molzen & French, 1989). Common marmosets are not endangered, possibly due to their adaptive nature. They inhabit multiple habitat types and have flexible feeding strategies depending on food availability, location, and seasonality (Rylands & de Faria, 1993; Stevenson & Rylands, 1988; Sussman & Kinzey, 1984). However, other related marmoset and tamarin species are endangered, such as the buffy-headed marmoset (*C. flaviceps*) and the GLT (*Leontopithecus rosalia*). These endangered Callitrichid species employ similar feeding strategies to common marmosets in different terrains and habitats. Therefore, the present study's apparatus could be tailored for other Callitrichids or other primate species.

Animals slated to be reintroduced into their natural habitats need to possess the necessary survival skills to obtain and process food and avoid predators (Spedding, 2000), otherwise introduction will not be successful (Castro et al., 1998). In particular, learning natural foraging patterns is imperative to survival after reintroduction (Kleiman et al., 1986). Captive animals, therefore, need to retain as many of their natural social and behavioural characteristics as possible (Redshaw & Mallinson, 1991). Environmental enrichment is an integral part of a conservation programme since enrichment addresses the physiological and psychological needs of captive animals, thus providing an environment for sustaining healthy, breeding populations (Morgan et al., 1998).

The GLT has been part of a reintroduction program, the GLTCP, for two decades. Kleiman et al. (1986) implemented a training program to wean reintroduction candidates from locating cut foods in a predictable location to searching for spatially distributed and/or hidden food. The current study's food bowls, cluster feeder, and dispersed feeders could be used to train reintroduction candidates to use natural foraging. The feeders could be modified to resemble features of the natural environment. In addition, not only could food be hidden within the feeders, but the

dispersed feeders could also be hidden within a more naturalistic environment to bring the reintroduction candidates a step closer to searching for food within the natural environment, in which food is not always centrally located.

4.4.3 Research Facilities

Australian, American, Canadian, and British government legislation requires researchers to replace, reduce, or refine (the Three Rs) the number of animals used in experiments (Canadian Council on Animal Care, 1993; Home Office, 1989; National Health and Medical Research Council, 1997; National Research Council, 1996). Use of more animals than is necessary would be considered unethical (Öbrink & Rehbinder, 1999). The Three Rs are used to limit the total number of animals used in experiments, and thereby improve the welfare for those animals that are excluded. However, this 'Three Rs' practice does not necessarily improve the welfare of those animals used in the experiments. Welfare and husbandry needs to be monitored, because a deficiency in those areas can lead to unreliable experimental results (Dickie, 1998; Maple & Finlay, 1989; Poole, 1997; Reinhardt & Reinhardt, 2002). The US National Research Council (1996, p.19) maintains that "good husbandry minimizes variations that can affect research results," thus fewer animals are needed to obtain reliable findings.

Enrichment devices can be implemented as part of maintaining appropriate husbandry practices and improving welfare. If the foraging devices used in the present study enhanced natural behaviours and activities in the current test subjects, they are likely to do so in subjects used for medical research. Therefore, this approach could potentially improve the results of experiments and reduce the number of subjects needed in the future. The current study's subjects had not previously exhibited recurrent abnormal behaviour, except one who plucked hair from her tail if she was isolated. Nonetheless, other non-human primates who are exhibiting abnormal behaviours may benefit from these foraging devices, especially because manipulation of these devices may be incompatible with exhibiting a stereotypy (Novak et al., 1998). Therefore, providing better analogues of the natural environment in the laboratory, through environmental enrichment, may render more reliable results. As Poole simply states, "Happy animals make good science" (Poole, 1997).

4.5 Suggestions for Policy and Practice

4.5.1 Systematic Studies

I believe that *all* studies investigating the benefits of devices as enrichment should be systematic, quantitative studies with statistical analysis. Studies that do not include these aspects confound the already subjective animal welfare field. When confronted with the ethical issues of maintaining animals in captivity, it does not seem prudent to rely on ideas or apparatuses that have been only *suggested* as appropriate for the species in question (Galef, 1999; Morgan et al., 1998). Such an inappropriate reliance on weak evidence may lead animal care-givers and researchers to employ flawed husbandry practices (Crockett, 1998). Evidence of this nature should be used only to suggest apparatuses or ideas for systematic assessment in future studies. Studies that provide mean data can show trends or patterns of responses to different experimental conditions. However, data from small sample sizes are often variable. Therefore, studies that include statistical analyses are superior because the variability of the data is considered in claims about real differences. Statistical analyses also present a comparable standard for other researchers.

4.5.2 Re-evaluating General Husbandry Practices

Both feeder types have enriching qualities and by current standards, could be labelled 'enrichment.' Enrichment devices are used to provide analogues of the natural environment in a captive context. However, once these methods or ideas have been 'proven' to be beneficial to different animal species, strategies that emulate a natural aspect of the animal's habitat may no longer be considered 'enrichment.' Instead, they should be considered a requirement in general husbandry procedures. There should not be any question that marmosets benefit more from being fed in feeders versus bowls, as

this is a more naturalistic feeding method and has been documented in the current study. Therefore, bowl feeding should be considered substandard.

The maintenance of animals in captivity is an age-old debate involving ethics and animal rights. The current situation is that there *are* animals in captivity. *Period.* While activists and scientists may argue over whether or not to have animals in captivity at all, we need to do what can be done to improve the lives of animals that are already in captivity. Research on animal welfare issues, such as this study, is a means to that end.

4.5.3 Legislation

In addition to general husbandry practices, the legislation that regulates maintenance of captive animals in Australia should be re-evaluated. The Australian policies and codes for maintaining animals in captivity lack any species or *Family* specific information even in the more-specialized *Non-human primates policy* (National Health and Medical Research Council, 2003). When compared to the codes for the UK, Canada, and the USA, Australia's policies are inadequate. To sufficiently attend to the needs of captive non-human primates, the Australian codes need to be re-assessed to include the psychological and behavioural needs of non-human primates on a *Genus* taxonomic level.

As means of measuring welfare improve, those devices, ideas, or methods that have been determined to be enriching should be integrated into standard legislative policy. The current study showed that species-relevant foraging devices induced natural foraging behaviours. In addition to these foraging devices, other methods that minimize the discrepancy between captive and wild non-human primates should become standard practice. Future research should continue to add to the available information on environmental enhancement and improving welfare and standard practices, and legislation should reflect the current research.

4.6 Limitations

Providing food in two bowls and feeders was a balance between standard husbandry procedures and not depriving subjects while also not overfeeding them. The UNE marmosets, as per standard husbandry procedure, typically received one food bowl in the home cage per marmoset pair, and the food bowl was left within the cage so food was available *ad libitum*. During the Bowl conditions, the marmosets received twice their daily rations with a full diet located in the Home Cage as well as the Exercise Room. Thus, the marmosets could have received a full feed from either location, so they were not coerced to enter the Exercise Room to sustain sufficient dietary intake.

Similarly, the marmosets were not deprived during the Feeder conditions. In these conditions, the additional foods from the diet were hidden within the feeders while the Basics were located in both food bowls. The Basics were not provided in the feeders for three reasons. The Basics provided the core of the diet, the marmosets were accustomed to continuous food access, and the feeders were present only for 20-40 minutes per day when. The Basic foods were not appropriate for feeder use as they fell apart easily. Therefore, the foods were separated during the Feeder conditions in an attempt to limit the overfeeding that was already part of the experimental design. In hindsight, even though the Basic foods would not work in the feeders, the additional foods should have been located in the bowls as well as the feeders. Also, if the food eaten from the feeders was weighed, the amount of the daily diet eaten from the feeders could have been determined. It was discovered after the experiment that even though the subjects had twice the amount of their standard diet available, no subject gained a significant amount of weight during the experiment. This was possibly due to the increased activity brought about by the experimental conditions. Therefore, the marmosets may have been able to adapt to the potential 'overfeeding.'

The current study included the Empty Room conditions as intermediate checks on order effects. To further eliminate order effects, two testing pairs should have received the DF condition then the CF condition, while the other two testing pairs should have received the reverse order. The Bowl and CBP conditions still could remain in their order before the Feeder conditions as there is a logical progression from the

marmosets having no food located within the ER to their learning that food was available in this room.

Small sample sizes can be a problem in non-human primate research (Kuhar, 1997; Tustin et al., 1996). Also, isosexual groupings are common in captive common marmoset facilities (J. E. Clarke, 1994). Four female pairs of common marmosets from three different families were used in the current study. However, the inclusion of males and more subjects housed in various family groupings would provide data more comparable to a wider range of housing conditions.

4.7 Suggestions for Further Research

Future studies could include variations on the current study's experimental procedure. For example, different species that utilize different feeding strategies or those that exhibit stereotypical behaviour could be studied to determine whether they could benefit from the present study's cluster and dispersed feeders. Similar to Novak et al. (1998) performance of some stereotypical behaviours may be incompatible with the use of these feeders. Common marmosets are exudativorous-insectivores (J. E. Clarke, 1994; Rylands & de Faria, 1993; Stevenson & Rylands, 1988). The present study's common marmosets preference for the clustered food distribution may reflect their wild conspecifics' use of habitat areas which include a higher density of gum-producing trees than other areas of the habitat (Scanlon et al., 1989). Other Callitrichid species are more frugivorous than exudativorous (Stevenson & Rylands, 1988). The current study's experimental procedure could be tested using more frugivorous species to see if these animals exhibit foraging strategies similar to their wild counterparts.

To gain a better understanding of the motivation that drives the use of the feeders, the feeders could be present *ad libitum*, similar to the food bowls. The feeders may maintain the subjects' attention throughout the day or may confirm Kuczaj et al.'s (2002) principle that variable enrichment presentation is more beneficial. Consumer/demand studies could be implemented to determine the effort the subjects are

willing to invest to obtain access to a feeder or to obtain food from within a feeder. In addition, a study in which the two feeder types are alternated or presented continuously over longer periods could help to determine when habituation or loss of novelty occurs. The current study's experimental design could also include a larger number of feeders and/or physiological data collection. More feeders could reduce intragroup aggression while to determine the physiological benefits of the study.

4.8 Conclusions

In conclusion, this systematic study determined that both feeders increased the space use by the study subjects. Both feeder types, cluster and dispersed, were beneficial, in various ways. The cluster feeder increased the time spent in the Exercise Room more than the dispersed feeders and this effect was sustained throughout the day, even though the feeder was absent. However, the dispersed feeders increased activity within the room more than the cluster feeder. Throughout all four experimental conditions, the study subjects moved within the High room sections the most and the Low room sections the least. However, the use of the Low room sections increased, provided there were dispersed feeders located within the sections. The cluster feeder also increased room use, but its effect was more localised. In particular, the cluster feeder shifted space use to the particular section in which it was located. As indicated by time spent with feeders and food bowls, the subjects preferred to interact with feeders rather than with food bowls. Of the two feeder types, the marmosets spent more time with the cluster feeder.

In addition to increasing room use, both feeder types also had advantageous behavioural effects. Both feeder types were effective in reducing self-directed behaviours, and the marmosets manipulated the feeders rather than huddle or allogroom. Sitting also decreased from Bowl to Feeder conditions and the type of sitting shifted from passive, unengaged sitting next to a light during the Bowl conditions to active, engaged sitting while eating during the Feeder conditions. For all these reasons, both feeder types, cluster and dispersed, positively affected the study subjects and were therefore, enriching.

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