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AN INVESTIGATION INTO THE SHORT-TERM EFFECTS OF ENVIRONMENTAL ENRICHMENT ON THE BEHAVIOUR OF PSITTACINES IN CAPTIVITY

By

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A thesis submitted in partial fulfilment of the requirements for
the degree of Doctor of Philosophy

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H. Elson.

Harriet L. G. Elson

I would like to dedicate this thesis to
Judy Taylor and Douglas Ferguson,
whose support made it possible

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Summary

AN INVESTIGATION INTO THE SHORT-TERM EFFECTS OF ENVIRONMENTAL ENRICHMENT ON THE BEHAVIOUR OF PSITTACINES IN CAPTIVITY

There is a lack of quantitative information available about the effects of environmental enrichment on avian orders, compared with the amount of similar research carried out on mammals. This is particularly surprising where members of the parrot family (Psittacidae) are concerned, as enrichment is widely regarded as essential for the welfare of captive primates, and there are well-documented parallels between the abilities and needs of primates and psittacines.

In this study, groups of psittacines were studied in basic enclosures in zoos in Ireland and Australia and daily activity budgets were compiled for each group and species. The results showed that the captive birds spent significantly less time in active behaviours (feeding and foraging, locomotion) than wild psittacines, and more time in sedentary behaviours (resting, preening). In order to see whether they would increase their levels of active behaviours when given the opportunity, various enrichment devices were designed to allow the captive birds to exhibit foraging behaviour. They contained the same foods as were present in the regular diet of the birds, which was also provided in feeding dishes as usual throughout the study.

When enrichments were present in the enclosures, the birds spent significantly less time inactive, and levels of preening also decreased significantly for all species of parrots and cockatoos studied. Lories, however, maintained the same levels of maintenance behaviour, regardless of the presence of enrichments. There was a significant increase in the amount of time all the birds spent foraging and, despite a concurrent decrease in time spent feeding from the dishes of prepared food, the total amount of time spent in feeding and foraging behaviours also increased significantly for all species. All the birds significantly increased the amount of time they spent in locomotory activity in enriched enclosures, with the exception of the lory species and a group of eight cockatoos, which were the only birds studied to be kept in an aviary large enough to allow sustained flying behaviour. The study showed that when enrichments were provided, the activity budgets of the birds approximated more closely to those of their wild conspecifics.

Further experiments indicated that species-specific enrichments, designed to allow the performance of wild-type, specialist, feeding behaviours, had the greatest attraction for the birds and were most effective in stimulating foraging behaviour. The psittacines also showed preferences for foraging at particular heights in their aviaries, and these too were consistent with what is known of the natural ecology of their species.

Experiments investigating the dietary intake of captive psittacines indicated that, in the presence of food-based environmental enrichments, they tended to consume a greater mass of food. It is possible that the increased levels of activity observed in the enriched birds would compensate for their increased calorific intake but, if not, then food-based enrichments could contribute towards long-term health problems such as obesity, in captive psittacines unless carefully rationed and their use monitored.

The birds studied all chose to expend energy in order to obtain nutrition from enrichment devices, rather than eating the same foods more easily available from a dish; an example of contrafreeloading behaviour. Experiments were carried out in order to examine the potential benefits of contrafreeloading, and the results did not support the information primacy hypothesis proposed by Inglis & Ferguson (1986), but suggested that psittacines in captivity are strongly and innately motivated to perform wild-type foraging behaviours.

Contents

Chapter 1

General Introduction

1.1 The Captive Environment

The research described in this thesis was carried out on groups of captive psittacines (parrots, cockatoos and lories) kept in zoos in Ireland and Australia. Although most research on animals in captivity has traditionally been carried out in laboratories, in recent decades the scientific community has begun to recognise that zoos and wildlife parks can provide unique opportunities for the study of a wide variety of species in a captive, and therefore controlled, environment (Kleiman, 1992; Ryder & Feistner, 1995; Hardy, 1996). As well as detailed studies of animal behaviour, physiology and reproductive biology, not possible in a wild setting, zoo populations have allowed behavioural biologists and psychologists to carry out research in a wide range of areas. For example, how cognitive mapping is carried out in Bornean orangutan (*Pongo pygmaeus*) (Citrynell, 2000) and the effects of young animals being prevented from dispersing from their natal groups in equids (a situation which is increasingly common in the wild as a result of habitat fragmentation) (Jordan, 2000) have both been understood primarily as a result of such research, as have the complexities of olfactory communication in cheetahs (*Acinonyx jubatus*) and giant pandas (*Ailuropoda melanoleuca*) (Lindburg *et al.*, 1985; Kaplan, 2003).

Although work carried out in zoos can shed light on the natural behaviour and behavioural ecology of captive animals, animals which are held in captivity, be it in a zoo, laboratory or farm, usually encounter an environment substantially different from the wild habitat in which the species evolved. The precise response of an animal to a captive environment depends on its natural history (Seidensticker & Forthman, 1998) but it will almost certainly be subjected to different selection pressures from its wild conspecifics (Hediger, 1964). For example, animals in zoos are usually protected from predation and disease, and are provided with food, shelter and potential mates. What is not always clear, however, is whether the captive setting provides animals with an environment which fulfils the needs which the species has evolved over many generations in the wild.

A ‘need’ can be defined as a requirement, which is fundamental in the biology of an animal, to obtain a particular resource or respond to a particular environmental or bodily stimulus (Broom & Johnson, 1993). Such a requirement may be for food or shelter, or it may be for a certain behaviour, such as grooming or nest-building. Control systems in animals seem to have evolved in such a way that animals are motivated to perform certain behaviours in particular circumstances (e.g. Hughes & Duncan, 1988; Spruijt *et al.*, 2001). For example, given the opportunity, in a rain shower captive Great Indian Hornbills (*Buceros bicornis*) will fly to the tops of trees and spread and flap their wings, in order to wet their plumage thoroughly. They will then 'strip' the water from their feathers using their beaks. This particular sequence of behaviours only happens in the presence of rain (Buri, 1993; pers. obs., 1999). This is an example of animals being motivated to perform certain behaviours in particular circumstances, but whether this constitutes a 'need', and whether the hornbills suffer if they are prevented from carrying out rain-bathing behaviour is difficult to assess.

In the scientific literature, the term 'need' is most often applied to vital activities such as the ingestion of food and the avoidance of predators, but also to the performance of behaviours observed in the wild, but which are not necessary for immediate survival (e.g. dust-bathing in domestic hens (*Gallus gallus domesticus*) (Vestergaard, 1980) and hunting behaviour in felids (Hughes & Duncan, 1988)). A requirement to perform these latter types of activities can be referred to as a behavioural or ethological need, although care should be taken as those terms are sometimes used inappropriately (discussed by Dawkins, 1983). It is clear that the needs of captive animals to perform particular behaviours may vary in their importance, and the consequences of not performing those behaviours may vary in their seriousness (Dawkins, 1990).

The assumption that the inability to fulfil a behavioural need in captivity (even if it results in no obvious physiological harm) causes suffering for the animal concerned, has been proposed but in many cases has not been demonstrated (Dawkins, 1983). As well as the degree to which the inability to express a need may compromise the welfare of a captive animal there is some debate in the published literature about what constitutes a 'need', as opposed to a preference.

It is thought that the performance of some behaviours, which do not result in a direct 'reward' or obvious advantage to the animal, may have evolved to be self-rewarding (Spruijt *et al.*, 2001). For example, rooting (a food seeking activity) is shown by captive pigs (*Sus scrofa scrofa*), whether food is obtainable by the process or not. Although it can be viewed as an appetitive behaviour, it appears to be under the control of a motivational system independent from that of consummatory behaviour. Because of this, the need to perform rooting behaviour is not satiated by the consumption of food, only by the expression of rooting itself (Rushen, 1985). In one study, for example (Breland & Breland, 1961) pigs were taught to carry tokens to a feed dispenser, in order to obtain food. After a time, however, the pigs stopped carrying the tokens to the dispenser and, instead, used their snouts to root the tokens into the ground. The hungrier the pigs became, the more vigorously they rooted. Examples such as this indicate that animals may be strongly motivated to perform behaviours which do not appear, in themselves, to be essential for the animals' wellbeing.

It is clear that a captive environment may not allow an animal to perform the full behavioural repertoire displayed by its wild conspecifics (e.g. without a suitable substrate available, hens cannot dust-bathe and pigs cannot perform functional rooting behaviour). Whether this compromises the welfare of the animal depends on the consequences of the behaviour not being performed.

1.2 Effects of the Captive Environment on Behaviour

1.2.1 Control

Behavioural development takes place in the environmental context in which an animal lives and in the wild it should develop the repertoire of behaviours normally exhibited by its species through evolutionary time. If it lives in a modified environment, however, some of the behaviours may not be expressed and others may be adjusted to suit the new conditions (McLean, 1997). One of the facets of a captive environment which is thought to differ considerably from the wild state is that, in captivity, animals do not have many opportunities to make decisions for themselves and can exert little control over their environment.

Research in the field of human psychology has looked at the effects of giving people more or less control over their environment and over events which affect their lives. Rotter (1966) proposed that feeling unable to control these things is inherently stressful for humans, and subsequent work by Rotter and others indicated that poor health and disease can be the result (e.g. Langer & Rodin, 1975; Lau, 1982). When added to the results of studies carried out in the same field on animal subjects, this research has major implications for the study and welfare of non-human animals in captivity.

In the wild state, animals interact constantly with their environment and learn that carrying out certain behaviours results in particular consequences. They adapt to changing environmental conditions using behavioural and physiological mechanisms, the regulatory range of which is determined by their genotype and experience (Taylor *et al.*, 2001). This gives them some measure of control over their environment and how it affects them. For example, a parrot in the wild state will ruffle its plumage and pant to increase heat loss and learns that it can avoid excessive heat in the middle of the day by perching beneath thick foliage. In captivity, animals are subjected only to the conditions provided by their human caretakers, and their ability to adapt to and predict those conditions is also limited by their captive environment. For example, an animal in the wild which experiences hunger can forage; performing behaviours which, it knows from experience, may result in the acquisition of food. In captivity, once the food ration allocated by its caretakers has run out, the animal is unable to appease its hunger, regardless of what behaviour it performs.

Research indicates that a substantial reduction in the controllability and / or predictability of events affecting a captive animal can, as with humans, lead to chronic stress, which may be an indicator of reduced welfare and which can result in disease (e.g. Wiepkema & Koolhaas, 1992; 1993). Control and prediction are, of course, connected, as gaining control over an aspect of an environment also increases, by definition, the predictability of that environment. In general, when an animal can not respond functionally to an event in order to ameliorate its effects (for example, when there is nowhere it can hide from a human entering its enclosure) the ability to predict the occurrence of the event becomes a more important factor in the animal's ability to cope with it (e.g. Weinberg & Levine, 1980; Abbott *et al.*, 1984).

Vertebrate brains are most sensitive to the occurrence of events which follow each other in a non-random way (Wiepkema & Koolhaus, 1992). A classic (albeit inhumane) experiment, which indicated the importance of predictability on the levels of stress and attendant disease experienced by captive animals, was carried out by JM Weiss in 1972, and further variations on the experimental set-up have been investigated since that time. In Weiss' study, he subjected two groups of rats (*Rattus norvegicus*), housed individually, to electric shocks (a third group acted as controls, and received no shocks). When the rats in group A were about to receive an electric shock, they heard a beeping tone; the rats in group B heard the tone as frequently, but it sounded randomly for them, having no connection to the shocking mechanism. They did, however, receive shocks of identical force, frequency and duration to those experienced by the animals in group A. The results showed that the rats in group A (that were able to predict when the shocks would occur, even though they couldn't avoid them) developed relatively little gastric ulceration during the experiment (the control group developed little or none). The group B rats, however, unable to predict when the shocks would occur, showed a significant amount of ulceration, which was thought to be a direct consequence of the stress they had undergone. These results indicate that it was the inability of the rats to predict the onset of a shock that was the main cause of the stomach lesions, rather than the electric shocks themselves. In a further, similar experiment Weiss obtained comparable results using weight loss, rather than ulceration, as an indicator of stress and reduced welfare.

It is not only a lack of predictability over negative events that can induce stress-linked responses such as stomach wall lesions, high corticosteroid plasma levels (Weiss, 1972) or lowered immune system capability (Visintainer *et al.*, 1982) (all found in group B rats after experiments based on those described above). A reduced ability to control or predict positive events (such as the acquisition of food) can also lead to comparable responses. For example, a study by Carlstead (1986) found that well-fed captive pigs showed increased stress responses (indicated by elevated plasma cortisol levels, variation in weight gain and an increase in frustration-induced aggressive behaviour) when the signals preceding each food presentation were unreliable.

The link between the performance of behaviour and appropriate functional outcome is one that is frequently lost in captivity with serious consequences for the psychological well-being of the animal (Shepherdson, 1994). There is growing evidence that animals in captivity perceive themselves as helpless and unable to change negative aspects of their environment, and that this influences the release of stress-related hormones (Dantzer *et al.*, 1983). Loss of control over their environment results in an increase in stress levels for captive animals. For example, mice (*Mus musculus*) that are placed in a novel environment or which are prevented from returning to a familiar environment once they have voluntarily entered the novel one, have increased levels of corticosterone, an indicator of increased stress. This does not occur if the mice are allowed to move freely between the novel and familiar environments, thereby exerting control over their surroundings (Misslin and Cigrang, 1986).

It has been demonstrated that captive animals will choose to control aspects of their environment, given the opportunity. For example, deer mice (*Peromyscus maniculatus*) which were trained to control their lighting using lever presses, turned off the light every time it came on (every half hour). If the light was automatically turned off instead, the mice turned it back on. The deer mice had a dislike of bright light, but it seems that exerting control of their illumination was sufficiently rewarding to override that aversion (Kavanau, 1963; 1964).

Joffe *et al.* (1973) also looked at the effects of giving some control over their environment to captive animals. Rats were reared in an environment where they could control the lighting, as well as presentations of food and water, by pressing levers (group 1). The control group (group 2) also had levers in their cages, but these gave the rats no control over food, water or lighting. The conditions experienced by both groups were identical, but were determined by the behaviour of the experimental group only; the group 2 animals had no control over their lighting, or food and water supplies. When the rats were tested, at 60 days old in a novel environment, it was found that those in group 1 were more active, explored more and showed less emotionality in novel situations (indicated by number of defecations) than the animals in group 2. Similar experiments, carried out on rhesus macaques (*Macaca mulatta*) by Mineka *et al.* (1986) also demonstrated that the animals reared with a degree of control over their environment (the macaques were able to control access to their food, water and treats) adapted better to novel situations than their conspecifics in the control group. They were bolder in the presence of a fear-provoking toy, were more eager to enter a novel room, explored it more after entering, and adapted more quickly to a stressful separation from their peers.

Lack of early experience in controlling environmental events can produce an animal which, later in life, adapts poorly to stressful events and which is less likely to investigate and learn about novel situations (Carlstead, 1996). Overmeier and Seligman (1967) termed this response 'learned helplessness', a phrase which has remained in use, despite the continuing debate on the actual psychological mechanisms involved. It is clear, from this and other research, that animals in captivity can be significantly affected by the levels of controllability and predictability in their environment. While a lack of these elements can cause stress to animals in captivity, too much predictability can also have the same effect.

1.2.2 Stress

Stress is a concept used in many different fields of study, and in the biological sciences there is much debate about how it should be defined. It was described by McGrath (1970) as an imbalance between environmental demand and response capability, and by Selye (1973) as the biological consequence of exposure to adverse environments. Moberg (1985) developed a more detailed 'model for response of animals to a stressful event'. In this model, the effect of the environment is to predispose the animal to the development of some pathological state. The preceding 'pre-pathological state' can be identified by any of a variety of abnormalities and inadequacies in behaviour, physiology, immune function and reproduction (Moberg, 1987a,b). This description of stress is limited by the use of pathology as a defining characteristic, as some adverse effects resulting from environmental limitations may not be considered pathological. Broom and Johnson (1993) therefore, proposed that stress can be defined as an environmental effect on an individual which overtaxes its control systems and reduces its fitness, or appears likely to do so. Although it is often difficult to measure fitness, it is thought that knowledge of the biology of a species can allow scientists to assess the likelihood of its fitness being reduced as a result of environmental circumstances (Broom & Johnson, 1993). The use of fitness in this definition enables a distinction to be made between the effects of short periods of unpleasant stimulation (e.g. due to a minor injury or receiving an injection) sometimes called acute stress, and long-term or chronic stress, which will reduce the lifetime fitness of the individual concerned. Stress in a captive animal can also be defined, more simply, as a state in which the animal is required to make extreme adjustments in its physiology or behaviour in order to cope with its environment (Fraser, 1993).

Chronic stress has been shown to result in elevated levels of pituitary-adrenal activity in animals, which can lead to inhibitory effects on reproduction, growth and digestion as well as causing reduced immune response, neuronal cell death, reduced fertility, depression and lethargy (Sapolski, 1987, 1989; Moburg, 1991; Shepherdson, 1994; Carlstead, 1996; Wingfield, 1997). Stress can also affect an animal's fitness in other ways. For example, attacks on newly born offspring by their mother have been recorded in captive Patagonian cavies (*Dolichotis* sp.)(Rosenthal, 1974) and small-spotted genet (*Genetta genetta* sp.) have been known to eat their offspring (Flint, 1975) when they became stressed as a result of enforced close proximity to human caretakers.

Threatening or aversive situations and events are experienced by both wild and captive animals, and a certain level of exposure to unpleasant stimulation is now thought to be beneficial for those in captivity (whether it is labelled 'stress' or not) and may be necessary for normal physiological and behavioural development (Weiss, Sunder & Becker, 1989). For example, Chamove & Moodie (1990) found that a group of captive cotton-top tamarins (*Saguinus oedipus*) which were exposed to stressful events of short duration, such as a bird of prey apparently passing overhead, showed a significant decrease in their levels of abnormal behaviour and an increase in positive social behaviours. The researchers concluded that short periods of intense stimulation such as this were beneficial to the tamarins. Too much stimulation or stress, regardless of the exact definition used is, however, considered detrimental to the welfare of captive animals (e.g. Wiepkema & Koolhaas, 1993).

An inadequate, and therefore stressful, captive environment may result in its inhabitants performing stereotypical behaviours. Such stereotypies are repetitive, invariant behaviour patterns with no obvious goal or function (Mason, 1991). For example, motor reactions such as pacing, rocking, hair or feather plucking, head swaying, and limb biting are commonly seen repetitive behaviours in caged animals. Not all stereotypies are caused by environmental inadequacies, however, some result from brain damage, psychiatric conditions or are caused by drugs (e.g. Robbins, 1976; Robbins & Shahakian, 1981). Despite the wide range of possible causes and symptoms, it can generally be said that stereotypies result from an abnormal organism-environment interaction (Carlstead, 1998).

Environmentally induced stereotypies develop from a range of behaviour patterns and those source behaviours may be identifiable in the physical appearance of the stereotypy (Mason, 1991). For example, oral stereotypies such as crib-biting, wind-sucking and repetitive licking and chewing of inedible objects, can arise in animals which in the wild spend much of their time grazing or browsing, but which receive a more concentrated, quickly eaten, diet in captivity and have limited opportunities to forage naturally (e.g. horses (*Equus caballus*) (Fraser & Broom, 1990); giraffe (*giraffa camelopardalis* spp.)(Kinahan & Marples, 2000)). While stereotypies can reflect the inadequacy of an environment, it may not be the current situation which has induced them. An animal may retain stereotypies that it has developed previously, even when it is housed in a new and adequate environment (Mason, 1991).

It has been proposed that, although they may result in physical damage (Mason, 1991) stereotypies actually help animals to cope with a sub-optimal environment and are, therefore, rewarding (e.g. Fox, 1971; Dantzer & Mormede, 1981). Some researchers suggest that stereotypies are reinforcing in their own right, perhaps by providing an outlet for a particular behavioural need, as with the oral stereotypies described above. These behaviours may be substitutes for normal consummatory activities (Wiepkema, 1985). Other research indicates that the performance of stereotypies can result in the release of opioids which have a calming effect on the animal (reviewed by Rushen *et al.*, 1990) but the evidence for this is correlational and sometimes inconsistent (reviewed by Mason, 1991). Whatever the possible benefits of performing stereotypical behaviours, their persistence in the repertoire of a captive animal is generally regarded as a reliable indicator of poor welfare, because they show that the animal has problems coping with its environment (Broom & Johnson, 1993).

Another type of behaviour which is often seen in captivity, and which has welfare implications, is that of excessive inactivity and lethargy (Chamove, 1898). As captive animals do not need to (and in many cases cannot) forage or hunt for their food, flee from predators, encounter new conspecifics or find their own shelter, the time they would spend in these activities in the wild becomes available for them to use in other ways. Animals may spend this time performing behaviours which are related to those wild-type activities. For example, stereotypic pacing often occurs in captive felids and other predators which would usually need to chase down or stalk their prey in the wild. Some animals held in zoos spend time begging for food from zoo visitors, despite the fact that they are well fed. This is an example of a substitute for foraging behaviour that has been adapted to the captive environment (van Keulen-Kromhout, 1978). Other animals engage in prolonged bouts of self-stimulating behaviour, such as head swaying, copraphagy or tail biting (Carlstead, 1996). Some captive animals, however, become lethargic and spend large portions of their time resting, even though their wild conspecifics did not evolve in habitats where such behaviour would be sustainable. This can result in problems such as obesity and muscle wastage (Bauck, 1998) as well as apathy and boredom (Wiepkema *et al.*, 1983). Animals exposed to chronically understimulating conditions (where, by definition, they have little control over their environment) can also respond poorly to stimulating or novel situations when they occur and may even die as a result of fatal shock syndrome (Snyder, 1977; Wood-Gush, 1973). Christian and Ratcliffe (1952) looked at fourteen zoo animals that were housed in small indoor cages and which subsequently died when stressed by transfer to a new cage, or disturbance by workers. In all cases, the adrenal cortex of the animal had atrophied, indicating the inability of the animal to sustain the correct physiological response to strong stimulation.

1.2.3 Wild-type Behaviour

It is thought that information about the needs of captive animals can be deduced from studies of their wild conspecifics (e.g. Broom & Johnson, 1993). The behaviour of a species in the wild, therefore, is often used as the desirable standard against which the behaviour, and hence the welfare, of captive conspecifics can be assessed (e.g. Heidiger, 1969; Farm Animal Welfare Council, 1986; Chamove & Anderson, 1989; Fraser & Broom, 1990). Activity budgets (i.e. the average length of time spent in different behaviours daily) can be compared for captive and wild groups of a species, and it is widely thought that any large difference between the two may indicate that the captive group is being kept in sub-optimal conditions (e.g. McGrew, 1981; Winskill *et al.*, 1996). However, not all departures of captive or domestic animals from the behaviour of their wild ancestors or conspecifics constitute a welfare problem (Dawkins, 1989). For example, captive giraffe may spend more of the day lying down than their wild counterparts, but this could merely be because lying down during the day is rarer in wild giraffe due to the increased risks of predation (Dalton, 1987).

We do not yet know how many species behave in the wild, and the species that have been well studied indicate that wild-type behaviour is often highly variable, and dependent upon local environmental conditions. Behaviour patterns in the wild have been found to vary with group size, gender, age, habitat and local weather (Harrison, 1983; Richard, 1985; Chamove, 1986; Shepherdson, 1998). This means that is can be difficult to tell whether changes in a species' behaviour in captivity are indicative of adversity, or merely appropriate adaptations to the new environment. It should also be remembered that wild animals may live in a wide variety of sub-optimal, stressful or atypical conditions themselves, and their activity budgets may reflect that. In baboons of the *Papio* genus, for example, the quality of habitat occupied by a population has been shown to affect the activity budgets of its members. In habitats where food is more scarce or dispersed the baboons will spend more of their day in feeding behaviours and less time resting. In addition, they will increase their rate of travel throughout the day, thereby freeing up more time for other activities (Dunbar, 1992). In the wild, animals usually have to contend with higher levels of danger from injury, disease and predation than they do in captivity, and those factors may also affect their behaviour. For example, alterations in predation risk can result in changes to feeding behaviours (e.g. Suhonen, 1993).

Another example of 'natural' habitats being sub-optimal has arisen from research on felids. It has been proposed that big cats have a 'need' to perform hunting behaviour (e.g. Beaver, 1980) but observations in the wild indicate that, given the opportunity, many big cats will choose to scavenge, rather than hunt, for all their food (Lindburg, 1988; Jackson, 1992) presumably because it is a more energy-efficient technique. However, there is good evidence that felids are, nevertheless, strongly motivated to carry out predatory behaviours, even in the absence of any desire to satisfy hunger. In the wild, cats such as leopards (*Panthera pardus*) and hyaenas (*Hyaena* spp.) perform 'surplus killings', particularly on very dark nights where their prey is less able to take flight (Shepherdson *et al.*, 1993).

The extent to which behavioural differences between wild and captive animals can be used as an indicator of welfare in captivity is, therefore, a matter of some contention. It has been argued that, although there may be some correlation between the expression of wild type behaviour in captivity and the welfare of the captive animal, in many cases it may be the consequences of the behaviour, rather than its expression, that results in benefits to the animal (Veasey *et al.*, 1996). For example, Lindburg (1988) found that the provision of carcasses to captive Amur tigers (*Panthera tigris altaica*) and cheetah (*Acinonyx jubatus* sp.) resulted not only in the expression of natural feeding behaviours, but in a concurrent improvement in oral health and a reduction in dental disease, compared with conspecifics fed formulated diets.

In some cases, however (as was clear from the discussion of behavioural needs in section 1.1) it is the performance, rather than the consequences, of a wild-type behaviour that is beneficial to the captive animal (e.g. rooting behaviour in pigs) and an inability to carry out that behaviour may result in poor welfare. A study by Dawkins (1989) comparing the behaviour of domestic hens and jungle fowl (*Gallus gallus*) (the wild ancestors of domestic fowl) indicated that the opportunity to perform foraging behaviour is important to hens, regardless of whether they find any food by doing so. Research has also shown that flocks of domestic fowl that have the opportunity to forage (i.e. behave in a wild-type fashion) show less cannibalism and feather-pecking than flocks which do not (Blokhuis, 1986).

Increasingly, the relevance of behavioural and ecological field data to captive management is being recognised by zoos and wildlife parks, although less frequently in laboratories and farms. The extent to which such data are used to affect changes in practice, however, is still limited in many areas of animal husbandry (Redshaw & Mallinson, 1991). For example, elephants (*Loxodonta* and *Elephas* spp.) are rarely kept in natural wild-type herd groupings in captivity, and unvarying, empty, relatively small enclosures, providing little stimulus and little control or choice over most aspects of day to day life are still commonly in use in many zoos (Redshaw & Mallinson, 1991).

1.2.4 Learning

As mentioned earlier, short periods of acute stress may be necessary for the welfare of captive animals. Specifically, short periods of acute stress may be vital for normal behavioural and physiological development (Weiss *et al.*, 1989). In many species, juveniles need to learn parenting, foraging and social skills from other group members. If they are prevented from doing this (e.g. as a result of being removed from the group at an early age, or because their environment does not allow the adults to teach the youngster certain skills) they may be behaviourally or reproductively compromised as adults (e.g. Mellen, 1992; Berman, 1990). For example, hand-reared sloth bears (*Melursus ursinus*) showed significantly higher frequencies of stereotypic and self-directed behaviours as adults than mother-reared individuals (Forthman & Bakeman, 1992).

There are phases in an animal's development, called sensitive periods, when exposure to specific stimuli result in the animal learning particular behaviours. Such learning, is permanent and varies both in type and duration, from species to species. For example, captive mallard ducks (*Anas platyrhynchos*) which were reared in elevated wooden nestboxes chose to use elevated boxes to nest in when they were released into the wild, as did their, wild-born, offspring. Conversely, those mallards raised in ground nests, chose to nest at ground level themselves (Hess, 1972).

If an animal does not encounter the specific stimuli necessary for development during the appropriate sensitive period, it may still be able to develop the behavioural traits later in life, but will do so less efficiently (Immelmann, 1975; Miller *et al.*, 1998). For example, domestic cats (*felis catus*) must be exposed to prey during juvenile development, or they do not kill efficiently as adults (Caro, 1979). A failure to provide learning opportunities at critical times in an animal's development in captivity can, therefore, result in reduced possibility of survival should it subsequently be released into the wild (Beck, 1995).

1.2.5 Novelty

Another aspect of animal behaviour which can be affected by the environment is response to novelty. The reactions of animals to novel objects and situations is a widely studied area, particularly in the fields of psychology, pest control and the development of aposematism. Neophobia can be defined as 'the initial avoidance of novel objects in an otherwise familiar environment' (Brigham & Sibley, 1998) although longer term avoidance of novel food items (in particular, by avian species) has also been described as 'dietary conservatism' (Marples & Kelly, 1999). The degree of neophobia exhibited by animals can vary, even between closely related species, and is thought to be an adaptation linked to various ecological factors (Glickman & Sroges, 1966; Mettke-Hofmann *et al.*, 2002). For example, experiments by Greenberg (1984) on wood warblers, indicated that the generalist opportunist feeder, *Dendroica castanea* was less neophobic than its more specialist relative *D. pennsylvanica*. He also found that young of the species conformed to this pattern in laboratory studies, and obtained similar results when studying generalist and specialist species of sparrow (*Melospiza melodia* and *M. georgiana)* (Greenberg, 1990). These results were similar to those reported in studies of different rat species (Brigham & Sibly, 1999).

Within a species, there are also wide variations in the levels of neophobia exhibited by individuals. Exploration and response to novelty have been shown to be affected by age, gender and genetics (Mench, 1998). In addition, the levels of exploration shown, the development of neophobia and subsequent dietary preferences have been found to be influenced by early feeding experiences (Fernandes, 1996) and the level of complexity of the rearing environment (Raach & Leisler, 1989). Social transmission of dietary preferences has been identified in, for example, macaques (*Macaca* spp.), baboons (*Papio* spp.), howler monkeys (*Alouatta pigra*) and meerkats (*Suricata suricata*) (review by Galef, 1976). Mitchell *et al.* (1977) found that Norway rats (*Rattus norvegicus*) which were taken from a large, frequently controlled population, displayed an initial neophobic reaction to novel food, while rats of the same species, taken from an island site, where there was little human control of the rat population, preferred the novel food to their usual diet from the first day of presentation. Norway rats have also been found to be easily trapped on land-fill sites, where the frequently changing environment makes a neophobic strategy impossible to sustain (Boice & Boice, 1968; Boice, 1971). This research indicates that the response of captive animals to novel foods or objects could be influenced by both physical and social aspects of their rearing and living environments.

Neophobia is thought to have evolved as an adaptive response to minimise the ingestion of harmful substances and to avoid previously unknown dangers in the wild (Fernandes, 1996). Despite the large amount of research on neophobia, however, there have been relatively few studies carried out to examine the ways in which the captive environment may influence response to novelty. One such study by Barnett (1956) compared the food preferences of wild and laboratory strains of Norway rat. The results indicated that the wild rats showed more highly developed flight and avoidance behaviour. Further studies (Barnett, 1958b; Calhoun, 1963) found that wild rats show marked avoidance of new foods, new or repositioned objects (including those containing familiar food) and strange noises, and that the introduction of these novel stimuli caused them to delay feeding from a familiar container. The laboratory rats, on the other hand, when tested in the same conditions, showed no delay in feeding from a novel container of food, and approached it as soon as it was placed in their cage. It should be noted that, although wild rats avoided novel objects placed in familiar surroundings, they approached and explored new areas and surroundings when they become available (Barnett, 1958a; Cowan, 1976) showing high levels of exploratory behaviour. The explanation of these results is unclear. The lack of neophobia exhibited by the laboratory strains of Norway rat could be a result of domestication (Barnett, 1958b) as neophobic animals would be selectively disadvantaged by 'laboratory natural selection' (Richter, 1954). Alternatively, it could be argued that laboratory rats resemble their wild ancestors in their responses to novelty, and that the wild rats of today have evolved be more neophobic as a result of selection imposed by human control measures (Mitchell, 1976).

Sackett (1972) looked at the effects of environment on the response of rhesus macaques to novelty by varying the degree of isolation of the test animals. The results showed that the macaques raised in normal conditions, or with their mother and other conspecifics, were least hesitant to enter a novel chamber, and spent longest investigating a novel object. Animals that had been isolated for twelve months were very hesitant in approaching and exploring the novel environment and objects. These results, combined with those from the studies on rats, indicate that, while neophobia or neophilia levels vary between species, a captive environment can cause changes to the animals' responses which would disadvantage them in the wild state.

1.2.6 Conservation of Behaviour

One of the stated aims of keeping animals in zoos is to aid the conservation of endangered species for posterity, research and education (e.g. Durrell, 1976). As behaviour is a consequence of interactions between both genetic and environmental factors, however, it is thought that failure to provide a captive environment which is at least functionally equivalent to that of the wild, will result in the loss of many forms and patterns of natural behaviours (Shepherdson, 1994; Markowitz, 1995; Ebenhard, 1995). As animals continually modify their behaviour to best fit their environment, either in the wild or in captivity (Veasey, 1996) a captive environment differing substantially from that encountered in nature could result in the erosion of morphological, behavioural or physiological traits necessary for survival in the wild, but not in captivity. This would be particularly likely for any traits which are expensive to maintain (Derrickson & Snyder, 1992). Captivity can also increase individual behavioural variability to the point where adaptive traits (or the ability to express those traits with the efficiency necessary for survival) are under-represented in the captive population as they are no longer strongly selected for. For example, studies on captive-bred Siberian ferrets (*Mustela eversmannii*) showed considerable behavioural variation between individuals, even though the entire stock originated from three females and two males (Miller *et al.*, 1998). In captivity, without proper care, therefore, unconscious artificial selection or the lack of natural selection may erode traits necessary for survival in the wild, particularly in very long-term breeding programmes (Derrickson & Snyder, 1992). However, some researchers contend that the stability of innate behaviour patterns is generally underestimated, and that there is little evidence that even deliberate domestication has caused behaviours to be eliminated from a species' repertoire (Carlstead, 1996). Some studies of feral populations, living in the wild after numerous generations of captivity and domestication, indicate that many behaviours may be recovered, even after generations of absence. For example, modern breeds of pig, living in semi-natural conditions in Scotland (Wood-Gush, 1988) and Sweden (Jensen, 1986) were found to show many behavioural similarities to wild boar (*Sus scrofa*) (Fradrich, 1967) despite so many generations of their ancestors having been domesticated and behaviourally restricted. Similarly, studies of feral flocks of domestic fowl, which had lived unrestrained for many years on an island off the coast of Australia, found that they showed behaviour which was very similar to that of wild jungle fowl (McBride *et al.*,1969).

Some researchers think that domestication often produces more placid, less aggressive animals with reduced fear reactions (Craig, 1981; Price, 1984) but tends to alter the intensity or frequency of different behaviour patterns by changing the release thresholds, rather than by adding or eliminating behaviours in the animal's repertoire (Price, 1998; Schutz *et al.*, 2001).

For example, fish that have been selected for high growth rates show reduced levels of antipredator behaviour and take more risks during foraging (Johnsson & Abrahams, 1991). Schutz & Jensen (2001) compared the behaviour of immature jungle fowl (wild-type) and white leghorn chickens (selected for high levels of egg production) in semi-natural conditions. They found that the jungle fowl were more active, more social, and performed more intensive foraging behaviour than the white leghorns. This research indicates that behaviours may be retained in captivity, even though unexpressed, but whether the behaviours can be performed with sufficient efficiency to allow the animals to survive in the wild is less clear. For example, Castro *et al.* (1998) monitored captive-bred golden lion tamarins (*Leotopithicus rosalia*) before and after release to the wild. They found that animals raised in standard zoo enclosures show the same behavioural repertoire as their wild conspecifics, but that they may not have the experience needed to fine-tune their behaviours or always to express them adequately in the appropriate situations. In studies where predator pressures have been reduced on wild populations, the animals responded correctly, but less efficiently, when a predator did appear (e.g. Morse, 1980; Coss & Owings, 1985; Loughry, 1988). It seems, therefore, that familiarity with and practice of a behaviour are both important in carrying it out with maximum efficiency. In this context it is interesting to note that the budgerigar (*Melopsittacus undulatus*), which has probably been under domestication longer than any other species of psittacine, is one for which feral populations are virtually unknown (Forshaw, 1989; Derrickson & Snyder, 1992) although several other parrot species have successfully established feral populations outside their natural range (Forshaw, 1989; Sanz & Grajal, 1998).

Where particular traits have been repeatedly selected for in a domestic species, they may be to the detriment of the animal if it were to live in a less artificial and controlled environment. For example, strains of broiler chickens and domestic pigs which have been selected for increased appetite over many generations, will become so obese in early life that, unless heavily restricted in their food intake, their reproductive fitness in later life will be reduced (Duncan, 1978). The existence of a flourishing captive population of a species is no indication that animals from that population retain the ability to survive in the wild.

Traits that have been unintentionally selected for in captivity may also affect the ability of animals to survive in a wild setting. Even in a flourishing captive population, some individuals will not breed, or will have a high proportion of unsuccessful attempts. This may be due to the animal failing to adapt well to its captive environment but, whatever the cause, the result is that those individuals will be selected against because they are not contributing to the future gene pool of their species (Frankham, 1995). Likewise, individuals which adapt well to their captive environment, and breed more readily or prolifically, could be over-represented in the captive gene pool of their species. This process of selection will be most intense in the first few generations after the transition from the wild to a captive environment (Price, 1984).

A crucial factor in determining the effects of captivity on the behavioural repertoires of a population is the selective pressures operating on the animals in the captive environment. Malmkvist and Hansen (2002) worked with two genetic lines of farm mink (*Mustela vison*) which differed in having either a confident or fearful reaction towards humans, over 10 generations. They found that offspring from a confident breeding line approached novel objects, food or conspecifics and investigated mazes, with a significantly shorter latency than those from the fearful line. This study highlights the way in which behaviours can change when animals which show low levels of fear towards humans are selected. In zoos and similar institutions, unintentional selection of animals with similarly fearless tendencies could occur. They may find their environment, with close proximity to human visitors and caretakers, less stressful than their more fearful conspecifics, and, hence, breed more successfully. In species with similarly divergent genetic lines to those found in mink, this could lead to captive populations being genetically and behaviourally different from their wild conspecifics. Results of a study by Mellen (1991) support this hypothesis. She found a positive correlation between the amount of friendly keeper interactions taking place with small exotic cats and their reproductive success. There are obviously species-specific differences in how a lack of fear of humans can effect the reproductive success of captive animals. For example, studies of great Indian hornbills (*Buceros bicornis*) in captivity have indicated that the birds which were more likely to approach their keepers spontaneously, were also significantly less likely to breed successfully (Carlstead & Kleiman, 1998).

It is clear that an absence of the selection pressures which would be present in a species' natural environment, and the presence of captivity-induced selective pressures, may allow behavioural traits to proliferate in captivity that would be disadvantageous in the wild (Carlstead, 1996). Occasionally, such effects are actively encouraged. For example, the fact that hand-raised birds are usually more tolerant of the presence of humans than parent-raised ones has been used in the development of a reintroduction strategy to restore cranes (*Grus* spp.) to their traditional breeding grounds in the Amur basin in Russia. The sites were abandoned as a result of human activity a few kilometres away and researchers hope that captive-bred young, released to join the wild flock, will pair with wild birds and breed closer to human settlements (Andronov, 1993). Whether other maladaptive behaviours will result from the birds being reared by humans is yet to be seen.

Although some behaviours may be maintained in captivity, despite an inability to express them, this will not be the case for those which are learnt by individuals and then passed on from generation to generation (Shepherdson, 1994). For example, Huber *et al.* (2001) studied learning in Keas (*Nestor notabilis*). The researchers showed two dominant members of a twelve bird group how to carry out a complex manipulative task (unlocking a 'model fruit' – a steel box fastened with three different locking devices) then tested the naïve birds on the same task, five who had observed an experienced bird perform the task and five who had not. They found that the keas who had watched an experienced conspecific showed a faster approach to the locking devices, extended persistence in their manipulative actions, more tactile exploration and greater success in opening the locking devices. Similar results have been found in studies on chimpanzees (*Pan troglodytes*) (Tomasello *et al.*, 1987). The diversity of such culturally transmitted behaviours (which also include activities as wide ranging as the rearing of infants, the identification of predators and the development of food preferences) has the potential to be lost much more quickly than does genetic diversity (May, 1991).

The loss of cultural traits, especially local adaptations, can result from small population effects, and so occur readily in captivity. The few individuals which were used to found a new population in captivity, for example, may not have happened to carry a particular trait with them; the group may have been founded by young animals that were isolated from their parent population before they acquired the trait, or an essential factor in maintaining the trait was not present in the environment in which the population was kept (McLean, 1997).

From the research outlined above, it is clear that genetic and behavioural aspects of an animal species can be altered unintentionally in captivity as a result of environmental effects. The ease and permanence of such changes is a still a subject of debate, but in situations where they may be undesirable (for example, when a species is being bred for reintroduction into the wild), providing a captive environment which is as functionally equivalent as possible to the natural environment of the species can reduce the effects of artificial selection pressures.

1.3 Environmental Enrichment

The concept of environmental enrichment has been around at least since the beginning of the 20th Century, but it is only in recent decades that it has started to develop into a scientific approach to understanding, and providing for, the physiological, psychological and behavioural needs of captive animals (Shepherdson, 1998). In general, the term 'environmental enrichment' means the provision of complex, diverse and functionally relevant surroundings, which increase the possibility that a captive animal can use its own behaviour to fulfil its requirements for health and fitness. Such requirements may include, for example, finding food, demarcating a territory, building a nest, maintaining a good physical condition, escaping conspecifics or hiding from perceived threats. An enriched environment affords an animal more of the behavioural opportunities found in the wild (Carlstead & Shepherdson, 1994) and there is increasing evidence that an animal with more behavioural options will be better able to cope with either boredom or stressful events (Carlstead, 1996).

The effects of environmental enrichment have been studied in various contexts since the early 1960s, in particular by psychologists looking at the effects of environmental stimuli and early environment on learning and behavioural development (Chamove, 1989; Shepherdson, 1998). In the psychology literature, 'enrichment' is used to describe any changes to a captive environment which increase its complexity, regardless of any biological relevance to the animal being studied. Since the mid-70s there has been an increase in research as interest in the practical applications of environmental enrichment has opened up new avenues of study (Dell & Rose, 1987). For example, research has been carried out into the effects of enriching the environment in the fields of mental retardation, ageing and recovery from brain damage in humans (Rosenzweig, 1984), as well as the areas of captive breeding for reintroduction, welfare and the education of zoo visitors in animals.

Successful environmental enrichment is achieved through the identification and provision of the environmental stimuli necessary for the optimal physiological and psychological wellbeing of an animal in captivity (Shepherdson, 1998). It is an increasingly popular method for improving the wellbeing of animals in zoos, laboratories and farms, because research has shown that appropriate enrichment can have highly beneficial effects on the behaviour and physiology of captive animals (Shepherdson, 1994). In addition to effects on other animals, environmental enrichment programmes providing human children with increased levels of stimulation and socialisation have been found to result in significant improvement in the children's performance in subsequent intelligence tests (e.g. Angoff, 1988).

1.3.1 Types of Enrichment

There are several different kinds of environmental enrichment, such as structural, object-based, food-based, olfactory and social enrichments, but they are only enriching when applied appropriately. Devices which enrich the captive environment for one species may cause chronic stress to another. For example, simple items such as visual barriers can have significant, species-specific effects on the social dynamics of captive animal groups. Providing visual barriers in a stump-tailed macaque (*Macaca arctoides*) enclosure was found to decrease aggression within the group, whereas such barriers increased aggression in pig-tailed macaques (*Macaca nemestrina*) (Carlstead & Shepherdson, 1994).

The so-called 'psychological space' of an enclosure can be increased by encouraging animals to make more use of the existing space (Chamove, 1989). Underused areas of an enclosure can be made more interesting and relevant to the animals by installing structural or object-based enrichment devices there. An enclosure can be made more complex by providing structures that allow the animals to make use of both the vertical and horizontal space available, for example, cargo nets, climbing branches and a variety of platforms can be used to increase the surface area over which the animal can move (Carlstead, 1996). In addition, the use of a wide selection of perches and climbing devices in an enclosure, of varying degrees of mobility and flexibility (e.g. fixed branches, ropes, chain, thin flexible branches, swinging tyres etc) can increase both the complexity and unpredictability of an environment designed for climbing animals or birds. The provision and use of such enrichments has been found to improve coordination and balance in monkeys (Catlow, 1995) and great Indian hornbills *Buceros bicornis* (pers. obs.) which were previously held in less complex environments.

One method of increasing environmental complexity is to provide captive animals with objects which they can manipulate. For example, a swinging boxing or rugby bag hung in a rhinoceros enclosure will elicit hours of rubbing and butting behaviour, as it responds to the animal's actions with movements of its own (Carlstead, 1996). Enrichment devices which contain food are commonly used in preference to other objects with many animal species however, as animals are usually inherently motivated to forage for food (Dawkins, 1990).

Food-based enrichments can be naturalistic or artificial in form. Some are designed to be very similar to items which animals would forage from in the wild. For example, Nadler *et al.* (1992) gave singly housed chimpanzees a cob of maize every other day, in addition to their usual biscuit ration. They found that the chimpanzees spent significantly more time feeding when the maize was provided, and showed a reduction in behavioural disorders. Other food-based enrichment devices are constructed from artificial materials, but designed to stimulate natural feeding behaviours. For example, Reinhardt (1993) gave rhesus macaques their usual daily biscuit ration on the mesh roof of their cage, instead of in a bowl. The macaques increased the time they spent foraging by a significant amount as a result, and demonstrated high levels of digital dexterity in their foraging behaviours. The macaques used foraging techniques similar to those which they would employ to extract food items from holes, shells or capsules in the wild. Alternatively, food-based enrichments may be artificial devices requiring manipulations that the animals would not need to perform in the same way in a natural environment. For example, Bloomsmith *et al.* (1988) provided chimpanzees with puzzle feeders containing popcorn, sunflower seeds or peanuts. In order to obtain the food, a chimpanzee had to put a finger into holes cut into the front of the feeder and push food items along horizontal shelves, with passage holes, until they dropped to a lower shelf. The exit hole was at the base of the feeder. There is no consensus in the literature on whether natural or artificial devices provide animals with the most effective enrichment.

The sensory complexity of a captive environment can also be improved through the use of appropriate enrichment. For example, scent trails can be laid in an enclosure, using essential oils or the urine of other species or conspecifics. In a study by Pankhurst (2000) the use of prey scents (branches scent-marked by fallow deer, *Dama dama*) resulted in increased exploratory behaviours in captive tigers (*Panthera tigris* spp.), and a reduction in stereotypic pacing. Where the space is available, the rotation of animals through different enclosures can also be enriching. For example, Stelvig and Sargent (2001) divided a large snow leopard (*Uncia uncia*) enclosure into three areas, one for each cat and one spare. They found that, when they gave the animals alternate access to the spare section, the male snow leopard increased the time he spent on three marking behaviours (spraying, scraping and cheek rubbing) and decreased the time he spent resting. The female showed an increase in the amount of time she spent in clawing (another marking activity). Both animals showed a large increase in their performance of behaviours related to scent marking responses: Flehmen, licking and scenting.

For social species, the presence of conspecifics can be a critical aspect of enrichment. Social partners are an excellent source of interactive stimulation, and allow an individual to interact with its surroundings to a greater degree than if it were alone (Carlstead, 1996). Appropriate numbers of individuals, sex ratio and age ratio within the captive group are important factors and have been shown to affect the expression of species-typical behaviours, as well as reproductive success (Kreger *et al.*, 1998). As discussed earlier, in order to develop into behaviourally and reproductively viable adults, it is necessary for the juveniles of many species to learn parenting and social skills from other group members (e.g. Beck & Power, 1988; Mellen, 1992; Berman, 1990). In many cases, animals may also benefit from the replication of seasonal or temporal variations in the make up of the group to mimic what would happen in the wild (Hutchins *et al.*, 1984; Caro, 1993). However, it must be remembered that not all wild animals live in optimal environments. For example, orangutans are usually solitary in the wild, but this may not be their preferred social grouping, merely one born of necessity in a habitat where food is frequently scare and widely dispersed.

When social species are kept in groups in captivity, the phenomenon of ‘social facilitation’, mentioned in section 1.2.6, can result in widespread interest in and use of enrichment devices by the group (Renner *et al.*, 1992). Social facilitation is defined as any increase in the frequency or intensity of a behaviour caused by the presence of conspecifics performing the same behaviour (Clayton, 1978; Gochfeld, 1980; Nicol, 1995). It has also been dubbed ‘contagious behaviour’ by Galef (1988).

Social facilitation has been found to occur in a number of behavioural categories including foraging and feeding (in e.g. hens, wood pigeons *Columba palumbus*, gerbils *Meriones unguiculatus* and turtles *Pseudemys nelsoni*). It has been shown that social facilitation of feeding in gerbils occurs particularly when novel food items are provided. This may aid animals to learn about the palatability of new foods which are familiar to other individuals in the group (Forkman, 1991). Other behaviours known to be influenced by social facilitation include preening, reproductive synchrony and antipredator defence (Palestis & Burger, 1998).

In a zoo environment it is thought necessary by many to promote natural species-specific behaviours in the animals on display. Not only might the ability to carry out natural behaviours aid the animal if it is released into the wild, but the opportunity to watch animals acting in a natural manner is an important factor in the education of zoo visitors (Young, 1995). In addition, animals often appear to be more motivated to perform species-specific wild-type behaviours than other activities they may be offered or trained to perform. For example, as with the pigs displaying rooting behaviour toward their ‘food tokens’ described in section 2.1, a racoon (*Procyon lotor*) was initially trained to exchange a coin for food, but subsequently spent most of the day directing natural feeding (including washing) behaviours towards the coin (Breland & Breland, 1961). It is important, therefore, when providing an enrichment device for a particular species, to take into account the natural behaviours of that species. In particular, if the enrichment device is food-based, the naturally occurring appetitive behaviours of the animal to be enriched should be considered and, where possible, opportunities to display them should be incorporated into the enrichment (Carlstead *et al.*, 1991; Young, 1995).

1.3.2 Effects of Enrichment

'Environmental enrichment' is a term that is widely used in studies of animal behaviour and welfare, but it is often vaguely defined. For the purposes of this study it is regarded as modifications to a captive environment which result in an improvement in the biological functioning of the animals held therein (see Newberry, 1995). The question then arises of what is meant by an 'improvement' in the functioning of the animals under examination. There are several ways in which the use of enrichment is regarded as improving the captive environment.

Work carried out by psychologists and physiologists mainly, although not exclusively, using rats has identified a particular set of physiological consequences associated with environmental enrichment. These include: Increased cortical thickness and weight, increased size, number and complexity of nerve synapses, and an increased ratio of RNA to DNA. Enriched animals also behave differently, showing fewer errors in maze problems, for example (reviewed by Widman *et al.*, 1992). In such studies 'enrichment' consisted of group, rather than solitary, housing or the presence of novel objects in a cage. It was found that enrichment using only novel objects resulted in increased object exploration (less fear, more exploration and interaction) by the rats in test situations. Animals that were only socially enriched, behaved the same way as unenriched ones in object exploration tests (Widman *et al.*, 1992; Hepper, 2001) but performed better than object-enriched animals in social situations (less fear, more exploration, more interaction) (Hepper, 2001). These results suggest that different types of enrichment may have differing and particular effects on some behaviours.

This is supported by the results of a study by Shepherdson *et al.* (1993) who looked at the response of small felids in captivity to two different food-based enrichments. The researchers found that presenting the cats with live fish in a pond (in addition to their usual food) resulted in the animals spending 60% less time sleeping, more time in active behaviours, especially hunting, and greater use of enclosure space. When the felids were presented with their usual food, hidden under a small pile of bush and provided four times a day instead of once, they showed increased levels of locomotion and exploratory behaviour and reduced stereotypic pacing, but showed no significant change in the amount of time they spent inactive or sleeping.

One area which environmental enrichment has been shown to affect is that of stereotypic behaviour in captive animals. As discussed earlier, the exact causes and effects of such repetitive behaviours are still under debate, but high levels of stereotypies are generally regarded as indicators that the animal either is kept, or has been kept in the past, in an inadequate environment. Enrichment has been shown to decrease levels of stereotypic behaviours in many captive animals. It does so in a variety of ways, for example by providing the stimuli the animal is motivated to look for, by reducing the motivation to perform an over-used behaviour, or by making the environment more variable and less predictable (Carlstead, 1998).

For example, in a study by Carlstead *et al.*, (1993) four leopard cats (*Prioailurus bengalensis*) were housed individually, in a building that also held lions (*Panthera leo* spp.), tigers and puma (*Puma concolor*). Stress levels (measured by urinary cortisol) and stereotypic pacing was chronically elevated in the animals. When their enclosures were physically enriched, by providing hollow logs, branches, boxes and platforms, both cortisol and pacing levels reduced significantly. The researchers hypothesised that the new cage 'furniture' allowed the animals to hide from the perceived threat of the big cats in nearby cages, thereby reducing their stress. The leopard cats continued to pace between feeding times, however, so their feeding schedule was made more unpredictable and more feeds were given. This led to a further significant reduction in pacing and a significant increase in exploratory behaviour. In addition, hiding the food in piles of bushes resulted in shorter pacing bouts and longer periods of exploration (Shepherdson *et al.*, 1993).

A singly housed American black bear (*Ursus americanus*) significantly reduced his stereotypic pacing when he was given the opportunity to dig and forage for most of his daily food ration (something he would do for about 18 hours a day in the wild, during the Summer and Autumn) instead of receiving it in a dish (Carlstead & Seidensticker, 1991). The manipulation of objects and substrates to find the food was the critical stimulation for the bear. When he was provided with the same amount of food, dispensed at random intervals from an automated feeder tree (thereby increasing unpredictability but not stimulating natural foraging behaviours), the pacing was not reduced (Carlstead *et al.*, 1991b).

It has been shown that simple forms of environmental enrichment can reduce the levels of stress-related hormones in captive animals (Carlstead, 1991) with benefits arising in the fields of reproduction and health, among others, as discussed in section 1.2. Vestergaard *et al.* (1997) looked at the effects of housing laying hens in cages with either a wire, or a sandy floor for two and a half years. Birds kept on wire showed a higher incidence of stereotypic behaviours, but there was no difference in the concentration of corticosterone (a stress-related hormone) between the two groups. The researchers then provided the wire-raised birds with access to sand. The birds had attempted to dustbathe, even on the wire floors, but there was a significant increase in dustbathing behaviour after sand was provided (dustbathing removes stale lipids which otherwise accumulate on the hens' feathers). They showed no change in corticosterone concentration but levels of aggression and stereotypic behaviour decreased significantly. When the sand-raised birds had their sand removed, they showed a significant increase in corticosterone concentrations but no increase in stereotypic behaviour. These results suggest that, while increased corticosterone levels are indicative of increased levels of stress, hens kept for long periods in conditions where they cannot dustbathe can develop behavioural patterns (i.e stereotypies, aggression, and ineffectual attempts to dustbathe - a vacuum behaviour) which ameliorate the stress of the condition.

One area in which enrichment has been shown to have particularly beneficial effects concerns animals' control of their environment in captivity. Many, if not all enrichments share an important characteristic: They restore to captive animals the contingency between the performance of a behaviour and the appropriate consequences (Shepherdson, 1994). As discussed earlier (section 1.2), animals allowed control over important aspects of their environment suffer less chronic stress, and its consequent adverse effects, than those who live in an environment which allows them no or little control. For example, rats and pigs which were subjected to a stress-inducing, frustrating experimental situation were able to inhibit their pituitary-adrenal stress response when provided with enrichment (Carlstead & Shepherdson, 1994). The enrichment devices used gave the animals the opportunity to perform behaviours such as chain pulling, drinking or wheel-running. In another study it was found that adding manipulable enrichment devices to the, otherwise barren, cages of rhesus macaques, resulted in the animals exhibiting lowered plasma cortisol levels and a reduction in abnormal or stereotyped behaviours (Line *et al.*, 1991).

Experiments on rodents, comparing those raised in enriched environments with those raised in impoverished ones, have shown that enriched captive environments also result in improved learning abilities (Widman et al., 1992) as well as qualitative and quantitative increases in exploratory behaviour (Renner, 1987; Widman & Rosellini, 1990). The performance of exploratory behaviour is vital for survival in the wild, as it enables individuals to obtain information about spatial details of their environment (Wiepkema & Koolhaus, 1992). An understimulating captive environment can result in animals showing reduced levels of exploratory behaviour; effects which can persist even if the animal is subsequently placed in a more complex environment (Mench, 1998).

Experiments by Dell and Rose (1987) showed that manipulation of the environment in which female rats are kept prior to mating can significantly modify the behaviour of future offspring kept in unenriched environments. Rats whose mothers were kept in enriched conditions (complex and variable with movable objects and a social group) were compared with rats whose mothers were kept in standard conditions (small social group in basic laboratory cages) and rats whose mothers had been kept in impoverished conditions (individually housed in basic laboratory cages), using open field and skinner box tests. The details of the results were difficult to interpret, but they clearly showed that the degree of enrichment of the pre-pregnancy environment can significantly influence offspring behaviour. Other studies have shown that female rats kept in enriched cages prior to and during pregnancy can confer anatomical and physical benefits to their offspring (including increased cortical thickness) as a result (Diamond *et al.*, 1984).

As discussed in section 1.2 , the complexity of the environment in which an animal is raised can affect its subsequent reactions to novelty. Experiments on moustached warblers (*Acrocephalus melanopogon*) were carried out by Raach and Leisler (1989). Three groups of birds were used: Captive-bred birds, bred in either a deprived (standard perches only) or an enriched (climbing structures, tubes, wood-wool, ribbons) environment, and wild caught birds. The added elements of the enriched environment were designed to replicate the salient physical properties of the birds' natural habitat. The researchers found that, when given a choice between the two artificial environments used for rearing, the wild-caught and enriched birds preferred the enriched environment; the deprived birds showed no preference. In follow-up experiments, the deprived birds were more reluctant to feed during neophobia trials and showed higher latency periods in ability tests. In contrast, there was no significant difference between the three groups in their response to curiosity tests which did not involve a food reward. These results support the theory that rearing animals in a deprived environment causes increased levels of neophobia which may, in turn, influence the animals' selection of habitat structures. This tallies with the work of Greenberg (1984) who postulated that innately high levels of neophobia in adult chestnutsided warblers (*Dendroica pensylvanica*) (which are specialist, not generalist feeders) might restrict them to foraging places which they explored in their youth. Lower levels of neophobia were found in related species of warbler that were more generalist in their feeding habits.

Whereas a complex and stimulating early environment can alter brain morphology and enhance other cerebral measures that affect behaviour later in life (Greenough & Juraska, 1979; Rosenzweigh, 1979), research has shown that dogs (*Canis lupis familiaris*) kept in a sterile kennel environment for the first 12 weeks on their life suffered shock when they were introduced to a more complex environment, from which they never recovered (Shepherdson, 1994). Animals which experience a complex environment early in life not only adapt to new experiences when they are older, but are also better able to employ cues in problem solving (Miller *et al.*, 1998). For example, Cheal (1987) looked at the effects of enrichment on Mongolian gerbils (*Meriones unguiculatus*). Gerbils exposed to a natural outdoor desert environment for an hour each month during development were better at finding food in a complex, novel environment than those raised in unenriched cages. The results of a second experiment showed that gerbils raised in large cages, enriched with pipes, rocks and ladders, were more successful in finding food in a complex, novel environment than those raised in small unenriched enclosures.

As discussed in section 1.2, with fewer opportunities to perform wild-type behaviours, captive animals often use their resulting 'spare time' to perform repetitive behaviours such as stereotypies or they may spend much more time inactive than their wild conspecifics. The provision of environmental enrichment can stimulate animals to increase their levels of activity (e.g. Van Hoek and King, 1997) and has also been shown to affect humans that have been institutionalised. Work by Chamove (1986) on schizophrenic patients that spent much of their time inactive in hospitals and day-care centres, looked at the effects of small amounts of extra activity on the patients' general behaviour (activities examined were swimming, keep fit, occupational therapy, work therapy and gardening). Patients showed significant improvements in their levels of social competence, irritability, social interest, tension / anxiety, movement disorder and psychotic behaviour. The psychological literature indicates that such activities teach skills which lead to a feeling of competence, and sociobiological theory suggests that evolutionary pressures have selected for humans who spend a part of their day in activity or work (Chamove, 1986). Studies of primitive tribes of hunter-gatherers , who are thought to most closely represent behaviour patterns through much of recent human evolution, found that women, in an average day, carry 25 kg in weight over a minimum of seven miles for a minimum of three hours (Blurton Jones & Sibly, 1978). Studies have indicated that self-injurious behaviour in humans and other animals may partly be caused by restriction of their activity levels. Environmental enrichment can ameliorate this by providing opportunities for humans and other species to engage in activities which engage the adaptive skills they have developed over their evolutionary history (Favell *et al.*, 1982; Chamove & Anderson, 1981; Chamove, 1986).

Another potential benefit of environmental enrichment is that it may make the presence of illness and disease easier to spot. It is particularly difficult to detect signs of illness in captive animals, as they tend to mask their symptoms well (Forthman Quick, 1984). If an animal has an enriched environment, however, any cessation of use of the enrichment devices can be quickly seen, and may indicate ill health in the animal. For example, a zoo exhibit provided servals (*Leptailurus seval*) with 'flying meatballs' to stimulate predatory behaviour (Markowitz & Woodworth, 1978). After a male serval had obtained food in that fashion for some time, he stopped abruptly. A medical examination revealed the presence of a hernia, which was easily treated at an early stage of development.

Environmental enrichment can also increase the reproductive success of captive animals both directly, by providing the social and physical environments necessary for successful reproductive behaviour and parental care and indirectly, by providing the developmental environment required for the growth of behaviourally normal and reproductively viable adults (Shepherdson, 1998). Chronic stress, which can have inhibitory effects on reproduction (Sapolski, 1989; Moberg, 1991) can be alleviated through the appropriate use of environmental enrichment (for example, in the study on leopard cats by Carlstead *et al.*, (1993) mentioned earlier, where the provision of enrichment significantly reduced levels of stress-related hormones). Research has shown the effectiveness of enrichment both prior to, and during reproduction. For example, Millam (1995) showed that a combination of enrichment strategies resulted in significant levels of egg production in pairs of orange-winged amazon parrots (*Amazona amazonica*) which had not previously laid eggs. Other work has shown that the provision of various enrichment devices increases egg production in commercial poultry (Bell and Adams, 1998).

Environmental enrichments, when inappropriately used, can have negative effects on captive animals. Preferred foods are often used in environmental enrichment in order to stimulate the performance of foraging behaviours such as dipping in termite mounds (chimpanzees), solving food puzzles and the use of other enrichment devices (Forthman *et al.*, 1992; Shepherdson *et al.*, 1993). As well as making sure that animals do not thereby ingest an unbalanced diet, in situations where animals are kept in groups, care must be taken to prevent dominant animals limiting the access of subordinate animals to the preferred food. Otherwise the dominant animals may suffer from obesity or malnutrition, while the subordinate animals may experience increased levels of stress and frustration (Baer, 1998).

Food-based enrichment devices which are designed for use over a prolonged period (for example, a wood block with holes drilled in it and stuffed with dried fruit and seed may take a parrot several days to tear apart and empty) may also be hazardous to the health of captive animals. In such instances care must be taken to ensure that the food does not spoil from prolonged exposure to warm temperatures or attract rodents and insects which can act as vectors for disease (Calle *et al.*, 1993; Scanga *et al.*, 1993; Baer, 1998).

1.3.3 Conservation and Enrichment

Many zoos are involved in captive breeding programmes for endangered species of animals, with the ultimate aim that they or their descendants can be successfully reintroduced to the wild. The International Union for the Conservation of Nature and Natural Resources (IUCN) has recommended that vertebrate taxa thought to number less than one thousand individuals in the wild should be considered as candidates for captive breeding programmes (IUCN, 1987). As discussed in the previous section, the use of appropriate environmental enrichment may facilitate reproduction in captivity but, unless it is followed by successful reintroduction into the wild, captive breeding is a conservation failure (Ebenhard, 1995).

Environmental enrichment has a vital role to play in ensuring that species do not lose either innate or learned wild-type behaviours from their repertoire while they are held in captivity (Mallinson, 1995). It is critical that animals which are released into the wild have experience of a sufficiently rich captive environment to allow the development, performance and maintenance of species-typical behaviours, necessary for survival after release (Shepherdson, 1998). In many of the reintroduction programmes carried out to date, however, the captive-born animals have not had the behavioural skills and experience to survive in the wild. Studies have shown that wild-born animals, introduced to the same sites as captive-born conspecifics, adapt quicker to their new surroundings and survive longer (Miller *et al.*, 1994) and that translocated wild animals have been found to adapt more successfully to their new surroundings than captive-bred introductees (Gordon, 1991). Miller *et al.* (1992) compared the behaviour of juvenile Siberian ferrets which were familiar with underground burrow systems in an enriched environment, with cage-raised conspecifics. When the animals were placed in an unfamiliar arena, the cage-raised ferrets spent more time on the surface, and less time underground, increasing their risk of predation. Research also showed that Siberian ferrets and black-footed ferrets (*Mustela nigripes*) raised in enriched environments were more proficient at killing prey after release to a natural environment (Miller *et al.*, 1992; Vargas, 1994), although all mustelids raised in captivity do have at least a rudimentary ability to kill prey when given the opportunity (Miller *et al.*, 1998). Other facets of predation which cannot develop in the absence of experience are learning where and how to search for prey, search images, the correct time to attack and specialised hunting techniques (Krebs, 1973; Lawrence & Allen, 1983).

In a reintroduction programme for golden lion tamarins, zoo-bred animals which lived in a free range, large wooded area showed enhanced behavioural adaptation on release into the wild compared with conspecifics reared in less natural environments (Bronikowski *et al,*, 1989). Conversely, some other attempts to improve the tamarins' survival skills, using smaller enriched environments, failed to confer any detectable long-term advantage on them. It is thought that this was because that the enriched cages did not adequately reproduce the challenges of the wild environment (Beck *et al.*, 1987). In the wild, tamarins must negotiate thin, flexible, mobile supports, such as terminal branches and lianas, navigate in three dimensions around a large home range, avoid predators, find food and shelter and behave appropriately towards conspecifics (Kleiman, 1989; Bronikowski *et al.*, 1989).

Reintroduction can be a valuable tool in conservation programmes. In 1994, Magin *et al.* calculated that 25 species of animal had been preserved in captivity following extinction in the wild. Most of them have been successfully reintroduced into their former habitat, including the Pére David's deer (*Elapharus davidianus*), the Californian condor (*Gymnogyps californianus*) and the Moorea tree snail (*Partula* spp.) (Mallinson, 1995). Where populations have been eradicated locally, but the factors causing the eradication have been partially or wholly corrected, it may be possible to re-establish populations from other sources (Soulé, 1987). In addition, the reintroduction of captive-bred animals can play a role in maintaining a species in the wild through a period of population stress. For example, such releases have aided the recovery of some populations of the peregrine falcon (*Falco peregrinus*) in the western United States during the period of subsiding levels of organochlorine contaminants which were largely responsible for the decline of the species (Cade *et al.*, 1988). Likewise, eggs and chicks produced in captivity were introduced into the nests of wild Puerto Rican parrots (*Amazona vittata*) to aid the survival and bolstering of the population in Luquillo Forest, along with a release of captive-reared adult birds (Snyder *et al.*, 1987).

Another main purpose of zoos is conservation education, and environmental enrichment in exhibits can make them more informative and interesting to zoo visitors (Shepherdson, 1998). For example, a study of zoo visitor behaviour by Altman (1998) found that animated activity by the zoo animals elicited the most visitor attention to behaviour, and that this, in turn, potentially facilitated visitor learning. The performance of stereotypies by the animals, however, tended to draw negative or critical comments from visitors. When enrichments which encourage species-specific behaviours are used in enclosures, the opportunities for visitors to learn about the natural history, ecology and behaviour of the animals is increased.

1.4 Avian Species in Captivity

There are approximately 9000 extant species of birds in the world today, compared with approximately 4500 species of mammals. They inhabit all the climatic zones, from the high Arctic to the Antarctic, and exhibit an extremely rich and varied range of behaviours. In terms of their distribution and variety of habitat, birds can be regarded as the most successful group of vertebrates and they are at least as well, if not better, represented in zoos than mammals (King, 1993). When it comes to mastering complex problems in a laboratory setting, bird species outperform many mammals in advanced learning experiments (Bohm, 1995) but, despite this being the case, the research and literature on zoo enclosure design and environmental enrichment is heavily biased towards mammals and mentions bird species relatively seldom (King, 1993). For example, although Markowitz gave many examples of enrichment in his ground-breaking book 'Behavioral enrichment in the zoo' in 1982, only one of the 199 pages of text was devoted to birds. Likewise, of the almost 100 talks and posters presented at the 5th international conference on environmental enrichment in 2001, only five referred to avian species (although the conference organisers had particularly asked for contributions about members of animal groups under-represented in the field of enrichment, such as birds and reptiles).

Some people consider mammals to be have a unique requirement for enrichment in captivity, and some even maintain that mammals, alone among vertebrates, experience a 'psychological need' to carry out behaviours which are unnecessary for their immediate survival (e.g. Poole, 1992). Bird species, according to Poole, are merely 'clever reptiles', although he admits that they have developed 'mammal-like attributes'. While recognising the possibility that the cognitive abilities of birds (and, hence, their psychological needs) may be found to be similar to those of mammals, despite differences in brain organisation, he does not believe it to be likely, and considers that birds are unintelligent, compared with mammals. Chapman (1990) claims that there is no neuropsychological basis for postulating the existence of suffering in birds or reptiles when their behavioural needs cannot be met, and that such suffering is specific to mammals. His view appears to be based on the assumption that, because birds and reptiles do not have the same brain anatomy as mammals, they cannot have developed comparative capabilities. This view is challenged by, for example, Dawkins (1992), King (1993) and Etienne (1984). King (1992) also points out that although birds and mammals are far apart in evolutionary terms, they have converged in terms of behaviours and abilities. This is particularly the case for psittacines and primates, which have many characteristics in common in terms of abilities, habitats and behaviours (see section 1.4.5).

Outside the parrot family, the group of birds with perhaps the greatest reputation for intelligence is the corvids. Members of the corvidae have been shown to exhibit excellent learning and memory skills and adapt well to novel situations. For example, rooks (*Corvus frugilegus*) at the Membury service station in England have learnt how to get food from the rubbish bins in the carpark, even though the bins are regularly emptied before the level of rubbish rises to within reach of birds perched on the rim. The bins are lined with black plastic bags, and the rooks have learnt to perch on the rim, lean over and grab a beak-full of black bag and haul it up over the rim. They then stand on the pulled up bag (to prevent the weight of the rubbish pulling it back into the bin) before reaching in and taking another beak-full of bin liner. Eventually, the rubbish rises within reach and the rooks throw pieces of food over their shoulders so that it collects on the floor, where they can eat it at leisure (Beynon, 2003).

Birds are generally very well adapted to catch and handle prey and have excellent food-finding abilities (Bohm, 1995). They are, therefore, interesting candidates for behavioural studies and are likely to benefit from environmental enrichment programmes in captivity. This particularly applies to species with advanced cognitive abilities such as corvids and psittacines. Further reasons why the study of psittacine behaviour is both important and difficult are summed up in this extract from a paper by Collar (2000): ‘Understanding of the complex environmental and social interrelationships of parrots is essential for their long-term *in situ* and *ex situ* management, but the behaviour of parrots, particularly in the wild, is calculated to defy the scientific investigator: Slow-breeding, wide-ranging, unpredictable, non-territorial, cryptic when perched, and capable (at least until recently) of detaching marking and tracking devices, they represent everything that is anathema to fast-track academic research study. Consequently, the scientific measurement of their ecological requirements remains in its earliest infancy’.

1.4.1 Psittacines

Psittacines are among the most highly threatened birds in the world, with more endangered species than any other bird family (Collar *et al.*, 1994). In global lists of species at risk (under protocols established by IUCN - The World Conservation Union, 1994) 90 (26%) of the world’s approximately 350 species of parrot are listed as threatened with extinction (compared with only 11% for bird species as a whole). Another 40 (11%) are listed as near-threatened (Collar, 2000). Of the remaining non-threatened species, almost all are declining in numbers, and many in range. The main threats come from habitat destruction and exploitation for the pet trade (Collar & Juniper, 1992). The situation is exacerbated by the reproductive biology of parrots, which is generally characterised by low rates of reproduction related to low clutch size, one clutch per year (with a few exceptions), low survival of chicks and fledglings, late age of first reproduction, large proportions of non-breeding adults and restrictive nesting requirements (Wright *et al.*, 2001). In addition, evidence is steadily accumulating that the security of many parrot species is prejudiced by their specializations in food and habitat use (including nest sites) (Collar, 2000). For example, some of Australia's *Psephotus* and other parrots depend on grass seed in the wake of natural fires as a seasonal dietary resource, and have died out where artificial burning regimes have allowed different plants to come to dominate in their feeding areas (Garnett, 1993; Garnett & Crowley, 1995).

Loss of suitable nest sites is thought to be one of the reasons for the decline of some psittacine species in the wild. Most psittacines are cavity breeders, with nests located in hollows in trees and palms. Mawson and Long (1994) studied the trees with hollows used for nesting by four species of parrot and one species of cockatoo in south-west Australia. The minimum calculated age of the trees ranged from 75 to over 200 years (Stoneman *et al.*, 1997). Such nest trees are used by 50 or more species of parrots and cockatoos in Australia and they may need to be more than 500 years old for some psittacine species to use. Another cause of decline in psittacine populations is poaching from nests to provide birds for the pet trade. Wright *et al.* (2001) calculated rates of mortality due to nest poaching in 23 studies of Neotropical parrots (covering 4024 nesting attempts, 21 species and 14 countries). They found that the average mortality rate was 30 % of all nests observed, ranging between no poaching in six studies which took place in areas known to have low levels of poaching or which concerned species of low commercial value, and over 70 % in four studies. The researchers concluded that poaching of parrot nestlings for economic gain was a widespread and biologically significant source of nest mortality.

Most rare species of psittacine have declined in number as a result of more than one environmental factor. For example, kakari (*Cyanoramphus novaezelandiae novaezelandiae* and *C. auriceps auriceps*) are parakeets endemic to New Zealand. After the arrival of European settlers their numbers declined as deforestation, disease, their persecution as crop pests and the numbers of introduced predators all increased (Greene, 1998).

The members of the parrot family have been glorified for centuries as tameable, adaptable cage birds in the bird keepers' literature and pet shops. They were kept by aboriginal peoples, and sometimes accompanied them on distant voyages, for example in the West Indies and Polynesia. The extent to which this contributed to the historical distribution of psittacines through the introduction of birds to new regions is largely, although not completely, undocumented, but may have been substantial (Wiley *et al.*, 1992). They are prized for their colour, longevity, intelligence and ability to mimic sounds (Millam, 1999) but notice is rarely taken of their biological requirements (Lantermann, 1997). Lantermann conducted a survey of 258 private parrot owners who kept their birds primarily as pets. The research showed that most of the parrots were kept in small 'traditional' cages, had inappropriately strong bonds to their owner, and showed high levels of behavioural and psychological problems, particularly after reaching sexual maturity. Significant modifications in behaviour result from the social isolation of parrots, and signs of sexual frustration and stereotypical behaviours occur frequently (Lantermann, 1989).

There are other problems which are also common in captive psittacines. If they are fed on high calorie diets, but are relatively inactive, then they are prone to fatty liver syndrome (hepatic steatosis) which can lead to liver failure, uncontrolled haemorrhage, severe fibrosis and death (Kollias, 1995). Adult parakeets, cockatiels, amazon parrots and some cockatoo species are well-known for their obesity problems in captivity. Inactivity and high levels of fat in the diet are again the principal factors (Bauck, 1995).

As mentioned earlier, psittacines are generally regarded as intelligent birds and this contention is supported by research into their abilities. Pepperberg and Funk (1990) tested four species of adult psittacines on object-permanence tasks. These tests are widely used to assess levels of understanding and intelligence in human children, as well as primates and other animals. Object permanence is comprehension of the idea that objects are separate entities that continue to exist when out of sight of an observer. According to Piaget (1953, 1954) development of the object concept is the earliest step in intellectual development. Each of the six stages in Piaget's scale of competence in this area shows progressive development of manipulatory skills and increasing awareness of both self and surroundings. All four species of psittacine tested displayed Stage 6 competence (following Uzgiris & Hunt, 1975). The species studied were: African grey parrot (*Psittacus erithacus*), illiger mini macaw (*Ara maracana*), parakeet (*Meloppsittacus undulatus*) and cockatiel (*Nymphicus hollandicus*). Piaget (1954) based on his work with human infants, proposed that stage 6 competence indicates that the subject is able to represent mentally the movements of an object that is absent from its perceptual field. Not all six stages of object permanence are reached by all species of animals (Chevalier-Skolnikoff, 1989) and the ability of psittacines to demonstrate full Stage 6 object permanence is indicative of their ability to both assimilate and use available environmental information (Pepperberg & Funk, 1990). Other animals which have been tested and thought to show Stage 6 object permanence include human infants (at about 2 years old); chimpanzees; lowland gorilla (*Gorilla gorilla* sp.) and white-throated capuchin monkeys (*Sebus capucinus* sp.). Dogs, cats (*Felis domesticus*) and some monkeys show Stage 5 levels of competence in object permanence tasks (Doré & Dumas, 1987).

In some situations, involving visual exercises, the mental capabilities and intelligence of psittacines have been estimated to be comparable to that of a five year old human child, but their emotional development is more usually equivalent to that of a two or three year old child (Davis, 1991). It should be noted that similar levels of ability between parrots and primates does not necessarily reflect the operation of the same cognitive mechanisms (Pepperberg & Kozak, 1986). Birds have very different brain morphology from mammals, especially in the forebrain. In the absence of a neocortex, it is thought that their higher behavioural functions depend on the intricate neuronal network of the external striatum (Etienne, 1984).

1.4.2 Avian Conservation

A variety of behaviours that are critical for population persistence have been found to have a learned component in wild populations of birds, and so could easily be lost in captivity. Such behaviours include long-distance migration patterns (Temple, 1978) and food preferences (Rowley & Chapman, 1986). Rowley and Chapman studied wild populations of galahs (*Cacatua roseicapilla*) and the slightly larger Major Mitchells cockatoos (*Cacatua leadbeateri*). These two species are sympatric throughout most of Australia and, occasionally, a galah will lose its nest-hole to a Major Mitchells pair but will leave an egg which the new owners of the nest will unwittingly raise with their own young. Such cross-fostered galahs tend to behave as, and associate with, *C. leadbeateri* and they ignore other galahs. They learn to fly and call like *C. leadbeateri*, although they sometimes use galah begging and alarm calls and might use galah flight patterns briefly on occasion, before quickly reverting to the typical slower *C. leadbeateri* behaviours. Even as adults, they continue to seek out and associate with *C. leadbeateri*. The cross-fostered galahs studied by the researchers in the field learnt to feed on all the favoured foods of *C. leadbeateri*, including those rarely if ever fed on by galahs (which have a less varied diet). The most extreme example of this was when cross-fostered galahs were seen, in the company of *C. leadbeateri*, hunting for wood-boring larvae. It is not known whether, with their smaller and weaker beaks, galahs would be able to obtain food in that manner, but the fosterlings certainly displayed typical *C. leadbeateri* feeding behaviour. Galahs in the area which had not been cross-fostered had never been seen to behave in the same way.

It seems, therefore, that some innate behaviour patterns may be modified by learning and their expression consequently altered in the adult. Through a combination of imprinting and subsequent learning, the innate patterns of *C. roseicapilla* behaviour were largely eclipsed. As a result, the cross-fostered birds were accepted by *C. leadbeateri* and allowed to fly, feed and roost in their flocks, whereas normally the two species remained apart. Tracking the environment for ripening foods, developing handling abilities with different foods when found, discovering and maximising the value of nesting assemblages and recognising predators are all skills which are learnt by psittacines. In the wild, they are taught to offspring by their parents and / or by older siblings or group members (Collar, 2000). In an inadequate captive environment, therefore, not only could learnt behaviours be lost from a population, but some innate behaviours could be inappropriately modified.

Several studies of birds have shown that immature individuals are often slower at prey detection or capture than adults, and may expend more energy per food item ingested (Magrath & Lill, 1985). Learning and experience are both necessary for the development of efficient foraging skills. Cannon (1979b) found that feeding skills were amongst the last behaviours to take full adult form in developing eastern rosellas (*Platycercus eximius eximius*) and pale-headed rosellas (*Platycercus adscitus adscitus*) in captivity, although young birds seemed to have abilities comparable to those of adults when only 44 days old. It is likely that differences in feeding skills could persist for longer, but that they were not apparent in the simple cage environment in which the parrots were reared, where they had their food provided in bowls (Magrath & Lill, 1985). Young herring gulls (*Larus argentatus*), for example, continue to improve their foraging skills over at least the first four years of their life in the wild (Grieg *et al.*, 1983). Animals which have a substantial learned component to their behaviour are, by definition, more difficult to keep and breed in captivity without losing some of their behavioural repertoire in the process. However, there are several factors which indicate that many rare species of psittacines may, nevertheless, be suitable candidates for captive breeding and reintroduction programmes.

Several arguments have been put forward to support the idea that birds may be generally more suitable for captive breeding and reintroduction programmes than mammals. A study by Berry (1983) which looked at the results of electrophoretic analyses of mammal and bird loci, indicated that bird populations tend to be less polymorphic, but more heterozygous than those of large mammals. If there is less genetic variation, but more inherent individual variation, on average in a population, it would appear that for a given number of individuals there would be a better genetic representation of the species as a whole. If this proves to be a finding which is generally applicable to avian and mammalian species, then birds may be less susceptible to genetic bottlenecks than mammals and so better suited to captive breeding programmes in limited space, particularly in situations where few individuals are available to participate in the programme. In many respects a captive breeding group is similar to an island population. It is worth noting, therefore, that over eleven percent of bird species are single island endemics, and some appear to have survived with very small populations for extended periods of time (Dixon, 1986). For example, the Chatham Island black robin (*Petroica traversi*), the Mauritius kestrel (*Falco punctatus*) and the Seychelles magpie robin (*Copsychus sechellanum*).

There are several specialised reproductive manipulation techniques that can be applied to birds in captivity, but not usually to mammals, such as double-clutching, artificial incubation followed by hand-rearing (or puppet rearing), fostering and cross-fostering. These methods can be used to increase population sizes quickly when necessary (see the examples of peregrine falcons and Puerto Rican parrots mentioned earlier), although the applications of cross-fostering and hand-rearing may be limited as maladaptive behaviour may occur (as seen in the galahs which were reared by Major Mitchells cockatoos, mentioned above).

1.4.3 Psittacine Conservation

Although the preservation of a species is best served by conservation methods associated with habitat, community and ecosystem preservation, the rapid decline and fragmentation of wild psittacine populations have often outpaced efforts to ensure their survival by such methods (Derrickson & Snyder, 1992). Captive breeding and introduction programmes, therefore, may well be necessary in order to conserve several species of rare psittacines.

Numerous feral parrot populations have been established through accidental introduction by humans (Wiley *et al.*, 1992; Sanz & Grajal, 1998) which may indicate that some parrot species at least have the behavioural and ecological versatility to adapt to new environments. Successful, deliberate reintroductions of endangered species of captive-bred psittacines to the wild have included: Yellow-shouldered amazon parrots (*Amazona barbadensis*) on Margarita Island, Venezuela (Sanz & Grajal, 1998) and red-crowned parakeets (*Cyanoramphus novaezelandiae cookii*) on Tiritiri and Cuvier Islands in the Hauraki Gulf (Taylor, 1985). Less successful attempts have been carried out with, for example, thick-billed parrots (*Rychopsitta pachychyncha*). Experimental releases of thick-billed parrots in Arizona were studied by Snyder *et al.* (1994). They found that captive bred birds, especially hand-reared ones, had poor survival rates due mainly to deficits in recognition of food sources, foraging ability and socialisation, as well as heavy losses to predators. In addition, there were no wild populations of the species in the reintroduction area, which is believed to have disadvantaged the introductees further as they did not have the opportunity to learn survival skills from wild-born conspecifics.

Parrots reared in captivity are at a considerable survival disadvantage, once released, compared to wild-caught birds. In order to increase their chances their captive environment must provide them with opportunities to develop appropriate predator avoidance and social behaviours, good physical condition and rudimentary flocking behaviour (Wiley *et al.*, 1992). This can be achieved through the provision of appropriate environmental enrichment, which can also be used to improve the birds' feeding and foraging abilities. It is important that parrots are familiar with the foods they will need to feed on after release. Not only do they need to develop an appropriate search image for the food items, but it may take them some time to learn proficiency in manipulating wild-type foods. For example, it takes young thick-billed parrots many months to become efficient in removing seeds from pine-cones (a staple natural food for the species) whether they are fledged in captivity or in the wild (Wiley *et al.*, 1992).

Many endangered species of birds have proved much more difficult to propagate in captivity than closely related non-endangered ones, possibly as a result of species specializations which are not catered for in the captive environment. For example, the Norfolk Island red-crowned parakeet (*Cyanoramphus novaezelandiae cookii*) proved to be problematic to breed in captivity, whereas the captive breeding of other *Cyanoramphus* subspecies has progressed relatively easily (Derrickson & Snyder, 1992). The use of environmental enrichment techniques may prove to be useful in providing the psychological, physiological or environmental requirements that are necessary to encourage breeding.

1.4.4 Avian Enrichment

As mentioned previously, there is a lack of published studies on the effects of environmental enrichment on avian species. Apart from the work done by Raach and Leisler (1989) outlined in section 1.3, most research that is carried out in this area seems to focus on hens, and the occasional species of parrot. A few other bird species have been studied, however, and some work has been carried out which identified possible negative effects of captivity on bird species. For example, Warkentin & West, (1990) studied merlins (*Falco columbarius*) which had been held in captivity for periods of seven months to three years. They were found to have significantly higher basal metabolic rates and body temperatures than more recently caught birds (2-7 days). This was thought to be due to the limitations of the captive environment, which prevented the merlins from performing the full range of their flying behaviours. Long-term captives may lose significant pectoral muscle mass while expending energy on the growth of organs such as the liver (although unlikely to be a positive change, the long term effects of this are unknown).

Dawson and Carey (1990) found that captivity affected the winter fat deposition of wild-caught goldfinches (*Carduelis tristis*) and lowered their resistance to severe cold. If this was due to stress or changes in behaviour in captivity, as proposed by the researchers, then the provision of appropriate environmental enrichment might be a means of avoiding it.

Some studies of the effects of environmental enrichment have been carried out on avian species. For example, Keiper (1969) studied captive canaries (*Serinus canarius*) and results showed that increasing the size of the cage or adding a swinging perch significantly reduced route tracing behaviour in the birds. Route tracing is a stereotypic behaviour where a bird or animal repeatedly follows a precise and unvarying path within their enclosure. When the canaries were provided with food-based enrichments ('seed bells', bird biscuits and millet sprays) instead of their usual diet in a feeding dish, they reduced their stereotypic spot-picking behaviour (where a bird pecks repeatedly at one place on a wall or other object).

Norgaard-Nielsen, *et al.* (1993) looked at the effects of providing enrichment for hens, in the form of sand and peat for dust bathing whilst they were being reared, and cut straw (obtained by the hens from a perforated plastic basket) during their laying period. They found that rearing with access to sand and peat reduced the later tendency to feather peck (causing damage to plumage and skin) and that the provision of straw in the laying environment had a similar, additional effect. It appears from the limited number of studies available that bird species respond behaviourally to species-specific environmental enrichment in much the same ways as mammals.

1.4.5 Enrichment for Psittacines

Many of the benefits of environmental enrichment, outlined earlier, are now regarded as vital for the well-being of captive mammals, and primates in particular. It is widely accepted that primates in captivity must receive regular, species-appropriate enrichment if they are to be well cared for and healthy, and to alleviate the problems associated with a lack of mental and physical stimulation in captivity (Reinhardt & Roberts, 1997). In the United States, environmental enrichment for some captive non-human primates is now mandated by legislation (APHIS, 1992).

The under-representation of birds in the field of applied enrichment may be particularly inappropriate where members of the parrot family are concerned, as psittacines have many of the same behavioural and psychological needs as primates in captivity and share many of the same ecological and behavioural characteristics in the wild (King, 1993). For example, psittacines and primates mostly inhabit dense forest, with a few species in grasslands or other more open areas. The vast majority of species in both groups are arboreal and extremely social (few primates or psittacines are truly solitary and many remain in social groups throughout the year). Vision is a primary sense and subtle displays involving colours and postures convey information among group members; vocal intraspecific communication is also extremely important. The majority of species are diurnal and both groups feed primarily on seeds, fruits and other plant material, though a few species are more carnivorous. Psittacines and primates both have 'tool using' members of their taxa (King, 1992a) and both groups include many species known to possess high levels of intelligence and learning ability (Pepperberg and Kozak, 1986 & Pepperberg and Funk, 1990). Manifestations of abnormal behaviours and boredom are common in both captive psittacines and primates and are well documented. In the wild, both groups tend to spend much of their day feeding and foraging. Primates in the wild spend between 25 % and 90 % of their day searching for and processing food (Clutton-Brock & Harvey, 1977) and the information available for psittacine species indicates that this range applies to them also (see Chapter 3).

Data from the wild is used by primate researchers to focus on the needs of primates in captivity, as making use of what is known about the biology and behaviour of a species under natural conditions is essential for improving its management in captivity. Awareness of the skills primates develop in the wild, and of the complex and intimate relationship between any primate species and its habitat, has focused interest on their need for environmental enrichment (Redshaw & Mallinson, 1991).

It seems probable that environmental enrichment techniques that have been shown to be beneficial for primate species will prove to be similarly beneficial for psittacines. From the evidence in the literature and from various avicultural websites, it appears that environmental enrichment is used more widely in zoos and aviaries that hold parrots than it has been in the past (e.g. Murray, 1993; Bauck, 1998) but it is still the exception rather than the rule and published research into the effects of enriching psittacines remains scarce.

Reed and Price (2000) looked at the effects of providing food-based enrichment for a pair of zoo-held hyacinth macaws (*Anodorhynchus hyacinthus*). The enrichment device consisted of a wooden log, suspended by a hessian rope from branches in the macaws' aviary, with 18 holes drilled into it to a depth of about 25cm. The holes were filled with four different types of nuts every time the device was presented to the birds. When they were enriched in this way the macaws spent significantly less time preening, resting and biting cage furniture. They spent 38% of their time foraging from or manipulating the enrichment device, thereby increasing the total amount of time they spent on feeding activities by 45%. The enrichment encouraged the birds out of the sheltered area at the rear of their cage, and into the centre where they could more easily be seen by visitors. In a similar experiment, Coulton *et al.* (1997) provided various psittacines with access to an enrichment device, consisting of a length of wood, with holes drilled in it, filled with seed or beans and covered with starch paper. Red-fronted macaws (*Ara rubrogenys*), thick billed parrots (*Rynchopsitta pachyrhycha*), green-winged macaws (*Ara chloroptera*) and yellow-backed chattering lories (*Lorius garrulus flavopalliatus*) were tested, and all except the red-fronted macaws used the enrichment device. The birds who used the food log showed increased levels of preening, but the researchers suggest that this was a desirable behaviour, augmented by the enrichment device.

Van Hoek and King (1997) looked at the effects of providing captive crimson-bellied conures (*Pyrrhura perlata perlata*) with a range of environmental enrichment devices. These consisted of fruit baskets, egg cartons, rolled up newspaper, hidden fruit, mineral block and ropes. In another experiment the perches in the enclosures were changed and willow branches added. Food and toys used as enrichments resulted in a significant decrease in the mean time spent preening (unlike in the Coulton experiment described above) while the perch changes resulted in a significant increase in time spent flying, hopping and climbing, and less time inactive.

Eight of the ten birds studied had plumage problems as a result of self-inflicted feather picking and plucking behaviours, possibly as a result of stress brought on by successive movements and separations of birds within the group. It is thought that although sometimes caused by a medical condition, self-harming, stereotypical behaviours such as these in captive birds may stem from excess preening which, in turn, originates as a displacement activity (used to fill in time which cannot be spent on more active behaviours, due to the limitations of the birds' enclosures) (Andrew, 1956; Fox, 1968). The effects of plucking and over-preening are detrimental to the health of birds, resulting in bare patches in the plumage and sore and lacerated skin (Bauck, 1998). In this study it was shown that in their baseline enclosures, the conures with plumage problems spent more time in preening and comfort activities, and less time vocalising and flying, than those birds with undamaged plumage.

1.5 This Study

This study was designed to examine the behaviour of psittacines in captivity, and how it is affected by the provision of environmental enrichment. Much of the published work on the effects of enrichment on captive animals uses experimental designs which look at the subject's responses to an enrichment device in a test arena, which it is placed in for a limited period of time before being returned to its usual accommodation. In economic terms such a set-up is called an 'open economy' because the test subjects have opportunities to carry out behaviours and access resources outside the experimental arena. The experiments carried out in this study, however, were performed in the birds' familiar enclosures. This meant that they lived with a range of choices, and associated costs and benefits, over a period of several days; a 'closed economy' in economic parlance. In this way the test animals were given the choice of continuing to behave as usual in their captive environment, or interacting with each enrichment device as much or as little as they wished. Testing animals in closed, rather than open, economies has been widely recommended for giving the most realistic view of animal priorities (Dawkins, 1990; Mason *et al.*, 1998).

Assessing which behaviours are of most importance to captive animals is one way in which researchers try to establish their 'behavioural needs' (Veasey *et al.*, 1996) and some work on the preference testing of captive animals has been carried out on domesticated species. For example, Tilbrook and Cameron (1989) placed rams with three ewes (*Ovis* spp.) which had long fleeces, and three ewes which had been recently shorn. They found that the rams preferred to mate with woolly ewes. Dawkins (1983) offered domestic hens a choice between entering a cage with a litter substrate but no food, and one with a wire floor which also contained food. Results from the experiments showed that the birds' preference for the presence of food over-rode their preference for a cage with a litter substrate when they were hungry. In other words, given the choice, hungry hens regarded food as more necessary than plumage care, but well-fed birds regarded the opportunity to dustbathe as more important than the opportunity to eat extra food. These results indicate that the preferences of a species can alter with circumstances.

Seeing how hard animals will work in order to access a particular environment or to interact with a particular enrichment, is another way of measuring the strengths of their different motivations and preferences. For example, Cooper and Mason (1997) showed that captive mink will push a heavier door to reach water to swim in than they will to reach a raised lookout platform or an empty compartment.

There is some debate over whether preference studies accurately indicate what is important to captive animals. Natural selection should result in animals exhibiting behaviours which increase their fitness but, of course, such behaviours evolved to increase fitness in the wild, not in a modified captive environment. It is certainly the case that, although animals are generally supposed to prefer that which is good for them (Broom & Johnson, 1993) not every expressed preference which has been studied has been found to be beneficial. For example, humans may eat too little or too much for good health, or may have a strong preference for drugs that will eventually kill them. Likewise, some captive rats (*Rattus norvegicus*), when given a wide range of foods to choose from, would only eat chocolate, which did not supply them with adequate nutrition. In fact they chose to tolerate extreme cold to eat the chocolate, despite the fact that a balanced diet was available to them in a warmer cage (Cabanac & Johnson, 1983). Some examples of preferences such as these may provide a short-term reward to the tested animals, although a prediliction for that reward could result in long-term adverse effects.

When an animal purposefully seeks stimulation, or chooses one environment or stimulus over another, it should be noted that it may not necessarily be because the effect is pleasurable. It may be because the stimulus is interesting or informative (Dawkins, 1976). Under normal conditions those things which animals show a preference for (i.e. which they find pleasurable or reinforcing in some way) in the short-term (at a causal level) are also beneficial for their long-term fitness or that of their species (at a functional level). This coupling of causation and function is sensitive to disturbances during ontogeny, or if the relationship is artificially uncoupled (Spruijt *et al.*, 2001). So, although for animals in the wild, the short-term welfare of the individual is usually synonymous with the long-term welfare of the animal or its species (Duncan, 1978), the same may not be the case in a captive environment. For example, certain strains of domesticated turkey (*Meleagris galloparvo*) have been selected for increased appetite and weight gain over many generations. As a result, the males will eat so much that they injure the females when they mount and tread them. By preserving her short-term welfare (by not mating and remaining injury-free), an individual female is therefore reducing her long-term fitness (by failing to reproduce and propagate her genes and her species) (Duncan, 1978). In the same way, humans suffer from obesity, diabetes or other problems if they continually follow preferences for energy-rich foods (that evolved to sustain their early ancestors, who had an active and physical lifestyle – see section 1.3.2) when they lead a sedentary existence in the modern world. Early experience can also have a strong effect on the development of preferences and could result in a less than optimal resource or activity being preferred (Broom & Johnson, 1993).

The language of consumer economics can usefully be applied to some aspects of the study of animal behaviour in captivity (e.g. McFarland & Houston, 1981; Dawkins, 1983; Tsunematsu, 2000). Although the economic methodology was originally designed to model how humans choose to spend their money in different circumstances, it can equally apply to how animals choose to spend their 'currency' of time. This approach can be applied to the assessment of animals' priorities in captivity, although it must be born in mind that, as with money, the priorities of the consumer may change with budget size.

In captivity, with sufficient food easily accessible, no new areas to explore and no predators to avoid, an animal's essential maintenance and survival activities can usually be carried out in a relatively short period of time. It is necessarily the case, therefore, that captive animals must have some elastic behaviours which they can perform to fill up the remaining time available to them. Bubier (1996) studied the effects of providing enrichment for domestic laying hens. She found that preening and social pecking at other birds were relatively elastic behaviours and may be used by the hens to fill their spare time. It is possible that repeated or continuous performance of such elastic behaviours can be detrimental to the long-term health or wellbeing of captive animals (Hughes & Duncan, 1988). For example, prolonged and frequent bouts of autopreening or pecking at other birds can cause considerable damage to hens' plumage and skin.

While long-term studies would be necessary in order to investigate many of the potential benefits of environmental enrichment described in this chapter, this study concentrates on what changes occur in the activity budgets of captive parrots and cockatoos during short-term enrichment programmes.

It was decided that preference should be given in the enrichment experiments to devices which would encourage expression of the whole complex of behaviours associated with feeding and acquiring food, as it is thought that the satisfaction of both the appetitive and consummatory phases of these behaviours may be important to the birds (Mench, 1998). Survival behaviours such as foraging for food are thought to be strongly internally motivated, with their satisfaction being a high priority behaviour for most animals (Dawkins, 1990). In their natural habitat in the wild, many species (including psittacines) spend most of their waking hours looking for, pursuing, gathering, handling, or hiding food (Shepherdson *et al.*, 1993; Carlstead, 1996) and environmental enrichments which promote such foraging activities are often preferred by animals over those which consist of inedible objects (e.g. Bryant *et al.*, 1988).

Previous studies indicate that, as with mammals, food-based enrichments are more stimulating to bird species than those which do not have a food component. For example, Bubier's work with domestic chickens indicated that searching for food items took priority over all inedible forms of enrichment (Bubier, 1996). It seems that in their natural form food items are inherently interesting to healthy animals and thus tend to elicit a range of manipulative and exploratory behaviours from them. These responses are known to occur even when satiation may not be the objective, whereas the rate at which inorganic objects occupy the attention of animals usually falls off rapidly unless these items are changed regularly (Lindburg, 1998). When enrichment devices are food-based, habituation does not appear to be a problem in most of the studies published to date, although there are exceptions (e.g. Plowman & Knowles, 2001). For example, in a study by Rapaport (1998) golden lion tamarins (*Leontopithecus rosalia*) were provided with a puzzle box containing grapes which they had to use specialised wild-type foraging behaviours to extract. They were given the device daily for 40 days but showed no sign of their levels of interest in it decreasing.

In a zoo setting, food-based enrichments may also have other advantages over inedible objects. Through the provision of wild-type feeding opportunities, species-specific feeding behaviours can be encouraged and explained to the visitor and the animals can improve their dexterity and foraging efficiency through their use (Mettke-Hofmann, 2000).

Data from wild birds were utilised in the study in order to ascertain the areas of psittacine behaviour that may benefit most from the provision of enrichment in a captive setting. As discussed earlier, behaviours in the wild vary with many factors, so comparisons with captive conspecifics that indicate, for example, that a species forages more in the wild than in captivity (e.g. Veasey *et al.*, 1996) does not indicate which of the two levels of foraging (or, indeed a third level), would be optimal for the species, or under what conditions. In this study, therefore, the birds were provided with their usual behavioural options (food, water, perches etc) plus food-based enrichments, which they could use if they so wished. They were then observed in order to ascertain whether changes in behaviour resulting from enrichment brought the birds' behaviour closer to the levels observed in the wild. More than one foraging device was provided in each experiment in order to avoid problems of aggression, arising through competition for food, which have been observed in some enrichment studies (Rapaport, 1998).

The original aims of this study were to observe individually-marked birds in the Dublin Zoo collection and how they responded to a variety of enrichments under conditions of varying day length, species composition and environmental complexity. It was also intended to study the reactions of the birds to novel stimuli, including the introduction of conspecifics, and to determine if those reactions varied depending on the birds' level of previous exposure to enrichments. In addition, it was planned to study the response of the visiting public to birds in enriched and unenriched enclosures respectively. Unfortunately, logistical problems at Dublin Zoo prevented the studies being carried out as planned and necessitated a move to carry out most of the observations of birds in Australian zoos (see Chapter 2 for more details).

This change meant that the observed birds could not be individually identified and the researcher had no control over which species were kept in mixed-species aviaries, what birds were introduced to, or removed from, aviaries or the size of the single-species groups.
As a result, the experiments were modified to focus on studying the behaviour of psittacines kept in typical zoo enclosures and to compare that with what is known of their behaviour in the wild, and also with their behaviour in an enriched captive environment. As well as examining the birds' activity budgets in different conditions, in order to ascertain which behaviours they were most motivated to carry out, several aspects of behaviour were examined in detail: The birds' preferences for different enrichment devices were studied to see how they compared with their species-specific behaviour in the wild. Other experiments looked at the psittacines' spatial use of their enclosures and the types and amounts of food they consumed when enriched.

A wide range of psittacine species were observed in a variety of captive settings in the study, rather than large numbers of individuals from one species housed in identical enclosures. In this way, any patterns of behaviour or responses to the enrichments which emerged as significant in the results would be more likely to be generally applicable to captive psittacines, rather than just to one species (which may not be typical of the taxon).

Chapter 2

Study Sites, Species, Materials & Statistical Analyses

2.1 An Introduction to Psittacines

Members of the avian order Psittaciformes are called psittacines. Systematists have always had difficulty classifying these birds (Forshaw, 1989) but recent works recognise three main groups, although the taxonomic levels the authors assign vary. The groups are cockatoos, parrots (including parakeets and conures) and lories & lorikeets (Juniper & Parr, 1998; Higgins, 1999). Data from biochemical, chromosomal, behavioural and morphological studies suggest that the parrot and lory groups are more related to each other than they are to cockatoos (see Higgins, 1999). The majority of lory and lorikeet species are distinguished from parrots, however, by the fact that they feed largely on nectar and pollen.

Psittaciformes is the third largest non-passerine avian order and is sometimes referred to as 'the parrot family'. It has more than three hundred and thirty constituent species, ranging from less than 20g to 2kg in weight, and most of those species are gregarious for at least part of the year. Psittacines are distinctive in appearance, but are often difficult to observe in the wild, especially as the majority of species are largely arboreal and, therefore, associated with tree-rich habitats (Gilardi & Munn, 1998; Forshaw, 1999). This may be one of the reasons why surprisingly little work has been carried out on the ecology of wild psittacines (Brice, 1992). They mainly eat plant parts, but also insects and other animals on occasion. The extant species are distributed mainly in the Southern Hemisphere, and are most prevalent in tropical and sub-tropical regions, although their range extends from 34°N to 55°S world wide.

2.2 Study Groups and Aviaries

2.2.1 Melbourne Zoo

Six groups of psittacines were studied in Melbourne Zoo, Victoria, Australia, totalling 45 captive birds as well a wild group of rainbow lories which lived in the area. Australia is generally arid to semi-arid, although temperate in the South-East and tropical in the North. Melbourne is situated on the South-East coast of Australia (approximately 37.8° S, 144.9 ° E). The average yearly rainfall in the area is 657 mm and the mean annual temperature is 19.8 ° C (data from the Australian Bureau of Meteorology).

2.2.1.1 Melbourne Zoo Parrot Group

The study group consisted of 16 birds, 5 species, all native to Australia (see Table 2.1). Each species was kept in a separate, well-planted aviary with opaque side walls. The species were, therefore, in visual but not acoustic isolation from one another, with the exception of the princess and scarlet-chested parrots which shared an enclosure.

Parrot Species	Number of Birds	Gender	Age	Birth Location	Wild Distribution
Golden-Shouldered *Psephotus chrysopterygius*	2	Female	6	Captivity	Endemic to Queensland in North-East Australia
		Male	5	Captivity	
Princess *Polytelis alexandre*	2	Female	~4	Unknown	Endemic to Australia. Confined to arid interior
		Male	~4	Unknown	
Scarlet-Chested *Neophema splendida*	3	Female	~1	Captivity	Endemic to arid mainland Australia. Arid inland zones
		Male	~1	Captivity	
		Male	~1	Captivity	
Australian King *Alisterus scapularis scapularis*	2	Female	>8	Captivity	Endemic to Eastern Australia. Found in forest and woodlands
		Male	~10	Unknown	
Bourkes *Neopsephotus bourkii*	7	Male	~4	Unknown	Endemic to inland Australia. Arid and semi-arid zones.
		Male	2	Captivity	
		Female	~4	Unknown	
		Male	~4	Unknown	
		Female	~4	Unknown	
		Female	~4	Unknown	
		Male	~4	Unknown	

Distribution information from review by Higgins (1999); all other data from ARKS records maintained by Melbourne Zoo. The ages of the birds were calculated for the year 2000.

Table 2.1: Details of the birds studied in the Melbourne Zoo parrot group

The enclosures were furnished and planted according to the natural habitat of the species kept in each. The golden-shouldered parrot enclosure (see Plate 2.1) had a sand substrate and was planted with grasses and a few shrubs typical of the arid areas of Australia. The enclosure shared by the princess and scarlet-chested parrots and that housing the Bourkes parrots were similar, with a sand substrate and the same types of plants. The king parrots are native to a more temperate area of Australia. Their enclosure (see Plate 2.2) had some areas of sand substrate, and others of wood-chip. It was planted with a mixture of large-leaved grasses, shrubs and bushes. All the enclosures had water pools, fixed branch perching and a shelf, 1 metre from the ground, on which feeding dishes were placed.

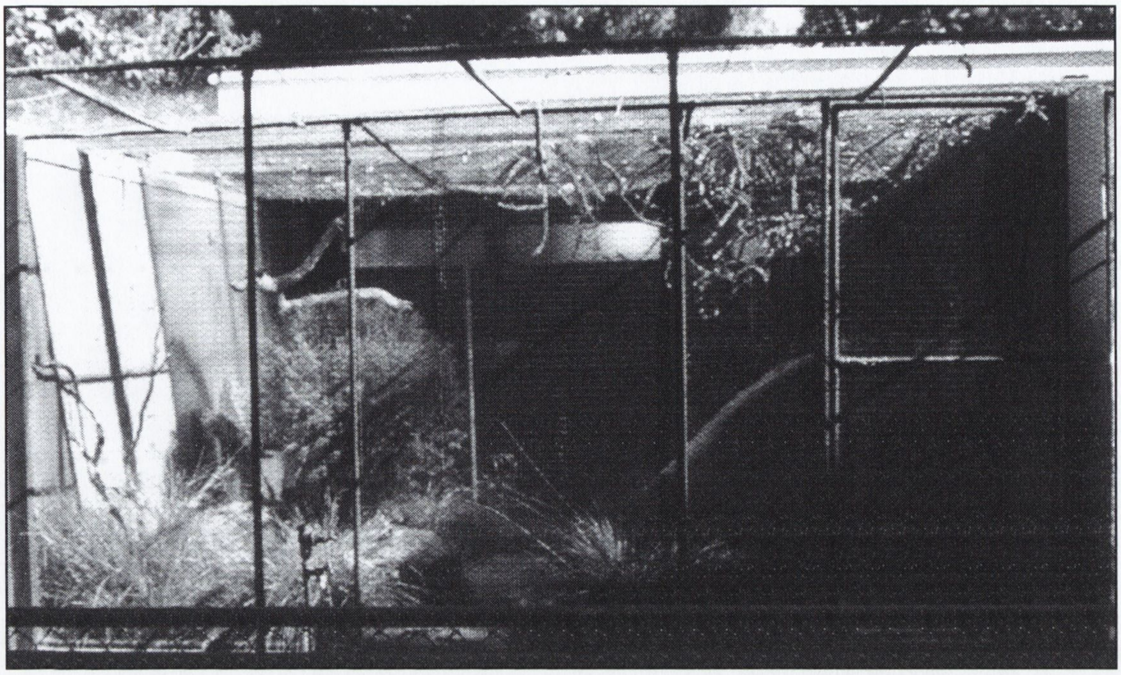


Plate 2.1: The golden-shouldered parrot enclosure at Melbourne Zoo

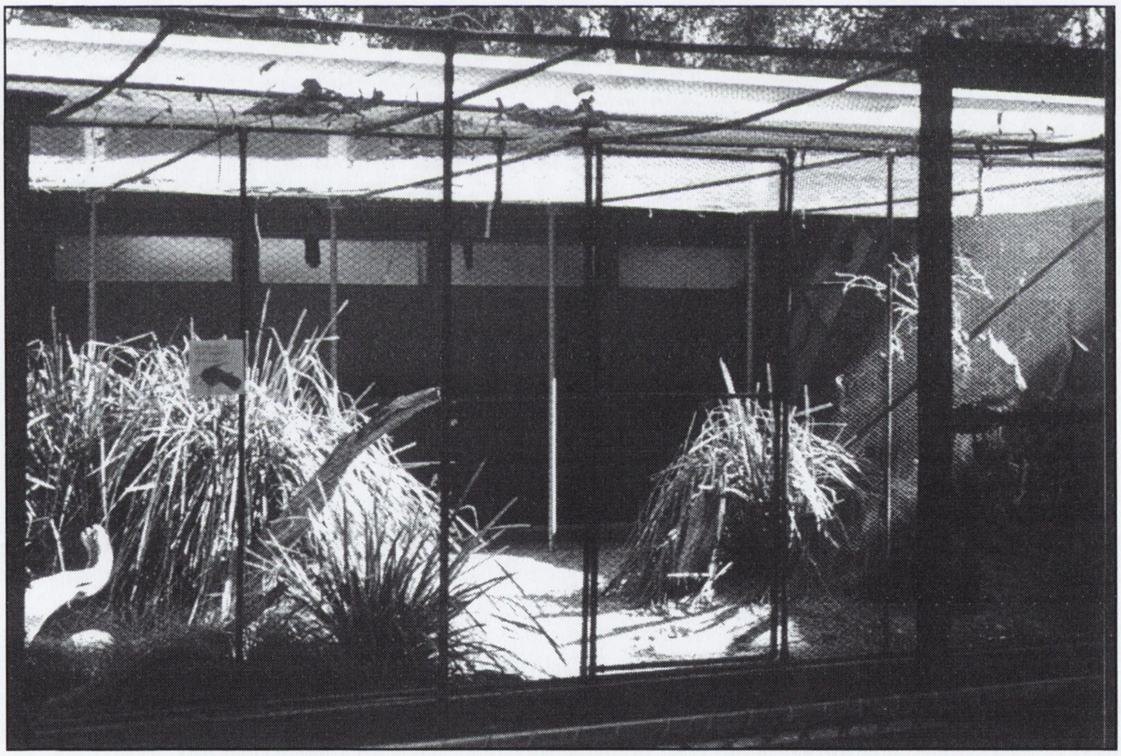


Plate 2.2: The king parrot enclosure at Melbourne Zoo

2.2.1.2 Melbourne Zoo Cockatoo Pair

The study group consisted of a pair of captive-bred Major Mitchell's cockatoos (*Cacatua leadbeateri*). Both birds were approximately 3 years old in the year 2000, and were housed in a well-planted enclosure next to the red lory pair (see section 2.2.1.4). The birds had visual and auditory contact with the red lories and with a pair of yellow-backed chattering lories, but not with any other captive cockatoo species. The aviary had areas of bark chip, sand and earth floor substrates and was furnished with a variety of logs and branches. It was planted with a grasses and plants from arid regions of Australia. Several branches of fresh eucalyptus browse were usually provided for the birds, and replaced once or twice a week, although browse was removed during baseline observations on the birds (Chapters 3 and 4). Food was provided in a feeder fixed to the wall, about 1.5m from the floor.

2.2.1.3 Melbourne Zoo Mixed Species Cockatoo Group

The study group consisted of 8 birds, 4 species, all native to Australia (see Table 2.2) which were housed in a large, mixed-species aviary at Melbourne Zoo (see Plate 2.3).

Cockatoo Species	Number of Birds	Gender	Age	Birth Location	Wild Distribution
Galah *Eolophus roseicapillus*	2	Female	~3	Unknown	Widespread throughout Australia. Populations, presumed feral, in New Zealand. Occur in a wide range of open habitats
		Female	~13	Wild	
Major Mitchells *Cacatua Leadbeateri*	2	Male	~3	Captivity	Endemic to Australia, mainly inland arid regions. Found in woodland, shrubland, grassland savanna and heathland
		Male	~3	Captivity	
Long-Billed Corella *Cacatua tenuirostris*	2	Female	~13	Wild	Endemic to Australia. Range restricted to extreme South-East. Found mainly in woodland and grassland
		Unknown	>14	Wild	
Greater Sulphur-Crested *Cacatua galerita*	2	Female	~15	Wild	North, East and South-East Australia. Also New Guinea and its associated islands. Usually found in or around timbered areas
		Male	~13	Wild	

Distribution information from review by Higgins (1999); all other data from ARKS records maintained by Melbourne Zoo. The ages of the birds were calculated for the year 2000.

Table 2.2: Details of the birds studied in the Melbourne Zoo mixed cockatoo group

The aviary had a deep layer of sand as a floor substrate and contained fixed horizontal metal perches, as well as being furnished with various logs and branches at different heights from the floor. The enclosure contained a water pool and a metal feeding trough at ground level. Large branches of fresh eucalyptus browse were usually provided weekly for the birds in water-filled containers, but these were removed during the baseline observations carried out for the experiments outlined in Chapters 3 & 4.

Plate 2.3: The Melbourne Zoo mixed cockatoo aviary

2.2.1.4 Melbourne Zoo Lory Group

The study group consisted of 4 birds of 2 species (see Table 2.3). The species were in visual and auditory contact with each other as well as with the pair of Major Mitchell's cockatoos which were housed adjacent to the red lories.

Lory Species	Number of Birds	Gender	Age	Birth Location	Wild Distribution
Red *Eos bornea*	2	Female	>4	Captivity	Islands of Amboina, Saparua, Buru, Ceram, Goram, Ceramlaut, Watubela & Kai Islands, Indonesia.
		Male	>4	Captivity	
Yellow-Backed Chattering *Lorius garrulus flavopalliatus*	2	Female	>4	Captivity	Northern Moluccan Islands, Indonesia.
		Male	>4	Captivity	

Distribution information from review by Forshaw (1989); all other data from ARKS records maintained by Melbourne Zoo. Ages were calculated for the year 2000.

Table 2.3: Details of the birds studied in the Melbourne Zoo lory group

The enclosures had wood chip as their flooring substrate, were furnished with a variety of fixed branch perches and were well planted with a variety of Australian plants and shrubs (e.g. see Plate 2.4). Each aviary contained two rocket feeders, one for the birds' nectar dish and one for their dish of seed and fruit.

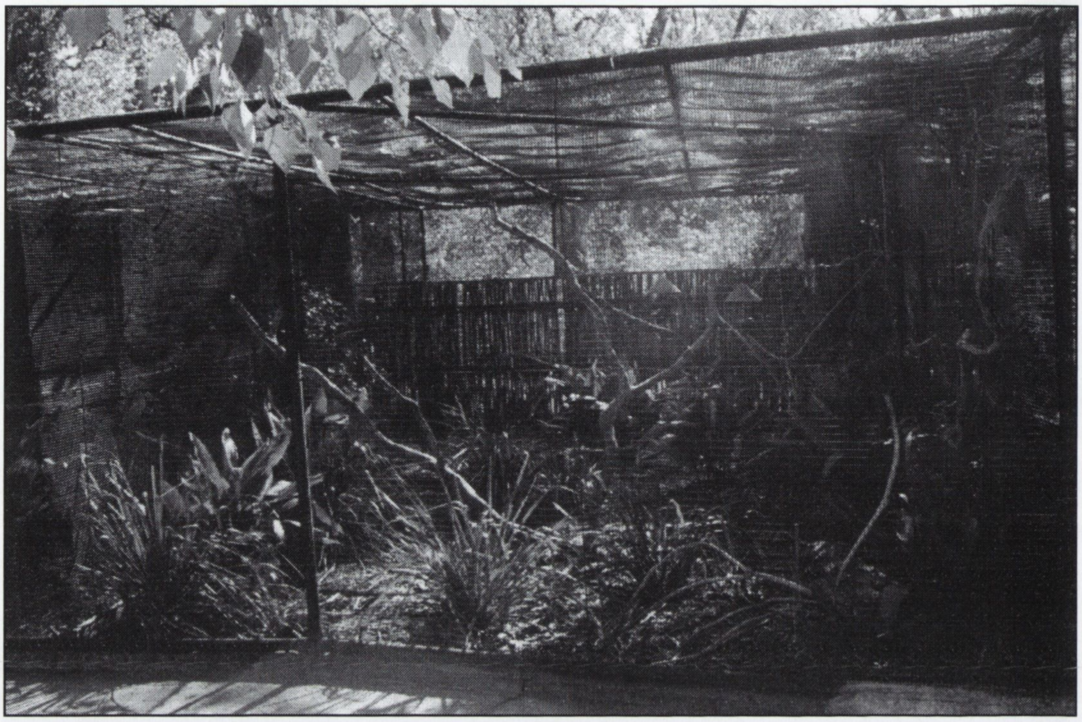


Plate 2.4: The yellow-backed chattering lory enclosure at Melbourne Zoo

2.2.1.5 Royal Park Wild Lory Group

A group of about 20 rainbow lories (*Trichoglossus haematodus*) a native species, was released from Melbourne Zoo into the surrounding Royal Park in the mid 1990s, and those birds bred to form the nucleus of the population of more than 200 individuals observed in the study. Ever since the original releases, supplementary food had been provided for the birds daily in the form of an artificial nectar mix which was supplied in three rocket feeders placed within the grounds of the zoo (see Plate 2.5).

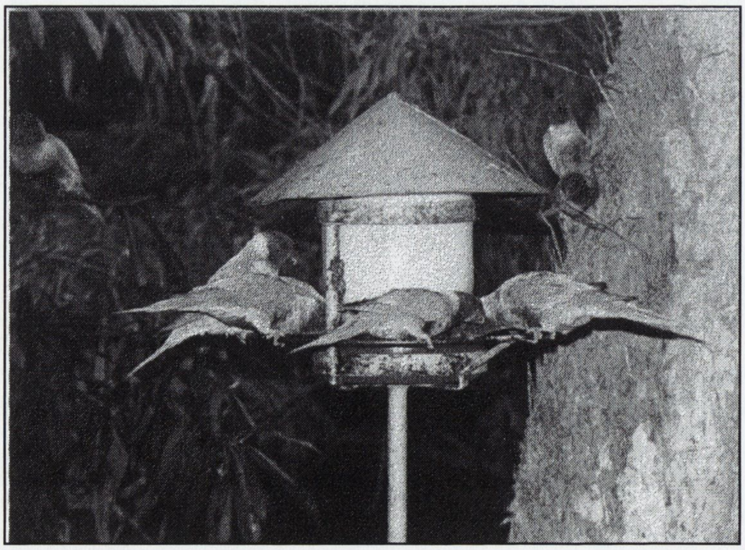


Plate 2.5: Wild rainbow lories feeding on artificial nectar mix from a rocket feeder at Melbourne Zoo

2.2.1.6 Melbourne Zoo Psittacine Group

The study group consisted of 8 species of psittacines, kept in 7 aviaries at Melbourne Zoo (see Table 2.4).

Species	Number of Birds	Gender	Age (Years)	Birth Location	Wild Distribution
Golden-Shouldered Parrot *Psephotus chrysopterygius*	2	Female	6	Captivity	Endemic to Queensland – North-East Australia
		Male	7	Captivity	
Major Mitchells Cockatoo *Cacatua Leadbeateri*	2	Female	~3	Captivity	Endemic to Australia, mainly inland arid regions. Found in woodland, shrubland, grassland and savanna
		Male	~3	Captivity	
Australian King Parrot *Alisterus scapularis scapularis*	2	Female	>8	Captivity	Endemic to Eastern Australia. Found in forest and woodlands
		Male	~2	Unknown	
Galah *Eolophus roseicapillus*	2	Female	~13	Wild	Widespread throughout Australia. Populations, presumed feral, in New Zealand. Occur in a wide range of open habitats
		Female	~4	Unknown	
Red-Tailed Black Cockatoo *Calyptorhynchus magnificus samueli*	2	Female	7	Captivity	Endemic to inland Australia. Found in forest, woodland, shrubland & savanna
		Male	5	Captivity	
Plum-Headed Parakeet *Psittacula cyanocephala*	2	Female	1	Captivity	Found in Sri Lanka, Rameswaram Island and the Indian Peninsula in wooded areas
		Male	~4	Captivity	
Monk Parakeet *Myiopsitta monachus*	6	Female	~2	Captivity	Found from central Bolivia & Brazil, south to central Argentina. Introduced to Puerto Rico; Some feral populations in the USA & Europe
		Male	~2	Captivity	
		Unknown	~2	Captivity	
		Unknown	~2	Captivity	
		Unknown	~2	Captivity	
		Unknown	~2	Captivity	
Conclurry Ringneck Parrot *Barnardius barnardi macgillivrayi*	4	Female	6	Captivity	Endemic to Australia and distributed through much of the country. Found in lightly timbered areas.
		Unknown	~1	Captivity	
		Unknown	~1	Captivity	
		Unknown	~1	Captivity	

Distribution information from reviews by Higgins (1999) and Forshaw (1989); all other data from ARKS records maintained by Melbourne Zoo. Ages calculated for the year 2000.

Table 2.4: Details of the birds studied in the Melbourne Zoo psittacine group

Some of the birds in this group were also studied in other experiments; these were: The female golden-shouldered parrot, one pair of Major Mitchells' cockatoos, the female

Australian king parrot and two galahs. The rest of the birds in the group were not used in any other experiments. All the species studied are native to Australia, with the exception of the plum-headed parakeets from Asia and the monk parakeets which are native to South America.

Each species was kept in a separate enclosure, except for the galahs and black cockatoos, which shared an aviary. Those cockatoos, the golden-shouldered parrots and the Conclurry ringneck parrots were housed in enclosures with a sand substrate and a variety of fixed perches. The other species were all housed in aviaries with a wood-chip substrate (except for the Major Mitchells cockatoos' enclosure, which had a floor of packed earth) planted with a variety of Australian plants and shrubs, and provided with a selection of fixed branch perches, much like the lory aviary shown in Plate 2.4. The feeding trays used were free-standing in all aviaries except for that of the Major Mitchells cockatoos, which was fixed to their enclosure wall about 1.5m from the ground. The free-standing feeders were about 1 metre tall, apart from one of the two in the galah and black cockatoo enclosure, which was only about 0.5 metres in height.

2.2.2 Healesville Sanctuary

One group of birds was studied in the Healesville Sanctuary, Victoria, Australia. Healesville is a zoo situated in the South-East of Australia (approximately 37.7° S, 145.5 ° E). The average yearly rainfall in the area is 1020 mm and the mean annual temperature 19.2 °C (data from the Australian Bureau of Meteorology).

2.2.2.1 Healesville Sanctuary Orange-Bellied Parrot Group

The Healesville Sanctuary is one of only two facilities which are currently engaged in captive breeding programmes for orange-bellied parrots (*Neophema chrysogaster*). 68 birds were released into the wild from the captive breeding programme between 1991 and 1999. The species, which is endemic to south-east Australia, is listed as Critically Endangered in the IUCN Red List Categories of Threat (1996) and is strictly protected under CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) as well as a variety of Australian legislation. The wild population is estimated to number about 200 birds, and they breed in a very restricted coastal range (Smales *et al.*, 2000). The stated aims of the captive breeding programme are to establish a captive population in case of catastrophic decline of the wild population; to augment the wild population through reintroductions and to provide opportunities for research and public education (Orange-bellied Parrot recovery Team, 1998).

At the Healesville Sanctuary most of the orange-bellied parrots were housed in off-limit facilities, away from areas open to the public, and dedicated to endangered species breeding programmes. The study group was observed in one such area.

Experimental Group	Number of Birds	Gender	Age (years)	Birth Location
A	8	Female	<1	Captivity
		Female	1	Captivity
		Female	4	Captivity
		Female	~6	Captivity
		Male	7	Captivity
		Male	1	Captivity
		Male	4	Captivity
		Male	4	Captivity
B	8	Female	~2	Captivity
		Female	1	Captivity
		Female	1	Captivity
		Female	4	Captivity
		Male	2	Captivity
		Male	2	Captivity
		Male	2	Captivity
		Male	4	Captivity
C	6	Female	~5	Wild
		Female	1	Captivity
		Female	3	Captivity
		Male	~5	Captivity
		Male	<1	Captivity
		Male	10	Unknown
D	6	Female	<1	Captivity
		Female	1	Captivity
		Female	~5	Captivity
		Male	1	Captivity
		Male	1	Captivity
		Male	~5	Unknown

Data from ARKS records maintained by Healesville Sanctuary. Ages were calculated for the year in which the birds were observed (2001).

Table 2.5: Details of the birds studied in the Healesville Sanctuary Orange-Bellied Parrot group

The 30 birds used in the study (see Table 2.5) were housed in pairs (one male and one female) in aviaries measuring 4.0m x 1.2m x 3 m high. The enclosures had sand as a floor substrate, with fixed perches, dry eucalyptus browse and nestboxes provided, but no other enrichment. The feeding platform in each enclosure was 1 metre high. Birds in some enclosures could see parts of their conspecifics' aviaries and all the birds were in auditory contact with the rest of the group.

2.2.3 Dublin Zoo

One group of birds was studied in Dublin Zoo, Ireland. Dublin is situated on the east coast of Ireland (approximately 53° N, 6° W) and experiences a mild temperate climate. The average yearly rainfall in the area is 733 mm and the mean annual temperature 9.6° C (data from Met Éireann, the Irish Meteorological Service).

2.2.3.1 Dublin Zoo Psittacine Group

The study group at Dublin Zoo consisted one pair of orange-winged amazon parrots, one pair of yellow-backed chattering lories, and one pair of citroen-crested cockatoos, all kept in separate enclosures. Two Moluccan cockatoos were housed in separate enclosures and there was a mixed species group in the sixth enclosure consisting of a pair of military macaws, and five blue-crowned conures (see Table 2.6).

All the birds were kept in outdoor enclosures with 24 hour access to heated indoor enclosures. They were in partial visual and auditory contact with the other psittacines in the group. The outdoor aviaries had a deep wood-chip substrate, a variety of fixed branch perches, and were of a variety of shapes and sizes. The indoor enclosures, connected to the outdoor areas by holes approximately 12 cm wide x 17cm high, ranged from 1m x 1m x 1m to 1.5m x 1m x 2m in size and their floors were covered with a layer of wood-chip. Feeding dishes were placed on the floors of the indoor enclosures, which were also provided with one or two fixed wooden perches and artificial light from 16.00-19.00 daily.

Species	Gender	Age (years)	Birth Location	Wild Distribution
Orange-Winged Amazon Parrot *Amazona amazonica*	Female	~5	Captivity	Columbia, Venezuela & the Guianas south to eastern Peru & southern Brazil. Also Trinidad & Tobago
	Male	~5	Captivity	
Blue-Crowned Conure *Aratinga acuticaudata*	Female	~10	Unknown	North-East Columbia & northern Venezuela, north-eastern Brazil & south-western Brazil to Paraguay, western Uruguay & northern Argentina. Found in woodland and shrubland
	Male	~10	Unknown	
	Unknown	2	Captivity	
	Unknown	2	Captivity	
	Unknown	2	Captivity	
Military Macaw *Ara militaris mexicana*	Female	4	Captivity	Mexico in specific areas. May occur in westernmost Guatemala. Found in wooded areas; may feed on plains
	Male	4	Captivity	
Moluccan Cockatoo *Cacatua moluccensis*	Male 1	11	Unknown	Central & northern Moluccas, Indonesia. Found in forested areas
	Male 2	~8	Unknown	
	Female	~7	Captivity	
Citroen-Crested Cockatoo *Cacatua sulphurea citrinocrista*	Female	~11	Unknown	Sunda in the Lesser Sunda Islands, Indonesia. Found in forested areas
	Male	~4	Captivity	
Yellow-Backed Chattering Lory *Lorius garrulus flavopalliatus*	Female	2	Captivity	Northern Moluccan Islands, Indonesia
	Male	3	Captivity	

Distribution information from reviews by Higgins (1999) and Forshaw (1989); all other data from ARKS records maintained by Dublin Zoo. Ages calculated for the year 2000.

Table 2.6: Details of the birds studied in the Dublin Zoo psittacine group

2.3 Materials

2.3.1 Enrichments

A variety of enrichment devices were used during the experiments and they are listed in alphabetical order and described in full in this section. The enrichments were designed to provide suitable edible components for the species being enriched, and also to encourage wild type foraging behaviours. Table 2.7 indicates the foodstuffs incorporated in each enrichment device and the behaviours it was designed to elicit.

Enrichment Device	Edible Components	Foraging Behaviours Encouraged	Suitable For which Psittacines
Banksia	flowers; nectar; pollen	fine manipulation using beak, tongue & feet	large ground-feeding cockatoos
Browse	leaves; leaf buds; sap	maintenance of balance whilst manipulating browse using tongue & beak	all birds except strict seed eaters
Corn Cob	fresh maize seeds	maintenance of balance whilst extracting & manipulating maize seeds using beak, feet & tongue	acrobatic birds eg lories
Flower Rope	flowers; nectar; pollen; leaf buds	maintenance of balance & fine manipulation of blossom using beak & tongue	lories & other nectar feeders
Forage Tray	dry seed mix &/or nuts in their shells	digging & scratching using feet & beak; manipulation of husks & shells using beak, tongue & feet	cockatoos & seed eaters which will feed at ground level
Fruit Branch	variety of fruits, corn cob pieces, green leaves & vegetables	maintenance of balance despite constant shifts whilst tearing away pieces of food, followed by manipulation using feet, tongue & beak	smaller fruit eating birds
Fruit Kebab	variety of fruits, corn cob pieces, green leaves & vegetables	climbing behaviours &/or tearing away pieces of food, followed by manipulation using feet, tongue & beak	any fruit eaters; best for climbers like lories
Millet Sprays	millet seed	fine manipulation of stem & seeds using feet, beak & tongue	small seed eaters
Seed Block	dry seed mix	maintenance of balance whilst manipulating seeds using feet, beak & tongue	all seed eaters except those who aren't acrobatic
Seeded Branch	dry seed mix	maintenance of balance despite constant shifts, whilst tearing off seeds followed by manipulation using feet, tongue & beak	all seed eaters especially acrobatic ones
Seeded Cone	dry seed mix	maintenance of balance whilst tearing off seeds, followed by manipulation using feet, tongue & beak	all seed eaters especially acrobatic ones
Seedpods	native seeds	breaking open & manipulation of seeds & pods using feet, beak & tongue	large native birds

Sprouted Seed Tray	sprouted seeds	pulling up of seeds using beak followed by manipulation of seeds & shoots using feet, beak & tongue	ground feeders which eat green shoots
Spiked Fruit & Vegetables	variety of fruit, vegetables and corn cob pieces	climbing behaviours to reach foods; maintenance of balance whilst tearing away pieces of food, followed by manipulation using feet, tongue & beak	all fruit eaters, especially larger birds
Stuffed Wood Block	dry seed mix and dried sultanas, cherries & raisins	maintenance of balance whilst obtaining seeds & fruit, followed by manipulation of food using feet, tongue & beak. Larger birds, particularly cockatoos, also tear apart the wood to get greater access to food & use it for beak maintenance behaviours	all birds, especially lories & large cockatoos and macaws

Table 2.7: Details and purpose of the environmental enrichment devices used in the study

2.3.1.1 Banksia (Plate 2.5)

Flowers were cut from *Banksia* trees (a genus of native Australian plants) with stem and twigs attached. The flower stems were then pushed 10 – 15 cm into the floor substrate of the enclosure.

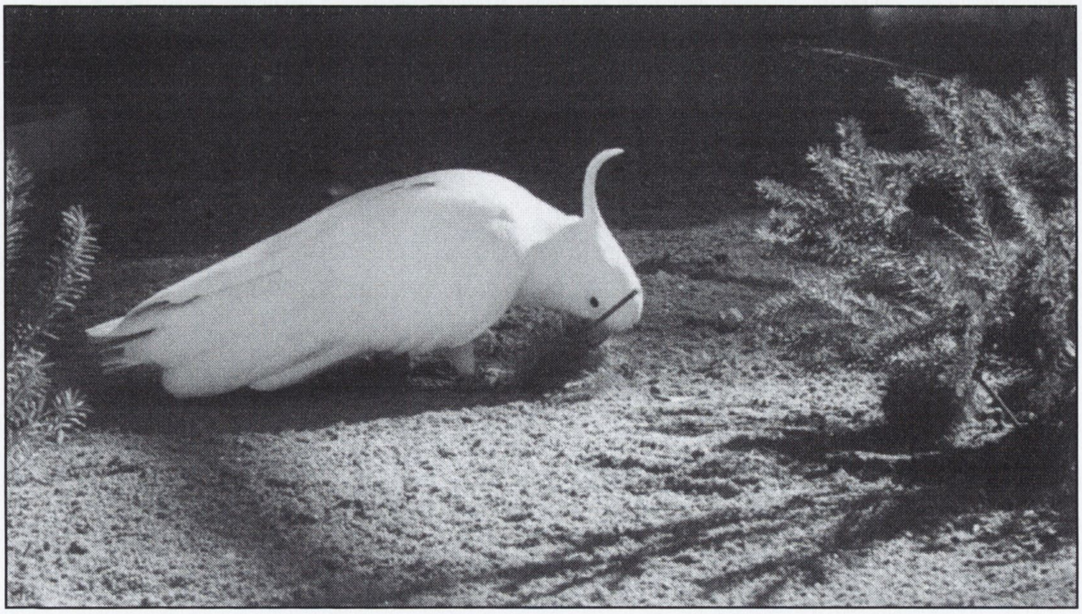


Plate 2.5: Greater sulphur-crested cockatoo manipulating a *Banksia* flower

2.3.1.2 Browse (Plates 2.6 and 2.20)

Branches of freshly-cut eucalyptus (*Eucalyptus* spp.) of different sizes (depending on the dimensions of the aviary) were tied to the sides of enclosures, or wedged upright between other trees and perches. The mixed cockatoo aviary was the only enclosure provided with water-filled containers for the browse, so the branches had to be changed more frequently in the other aviaries in order to keep a constant supply of fresh leaves available.

2.3.1.3 Corn Cob (Plate 2.7)

A whole cob of corn, complete with husk, except for the removal of one strip to expose the maize kernels, was pushed lengthways onto a metal skewer. The point of the skewer had been flattened, and blunted somewhat, and a hole had been drilled through the flattened tip. Once the cob had been pushed down the skewer, to rest on the looped end, the whole device was suspended from the roof or side netting of the aviary by a wire passed through the drilled hole.

Plate 2.6: Yellow-backed chattering lory chewing on the bark of a branch of eucalyptus browse

2.3.1.4 Flower Rope (Plate 2.8)

A length of about 1 metre was cut from a new coil of hessian rope. One end of a doubled piece of wire about 40 cm long was plaited in with the main cords of one end of the rope, then unravelled rope from the coil was used to bind both ends. The protruding wires were bent into a hook so that the rope could be hung from the mesh ceiling or wall of an enclosure. Flowers were picked daily from in and around the zoo (in areas free from pesticides). The main types used were sprays of blossom from native eucalyptus, acacia and *Callistemon* trees, as well as *Banksia* flowers, but other assorted blooms growing in the area were also used in small quantities. The stems of the flowers were pushed between the strands of the rope to hold them firmly in place and the protruding woody stems of the tree blossom and *Banksia* also provided horizontal perches for birds investigating the rope.

Plate 2.7: Red Lory pecking at a corn cob

2.3.1.5: Forage Tray

There were two different types of forage tray used in this study. For larger parrots and cockatoos a tough plastic storage tray had holes burnt into its floor, to prevent the accumulation of moisture, then it was filled half full with pieces of wood-chip (Plate 2.9). Dry seed mix and nuts in their shells were stirred into the substrate so that the birds had to peck and dig to find the food. The dry seed mix used was that fed to the birds in their normal daily diet. For smaller parrots the forage trays were made out of the large plastic ‘saucers’ used to stand flower pots in. Small holes were put in the floor of the tray, then it was filled with sand, and dry seed mix was stirred into the substrate (Plate 2.10).

Plate 2.8: Yellow-backed chattering lories feeding from eucalyptus and acacia blossoms above a *Banksia* bloom on a flower rope (most of the flowers provided had already been pulled out and shredded by the birds)

Plate 2.9: Major Mitchells cockatoo looking for nuts and seed in a forage tray filled with wood-chip

Plate 2.10: Princess parrots foraging for seed in a forage tray filled with sand. Scarlet-chested parrots can also be seen approaching the tray

2.3.1.6 Fruit Branch (Plate 2.11)

A branch of eucalyptus or *Hakia* wood about 50 –70 cm long was trimmed and a hole drilled through the centre of it. A rope was then threaded through the hole. For birds with stronger beaks, such as the king parrots, the rope was plaited with wire, for smaller parrots the hessian rope alone was used to suspend the branch horizontally from the enclosure roof.

Bullet-headed nails about 12 cm long were hammered part of the way into the branch at an upward-pointing angle, and whole fruit and vegetables, or large pieces thereof, were pushed onto them. The branch pivoted about the axis of the rope and moved considerably when a bird landed on it or took off from it. In addition, as food was eaten from the device, its balance and stability was altered. This meant that the birds not only had to tear apart and process the food provided on the enrichment before eating it, they had to use both wing and leg muscles in order to balance whilst doing so.

It is worth noting here that the majority of psittacines tend to hold their food in one foot, and bring that foot up to their beak in order to take bites of the food (see Forshaw, 1989). This means that food has to be cut up into pieces small enough to be held by the foot before the bird actually ingests any. Whereas food tends to be pre-chopped into suitably sized pieces for captive birds, providing them with larger pieces means that they have to do the 'chopping' and pulling apart themselves, using beak and feet.

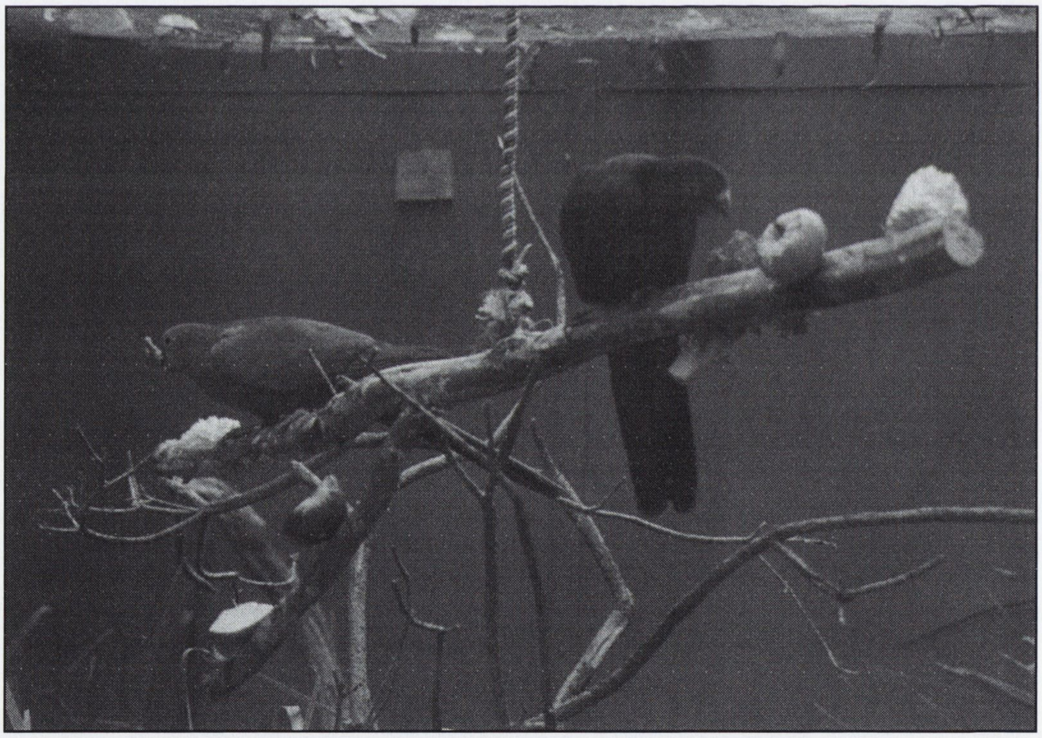


Plate 2.11: Australian King Parrots feeding from fruit and vegetable pieces on a fruit branch

2.3.1.7 Fruit Kebab (Plate 2.12)

Pieces of fruit and vegetables were threaded onto a piece of wire about 30cm long. The ends of the wire were bent over, allowing the kebab to be attached to the wire mesh walls of the aviary. For less agile birds the kebab was positioned above a perch to make access to it easier (see Plate 2.12).

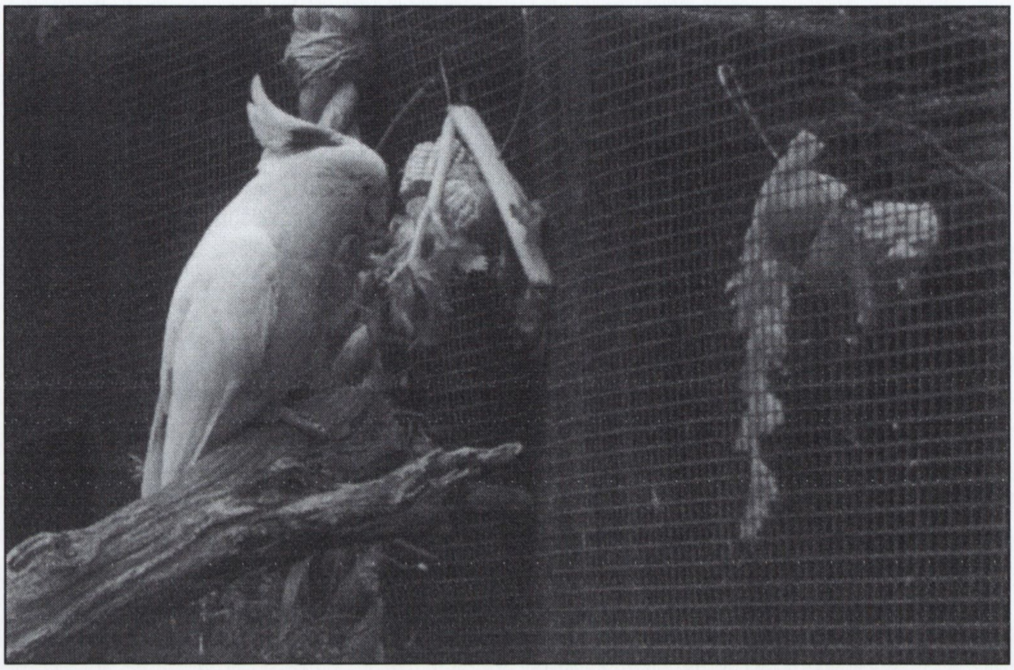


Plate 2.12: Major Mitchells cockatoo feeding from a fruit kebab. The kebab in the neighbouring red lory enclosure can also be seen.

2.3.1.8 Millet Sprays

Sprays of *Panicum* millet that had their stems left on were bought from pet shops or aviculture suppliers. These were presented to the parrots that usually received millet seeds in their food dishes, in three different ways. They could be attached, using wire or plastic ties, to objects in the enclosure (such as the wire basket shown in Plate 2.13), they could be stuck into holes drilled in planks of wood which were placed on the floor of the aviary (see Chapter 8) or their stems could be stuck into cracks in various perches in the birds' aviaries (see Plate 2.14). In all three situations, the birds had to manipulate the sprays to obtain the millet seeds, which then had to be de-husked before being ingested.

2.3.1.9 Seed Block (Plate 2.15)

Blocks of seed, moulded to various shapes can be purchased from most places selling pet supplies. They consist of a mass of dry seed (usually a mix of millet, sunflower seed, sorghum, canary seed and hemp) stuck together with an edible adhesive, with a wire hook fixed through the centre. The blocks were suspended from branches in the psittacine aviaries.

Plate 2.13: Blue-crowned conures feeding from millet sprays tied to the frame of a wire basket in their enclosure

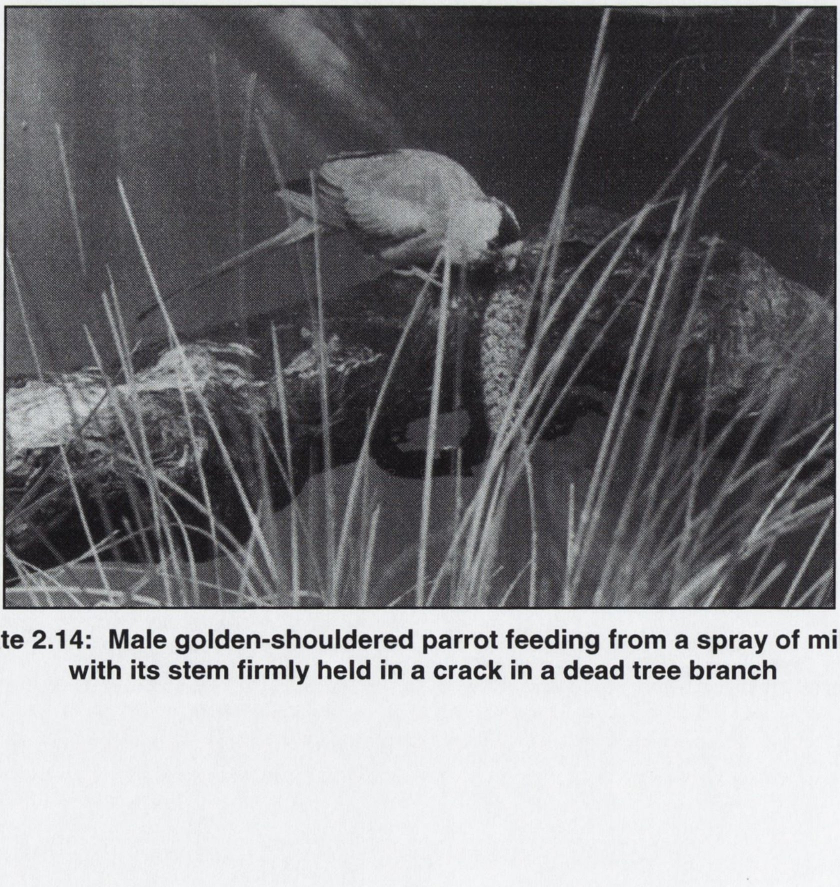


Plate 2.14: Male golden-shouldered parrot feeding from a spray of millet with its stem firmly held in a crack in a dead tree branch

Plate 2.15: Major Mitchells Cockatoo feeding from a seed block

2.3.1.10 Seeded Branch (Plate 2.16)

The seeded branch was constructed in the same way as the fruit branch (see section 2.2.1.5) but no nails were used. Instead, the branch was covered with a layer of water soluble PVA (poly-vinyl acetate) adhesive, and then coated with dry seed mix. The seed mix used was the same as that fed to the birds in their usual daily diet.

A seeded log was made for use in the mixed cockatoo enclosure by painting PVA onto part of a log resting on the floor of an enclosure, then coating the glue with seed.

2.3.1.11 Seeded Cone (Plate 2.17)

Large open pinecones were collected and an eye screw was fixed into the top of each. From that, the cone could be suspended from a perch using wire or plastic ties. The cones were covered with PVA and coated with dry seed mix in the same way as the seeded branch (section 2.3.1.10). To make a stuffed cone, dried fruit (sultanas, raisins and cherries) were pushed deep into the spaces between the scales of the cone, prior to the outside of the cone being coated with PVA and seed.

Plate 2.16: Golden-shouldered parrots feeding from a seeded branch

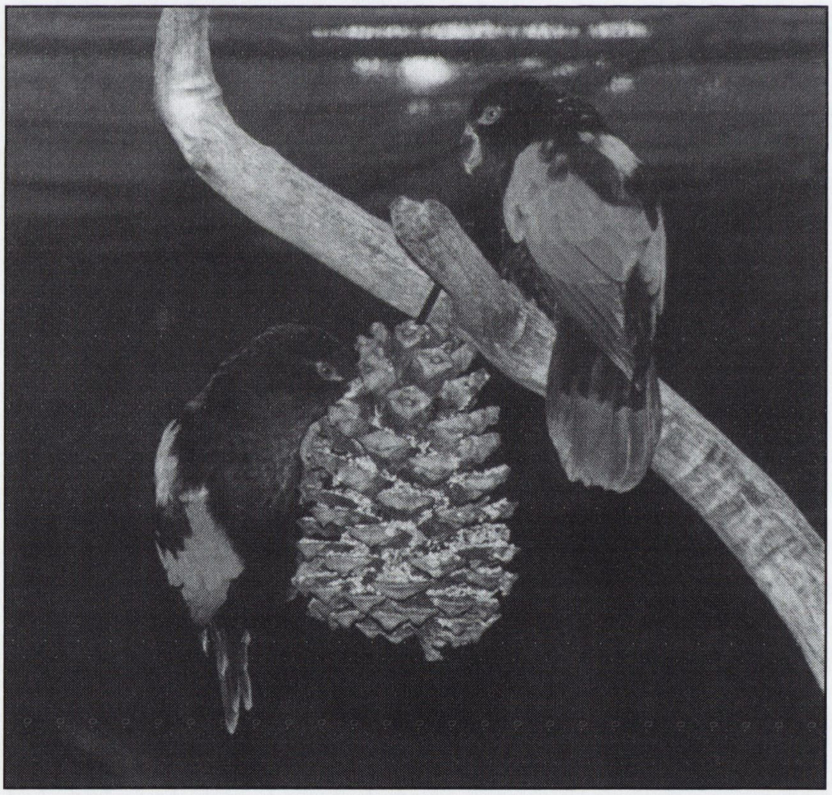


Plate 2.17: Yellow-backed chattering lories feeding from a stuffed seeded cone

2.3.1.12 Seedpods (Plate 2.18)

Ripe cones and seedpods were collected from various native species of eucalyptus, *Banksia* and *Hakia* trees and scattered on the floor of an enclosure. The species chosen were those that psittacines had been seen to feed from in the wild, according to personal observations and records taken from a review by Higgins (1999).

Plate 2.18: A pile of the native cones and seedpods used for enrichment in the mixed cockatoo enclosure

2.3.1.13 Sprouted Seed Tray (Plate 2.19)

Dry seed mix was sown in a plastic seedling tray filled with earth and sand. The seed shoots were grown to a height of about 8 cm before being moved into the enclosures. For the smaller birds, the whole tray was placed on the floor of the aviary, for larger ones that could chew the plastic of the tray, the earth and seedlings were lifted out of it and placed on the aviary floor like a turf of grass.

2.3.1.14 Spiked Fruit and Vegetables (Plates 2.20, 2.21 and 2.22)

A variety of whole fruit and vegetables, or large pieces thereof, were pushed onto 12cm bullet-headed nails which had been hammered part way into branches and logs, positioned at various heights in an enclosure. In some aviaries the food items could also be pushed onto the twigs of branches furnishing the enclosure. As the fruit and vegetables were pecked and shredded by the birds, pieces fell to the ground, thereby providing scattered 'floor food' for the birds to forage for.

Plate 2.19: Scarlet-chested parrots foraging from a sprouted seed tray

Plate 2.20: Major Mitchells cockatoos feeding from fruit and vegetables spiked on nails on a high perch. Food can also be seen spiked on twigs on the left of the picture and branches of fresh browse are visible on the right.

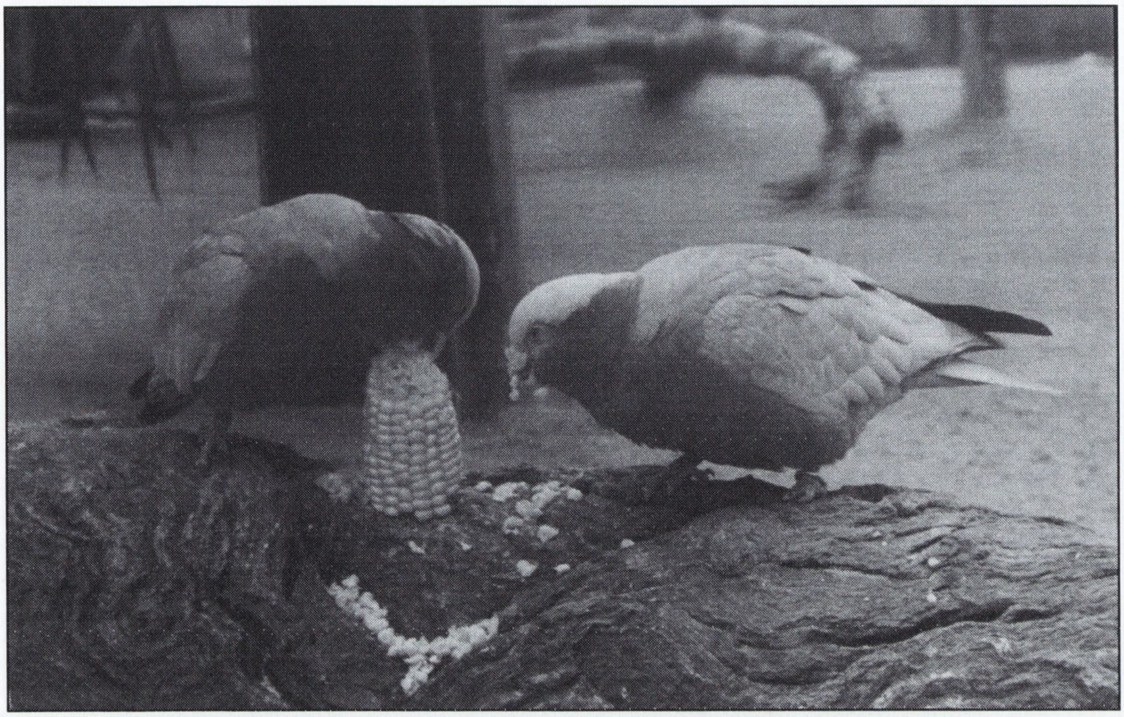


Plate 2.21: Galahs feeding from corn on the cob spiked on a nail

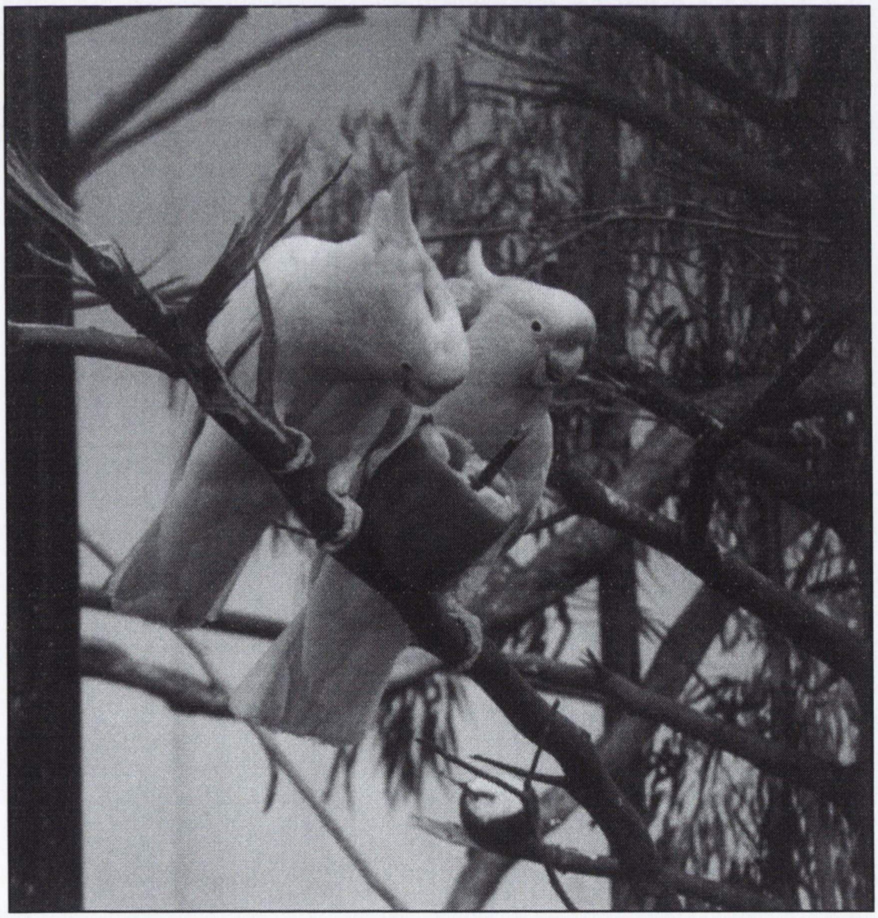


Plate 2.22: Major Mitchells cockatoos investigating a green capsicum pepper spiked on the twig of a fixed branch perch

2.3.1.15 Stuffed Wood Block (Plate 2.23)

The wood block enrichment consisted of a piece of eucalyptus log split with an axe, and then drilled with holes of various sizes. Some holes were drilled right through the block of wood, while others went in only a centimetre or two. An eye screw was attached to the block so that it could be suspended by wire or a plastic tie from a perch, and the holes were packed with a mixture of dried fruit (sultanas, raisins and cherries) and dry seed mix.

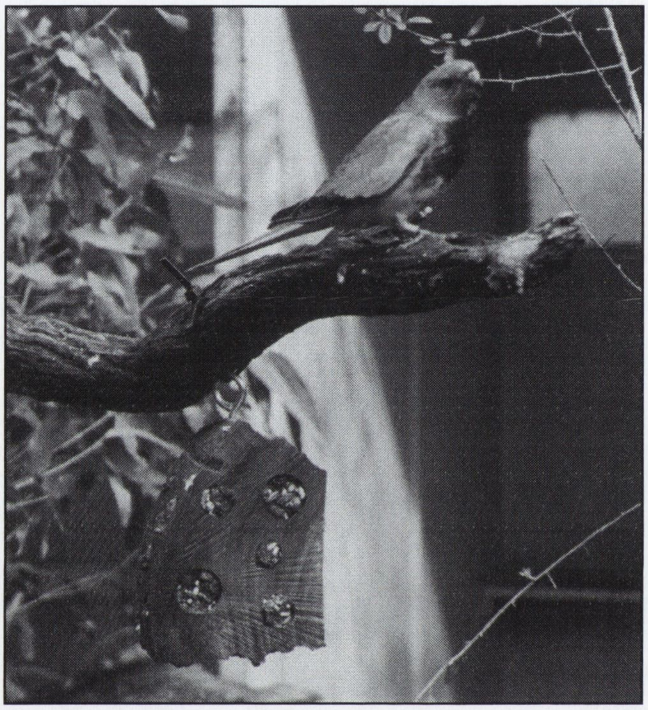


Plate 2.23: Stuffed wood block and a male scarlet-chested parrot

2.3.2 Measuring Equipment

Four climatic variables were recorded every hour in the vicinity of the experimental aviaries throughout the study. These parameters were selected for investigation because they have all been found to effect mammalian or avian behaviour in other studies (eg Bockisch *et al.,* 1999; Shinura *et al.,* 2006; Hayes & Huntly, 2005; Dabbert & Martin, 1994). Ambient temperature in the shade was measured using a Diplex Thermochip 900 electronic thermometer. Recordings were accurate to 0.1°C. The relative strength of wind speed was measured using a hand-held Negretti and Zambra low speed anemometer. The number of rotations per 5 second period were recorded, accurate to the nearest rotation. Relative humidity was measured using a Grant Squirrel Meter which gave recordings accurate to the nearest 0.5%. Light intensity was measured using a digital Lux Hi Tester which had a range of 0-20000 lux. Recordings of light intensity were accurate to the nearest 0.5 lux. In the experiments where food was weighed, mass was measured using Salter electronic scales, model 323, which had a range of 0-5kg. Recordings were accurate to the nearest 0.5g.

For each experiment that was carried out, the climatic parameters were compared for the baseline and enriched environments. Any significant difference between the two could mean that the birds' behaviour was differentially affected in the experiments and effects of enrichment could be confused with the effects of weather conditions. In the majority of experiments there was no significant difference between the mean climatic conditions during the baseline observations and those taken when the enclosures were enriched, or between those taken during different enrichment regimes. Where significant differences did occur the details are discussed in the relevant chapter. Observations were not taken on days where heavy rain fell for more than 1 hour, as heavy, continuous rain has been shown to affect the behaviour of wild psittacines. In particular it can cause them to alter their daily patterns of behaviour (Noske, 1980).

2.4 Statistical Analysis

2.4.1 Zoo Research

Zoo-based research has to deal with a number of methodological challenges resulting from the nature of the zoo environment. These typically include the availability of only a small number of any one species, and the fact that the researcher rarely has control over variables such as group sizes, gender or age mixes and enclosure size, location and structure. Animals are primarily housed with regard to their welfare, natural social grouping and efficacy of display rather than the ease with which robust research can be carried out on them. This leads to problems with accurately studying the animals' behaviour and response to different conditions and stimuli, since inferential statistics techniques were not designed to analyse data sets where assumptions of independence and random sampling could not be met (Kuhar, 2006). Lack of independence of data points can lead to pseudoreplication and, therefore, inaccurate P-values and an increased risk of type I errors. Nevertheless, inferential statistics are frequently used in the published literature despite the fact that the data to be analysed does not fulfil the assumptions attendant on their use. They are sometimes used through miscomprehension of statistical tests, their application and limitations. Sometimes, particularly in zoo-based research, they are used because there is no other, more statistically valid way, to analyse a particular data set and the researcher faces a choice between running a flawed statistic to appease an editor or reviewer and allowing information that is valuable to the zoo community to remain unpublished (Kuhar, 2006).

Some sciences which are prone to the problems associated with a lack of independence, such as ethology and ecology, have examined whether statistical analysis was being correctly used in their field and, in particular, how widespread pseudoreplication was in the published literature (e.g. Machlis et al 1985; Johnson 1999) but it is only recently that zoo biologists have begun to do the same (e.g. Kuhar, 2006; Plowman, 2006). A review of articles published in Zoo Biology between 1999 and 2004 showed that 146 articles used inferential statistical analysis, of which approximately 40% showed evidence of pseudoreplication (Kuhar, 2006).

If zoo research is to move forwards, it is essential that guidelines are agreed for tackling the evident statistical challenges involved. The British and Irish Association of Zoos and Aquariums (BIAZA) has recently made progress in this regard by putting together a group of zoo researchers, statisticians and ethologists to develop just such guidelines (Plowman, 2006) which, it is hoped, will also be adopted by the North American zoo community. These guidelines are needed to advise researchers on how best to deal with the statistical and methodological challenges encountered in zoo research. Previously, the advice available was varied and often conflicting. For example, as a graduate student Christopher Kuhar discussed these issues with numerous statisticians, only to receive just as many different answers in reply. As he puts it: "Within the field of zoo biology there are no guidelines as to what is acceptable, which rules are okay to bend and when you may bend them without going to statistics jail… It is not uncommon to have one set of reviewers allow a certain statistical technique, but then have another set who refuse to permit such analyses to be used" (Kuhar, 2006).

A scrutiny of the published research in zoo biology and the methods of analysis used would certainly confuse anybody trying to ascertain which rules were 'okay to bend'. Some authors justify a degree of pseudoreplication and lack of independence in their data sets by arguing that their findings apply only to their study group, and not necessarily the wider population of the species under examination (eg Patton et al, 2001). Others have protested against the strict adherence to an arbitrary significance level (typically P=0.05) that is used as an absolute criterion for determining if an effect exists. They claim that the authors, who make the complex decisions regarding study design and experiment execution, should be allowed to determine whether the resulting data are practically or biologically significant, regardless of the level of statistical significance (e.g. Kirk, 1996). There are concerns that, by focussing on a P-value, practical differences that are apparent from a graphical representation of the data, but do not show significance in statistical testing, may be ignored (Kuhar, 2006). At least one author (Young, 2003) has recommended the use of pooling and pseudoreplication ‘when no other option is available’. Hopefully, these issues will ultimately be resolved. In the more immediate future, inexperienced zoo researchers will be able to study the BIAZA guidelines before designing their experiments. Through the use of randomisation tests, other recommended statistical techniques and recently developed statistical software which is appropriate for studies using small samples, they should be able to produce statistically robust conclusions from their data.

2.4.2 This Study

As discussed above, a major difficulty with zoo-based research is the low number of animals in the groups available for study. This can be partially circumvented by using individuals as their own controls in repeated measures analyses (Saudargas & Drummer, 1996). When this study was planned, it was intended to use that sort of experimental design in order to study the responses of psittacines held at Dublin Zoo, Ireland to a variety of environmental enrichments, including structural changes to enclosures, changes to social groupings and food-based enrichments. The zoo agreed to have all the psittacines ringed so that they could be identified individually for the purposes of the study. Unfortunately, due to some changes in zoo personnel before data collection started, and subsequent decisions concerning the psittacine collection, the ringing was not carried out. Other alterations to the collection meant that husbandry regimes and enclosures were altered and birds were added and removed from the aviaries without prior consultation. This resulted in several half-completed data sets having to be discarded as the conditions were changed partway through an experiment.

Once it became clear that only limited research could be carried out at Dublin Zoo, a new site was sought where the majority of the behavioural observations could be collected. Melbourne Zoo, Australia allowed the research to be carried out there on their psittacine collection and, although their birds were not individually identifiable, the fact that it was possible to halt or control all husbandry, grouping and dietary changes throughout the study, made research into the effects of some environmental enrichment on their psittacines possible. The focus of the research was altered to accommodate the change of location and in order to remove any need to make changes to the structure of the birds’ aviaries or their social groupings. Instead it was decided to concentrate on food-based enrichment devices and their effects as well as comparisons of wild-type and captive activity budgets. After consultation with experienced researchers and academics, it was decided that the study's methodology would be based on that recommended and used widely in published, peer-reviewed literature at the time (1998-2001), where experimental groups are used both as their own controls and in the production of replicates over the duration of the experiment (e.g. Traylor-Holzer & Fritz, 1985; Brockett *et al.*, 1999; van Hoek & King, 1997).

Neither the repeated measures nor independent design statistical tests currently available to biologists were originally constructed for use on data sets of the form used in this study. As a result of the small sample groups and the consequent design of the experiments (with the exception of that described in Chapter 8) the same birds or species were used both as their own controls, and in the production of replicates on concurrent days of an experiment. In other words, a bird may have been observed in a baseline enclosure for five days (five replicates) and then in an enriched environment for five days. The baseline and enriched data were then compared. Independent t-tests and one-way ANOVAs (analysis of variance) were applied, together with Levene's test for equality of variance and Bonferroni post hoc tests. These all assume that the replicates of an experiment are each obtained from different individuals in a population. This means that, in theory, the significance of the results of this research could be compromised. However, despite theoretical flaws, these tests have been found to be robust enough to make them valid for use in experiments such as those outlined in this study, where the data have a normal distribution. They have been widely used in zoo research in recent years for this reason (e.g. Healy & Marples, 2000; Weeks, 2002; Wesserle, *et al.*, 2002; Mitchell, 2002).

To determine whether to use parametric or non-parametric analysis techniques, normality was assessed for each data set. The assumption of normality is a prerequisite for the parametric techniques which were applied in the study (t-tests, one-way ANOVAs) although both have been reported to be robust to deviations in normality (Tabachnik & Fidell, 1996). The data sets were explored graphically using histograms, boxplots and normal probability plots. Normality was also tested using the Kolmogorov-Smirnov statistic with a Lilliefors significance level, and the Shapiro-Wilks statistic (Coakes & Steed, 2001). The graphical representations of the data sets were examined to see if they indicated a normal distribution and, if that was indeed the case, the results of the statistical tests were also checked. If the statistical significance level was greater than 0.05, then normality was assumed. Where data did not have a normal distribution, the Mann-Whitney U test was applied.

Paired t-tests were used to compare the behaviour of captive and wild birds (Chapter 3) and the enrichment preferences of captive psittacines (Chapter 5). These tests are robust to violations of the normality assumption (Jaccard & Becker, 1997) which was important given that the distribution of the data from wild birds was not known in detail.

Period and carry over effects (Diaz-Uriarte, 2002) were not a cause for concern in this study, as it looked at the effect of enrichments, on previously unenriched birds, over several days. The identification of any habituation to the enrichments during the experiments was an important factor in the ascertaining the effectiveness of the enrichment devices, and interest in the enrichments could have increased or decreased during the course of an experiment. The use of data from a group on each of five days would give a better indication of any such response than would data which was collected from separate birds for each replicate. Unless the birds were kept in complete isolation from each other, the latter technique would not have resulted in independent data from each bird, as psittacines are social species and individuals are likely to be affected by the behaviour of other group members.

Social facilitation, as discussed in Chapter 1, is a common phenomenon in social species such as psittacines and can affect any animal which is not kept completely isolated from its conspecifics. In this study, any behavioural changes resulting from social facilitation would increase the chance of a pair or group acting like an individual. In other words, behavioural variation in an experimental group could be reduced. As it would seriously compromise both the welfare and the behaviour of a psittacine bird to keep it in solitary conditions, that option was not considered for this study and therefore, the influence of social facilitation could not be controlled for.

Unfortunately, despite much consultation with zoo researchers and other academics throughout, no doubt was cast on the validity of the methodology and statistical analyses used in this study until after all data had been collected and it was impossible to re-collect it in a different way. This being so, it was decided that, rather than discard the research, the data should be presented in the best way available, while recognising concerns about the statistical validity of the results. There were several arguments that supported this decision:

Firstly, the lack of independence of data arising from the effects of the statistical problems outlined above were limited by the aims of the study. As mentioned in Chapter 1, studies were carried out on several different species of psittacines, and at different holding facilities, both to examine in detail the response of psittacines to enrichment, and to see if general effects of enrichment were consistent in different populations of birds. In total, 28 species of psittacines were studied in captivity (99 individuals). Birds were observed in three different zoos, one in the Northern and two in the Southern hemisphere, covering a range of climatic conditions.

This conforms to the advice given in the BIAZA guidelines (Plowman, 2006) which state: "If the research question refers to only one particular group of zoo animals (eg the effect of enrichment) general assumptions about a greater population are actually not necessary. In these cases a high external validity of data is not required. For example, if one is interested in finding out whether individuals in a specific group are positively affected by a new enrichment, then it is not important to question whether the animals are independent or not. That animal A affects animal B's usage of the enrichment in such a way that both profit, will not affect the interpretation of the results; one is simply interested to know if all individuals benefit. The observation may need to be repeated to ensure the enrichment is still effective if one of the animals is removed, as he/she may have been the facilitator, but the immediate question of whether enrichment benefits this specific group with its current composition, has been answered; the aim was not to extrapolate the findings to the wider population. Statistical tests can be performed (by violating the assumption of independence), but it must be explained that the lack of social independence is unimportant for the reasons given above. In some cases, follow up studies on other groups can then determine if the same trends can be found for the wider population."

Secondly, the lack of independence suggests that the results of this study should only be applied to the group of birds under investigation. However, as psittacines usually are (and certainly should be) kept in same-species pairs or larger groups, any general effects apparent in the results of this research may well be applicable to birds kept in other institutions. The fact that experiments were carried out on several different groups, living in different conditions, supports the argument that results which prove to be consistent across the study groups may well be applicable to the wider population of captive psittacines.

Thirdly, scan sampling methods were used in order to ascertain the activity budgets of the study birds, as recommended in the BIAZA guidelines (Plowman, 2006). In order to reduce the likelihood of temporal dependence of data points, behavioural observations on the birds were taken every two or four minutes for the first 30 minutes of every hour and then averaged. There was then a 30 minute gap before the next round of observations was taken.

Finally, in order to examine the validity of the results of the experiments which monitored changes to activity budgets in the presence of enrichments, but suffered from a lack of independence of data points, observations were also carried out on a group of 28 orange-bellied parrots, kept in pairs (see Chapter 8). The data-sets taken from this group were much more robust and, hence, would give credence to the results of the other psittacine experiments if their conclusions concurred. In the same way, the experiments carried out on dietary intake (Chapters 7 and 8) which used the aviary as the experimental unit were robust in their methodology and analyses, so their results, if in accordance with those of other chapters, will support the validity of their results and conclusions.

In addition to careful consideration of the results of the quantitative analyses performed, the qualitative trends and tendencies indicated by the collected data were also noted for each experiment of the study. It is now more than twenty years since Hurlbert (1984) called for editors to be liberal in accepting good articles that did not use any inferential statistics when they could not be applied correctly. Although journals are often reluctant to publish results where the conclusions are not based on statistically significant results, qualitative analysis can provide a useful indication of real effects (Kuhar, 2006).

Chapter 3

A Comparison of Wild and Captive Behaviour in Psittacines

3.1 Activity Budgets

Introduction

This chapter will examine the behaviour of a variety of psittacines in the wild and compare it with the behaviour of psittacines kept in basically furnished aviaries in a captive environment. In the general introduction (Chapter 1) the relevance to captive species of data collected from observations made in the wild was discussed. It is of particular interest in the context of this project, as future chapters will be examining the effects of environmental enrichment on the behaviour of psittacines in captivity and test the hypothesis that food-based enrichments can cause these birds to behave in a more wild-type manner. As a preliminary to that, it is necessary to establish how birds behave in basic enclosures using data from the wild as a focus for comparison.

One way in which wild data can be compared with those taken from conspecifics in captivity is through the compilation and comparison of activity budgets. The majority of psittacine species, including those studied here, are diurnal in behaviour so it was decided to observe the birds from the first hour after first light to the last hour in which they could be seen clearly. For the purposes of this thesis, that duration will be referred to as ‘dawn until dusk’ and the activity budgets refer to this period unless otherwise specified.

It was important to gather information about the birds’ behaviour at all hours of the day as the daily activity patterns displayed by psittacines (eg Barclay, 1976; Westcott, 1988; Emison, 1994) indicate that they tend to spend certain periods of the day in particular activities. Activity budgets based on observations from discrete parts of the day only would therefore be likely to provide an inaccurate picture of the birds’ complete daily activity. In addition, in future chapters, activity budgets will be compared for birds kept in different conditions in captivity. Should the time spent in, for example, resting behaviour in the morning, decrease in enriched conditions, it would be necessary to observe the birds throughout the day in order to find out whether resting behaviour increased in the evening, for example, thereby compensating for the earlier decrease. Instances of animals’ behaviours varying in this way are to be found in the published literature (e.g. Kinahan & Marples, 2000).

A literature survey was carried out in order to find out more about the behaviour of psittacines in the wild, and the limited data that related to the activity budgets of wild populations of psittacines was collated. The studies of activity budgets in the wild collected their data in one of two ways. In some of the studies the researchers used instantaneous sampling methods to observe the behaviour of identified individuals in a flock (eg with 30 second sampling intervals, Magrath & Lill, 1983). In other studies the researchers scan-sampled the flocks to see what proportion of the total number of birds were performing particular behaviours at the time of day observed (eg Emison & Nicholls, 1992). All studies from which data pertaining to activity budgets have been taken were carried out from dawn to dusk (with observations covering the whole period), over many weeks or months observing large numbers of wild birds in a pre-determined area of land.

In order to compare this wild behaviour with that of captive psittacines, activity budgets were determined for a variety of species held at Melbourne Zoo. The birds were scan sampled several times an hour from dawn until dusk on five days, their behaviour noted and the proportion of the observations that were spent in each behaviour were calculated. These data were extrapolated in order to calculate the percentage of daylight hours that were spent in each behaviour by each species or group of birds.

Studies of wild birds have shown that one of the species observed at Melbourne Zoo, the Bourkes Parrot, does not conform entirely to usual psittacine diurnal behaviour patterns. Bourkes parrots have been reported to be active before dawn, after dusk and, occasionally, on moonlit nights (Fisher, 1972; Higgins, 1999). The species tends to live in arid conditions in the wild, where visits to water, for example, may be safer at these times. As a result, the captive activity budgets calculated for this study may not be quite complete for the Bourkes Parrots, as they will not include any activity taking place before dawn or after dusk.

Parrots, cockatoos and lories were observed separately in this study as they are regarded as being taxonomically separate groups (see Chapter 2, section 2.1) and, therefore, may have distinctive behavioural differences. The lories, parrots and the pair of Major Mitchells cockatoos studied, were kept in baseline enclosures that were well planted with shrubs and bushes, had sand, earth and / or woodchip floor substrates and a variety of fixed perching provided (see Plates 2.1, 2.2 & 2.4). The mixed cockatoo group baseline enclosure had a deep sand substrate and a large selection of metal and wooden perches, but no living plants (see Plate2.3).

3.1.1 Parrots

Methods

The birds of the Melbourne Zoo parrot group (see section 2.1) were observed in their unenriched baseline enclosures during the Winter month of June 2000. The birds in each enclosure were observed every 4 minutes, for the first 30 minutes of every hour (a total of 8 times an hour) from dawn until dusk (07.00 – 17.00) and the behaviour each bird in the enclosure was engaged in was noted. Instantaneous scan–sampling methods were employed (following Altmann, 1973; Martin & Bateson, 1998). Trial data collections were carried out for three days in this manner before the experiment began, in order to accustom the birds to the presence of an observer. During this period an ethogram was compiled for the parrot group classifying all of their behaviours and activities (see Table 3.1). As described in the Table 3.1 below, when referring to captive behaviours for the purposes of this study 'feeding' is taken to mean the consumption of food from prepared dishes, while 'foraging' refers to all other feeding behaviours, both appetitive and consumptive.

Description of Behaviour	Classification
inactive with eyes closed	resting
inactive with eyes open; head may be moving	alert
walking, climbing, hopping or flying	locomotion
autopreening, scratching, stretching, toe nibbling, feather shaking	maintenance behaviour
eating prepared food from dishes	feeding
feeding behaviours which involve: eating any food items not provided in dishes; pecking or tearing at any non-food objects, whether ingestion occurs or not	foraging
ingestion of water from pools or bowls	drinking
washing, shaking and preening of feathers in standing water	bathing
allopreening, mating, attacks on another bird	social interaction
calls of any type	vocalisation
interaction with humans, usually indicated by the bird approaching a person	human
all behaviours not included in another category	other

Table 3.1: Ethogram of the Melbourne Zoo psittacines explaining the classification of behaviours used throughout the study. Vocalisations can occur while the birds are performing other behaviours, so were not included in the activity budgets

After the three day acclimatisation period during which the ethogram was compiled, the same observation procedures were carried out for 5 days, with the behaviour of each bird being recorded 8 times every hour from dawn until dusk. This gave a score out of 8 for each bird, for each behaviour, for each hour of daylight on each of five days. The data collected was transferred from checksheets to computer data files (SPSS version 10.0), converted to mean percentage time spent in each behaviour, and then activity budgets were calculated for each species observed.

Qualitative Results

The captive birds tended to spend less time on active behaviours, such as feeding and moving around, than the wild parrots studied. Instead, the captive birds showed a tendency to spend more time on static behaviours such as preening and resting.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with caution).

REFERENCE	SPECIES	DIET	ACTIVITY BUDGET DATA (%)	FORAGING DATA
Jones 1983	Cockatiel *Nymphicus hollandicus*	Seeds of grasses, shrubs & trees, agricultural grain; also fruit and berries.	Post roost activity: 5 Am feed: 12 Pm feed: 13 Pre-roost activity: 6	>25%
Magrath 1983	Crimson Rosella *Platycercus elegans*	Buds, seeds, insects, fern sori	Feeding: 38 Inactive: 42 Maintenance: 5	38%
Barclay 1976	Red-Rumped Parrot *Psephotus haemotonotus*	Seeds and herbs	Feed/drink: 32 Inactive/preen: 34 Fly: 26 Roost: 7	32%
Westcott 1988	Red-Rumped Parrot *Psephotus haemotonotus*	Seeds & herbs	Foraging: ~40 Inactive: ~44	~40%
Mean Total				**34%**

Table 3.2: The mean percentage of daylight hours spent in feeding and foraging behaviours by four populations of wild parrots, and details of the data on activity budgets found in the wild parrot literature. All data were collected during the Winter.

When the available literature was examined (Table 3.2) it appeared that wild parrots tended to spend more time in feeding and foraging behaviours and locomotion and less time in maintenance behaviours and inactivity than the captive birds observed at Melbourne Zoo. For example, in the wild, crimson rosellas (*Platycercus elegans*) were reported as spending 5% of the day in maintenance behaviours, red-rumped parrots (*Psephotus haematonotus*) were observed to spend 26% in locomotion during the Winter. The captive parrot group, however, spent a mean of 15% of the day in maintenance behaviours and 12% in locomotory behaviours (Table 3.3).

SPECIES	WILD DIET	ACTIVITY BUDGET (%)	FEEDING & FORAGING DATA
Golden-Shouldered Parrot *Psephotus chrysopterygius*	Fallen seed, seed from grasses, flowers, occasionally insects	Rest: 17 Alert: 37 Maintenance: 14 Locomotion: 6 Feeding & Foraging: 16 Other: 10	16%
Princess Parrot *Polytelis alexandre*	Seeds of grasses, flowers, nectar & leaves	Rest: 21 Alert: 27 Maintenance: 21 Locomotion: 11 Feeding & Foraging: 14 Other: 6	14%
Scarlet-Chested Parrot *Neophema splendidia*	Seeds of grasses, shrubs and trees. Mainly eat fallen seed	Rest: 5 Alert: 32 Maintenance: 12 Locomotion: 18 Feeding & Foraging: 30 Other: 3	30%
Australian King Parrot *Alisterus scapularis*	Mainly seed, also fruits, berries, flowers and nectar	Rest: 8 Alert: 45 Maintenance: 13 Locomotion: 9 Feeding & Foraging: 18 Other: 7	18%
Bourkes Parrot *Neopsephotus bourkii*	Seeds of grasses, herbaceous plants, trees and shrubs	Rest: 9 Alert: 45 Maintenance: 17 Locomotion: 8 Feeding & Foraging: 16 Other: 5	16%
Mean Totals:		**Rest: 11** **Alert: 37** **Maintenance: 15** **Locomotion: 10** **Feeding & Foraging: 19** **Other: 8**	**19 %**

Table 3.3: The mean percentage of daylight hours spent in feeding and foraging behaviours by the Melbourne Zoo parrot group during the Winter. Activity budgets are shown for each species, but activities performed for less than 1% of the day are classified as 'other'. The information on the wild diets of the birds is taken from a review by Higgins (1999).

The wild parrots lived in larger flocks than the captive birds and spent more time engaged in social interactions according to the literature (this is called pre-roost or roost activity by Jones, 1983 and Barclay, 1976). Data were unfortunately very limited on the behaviour of most of the species in the wild, but sufficient feeding and foraging data were available to compare that from wild and captive birds which fed on similar diets (see Tables 3.2 & 3.3). They were found to be significantly different (independent t-test: t=3.40, df=7, p=0.012) with wild birds spending significantly more time in feeding and foraging behaviours than the captive group studied. The data available also indicated that on average the wild parrots spent 42% of their time inactive or in maintenance behaviours, while the captive parrots spent a mean of 63%, rendering their levels of these behaviours significantly higher than those of the wild birds (independent t-test: t=4.4, df=4.8, p=0.007). Due to the inescapable non-independence of the captive data collected, these analyses should be treated with caution (see Ch. 2.4) and this should be borne in mind during the discussion of results, but a trend of greater activity in the wild than in captivity appears to be present.

Discussion

It is clear that wild parrots spent significantly more mean time in feeding behaviours than the captive group at the same time of year, despite the unusually high levels of foraging behaviour showed by the scarlet-chested parrots (see Fig. 3.2), a feature which will be discussed further in Chapter 4. The extra time used for foraging by the wild parrots appeared to be spent in inactivity and maintenance behaviour by the captive birds.

It should be noted that despite dietary and ecological similarities, the wild species for which data were available are not the same species as were studied in captivity, although the red-rumped parrot is closely related to the golden-shouldered parrot. There may well be differences in the levels of foraging shown by different species, but it is unlikely that the extreme difference seen in mean percentage time spent feeding and foraging between the wild and captive groups examined here is due entirely to species differences.

3.1.2 Cockatoos

Methods

The birds of the Melbourne Zoo cockatoo pair (see section 2.2) and the Melbourne Zoo mixed cockatoo group (see section 2.3) were observed in their unenriched baseline enclosures using the methods outlined in section 3.1.1. The pair of Major Mitchell's cockatoos was studied during the Autumn month of April 2000, and the mixed species group was studied during the Winter month of August 2000, each study being preceded by a three day acclimatisation period as described in section 3.1.1. Each bird was observed 15 times in every hour (every 2 minutes for the first 30 minutes of every hour) from dawn to dusk (07.00 – 18.00) for 5 days and their activity budgets calculated. The ethogram displayed in Table 3.1 details all the behaviours observed in the captive cockatoos.

Qualitative Results

Like the parrots examined in the previous section, the wild cockatoos for which data were available showed an overall tendency to spend more time in active behaviours, such as foraging, and less time inactive, than did the birds studied in a captive environment.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with caution).

As with the parrots, it is clear that, although there was considerable variation between the wild data collected for each species, the captive cockatoo group spent significantly less mean time in feeding and foraging behaviours than the wild birds studied (independent t-test; t=3.821, df=7, p=0.007) (see Tables 3.4 and 3.5).

REFERENCE	SPECIES	DIET	ACTVITY BUDGET DATA (%)	FORAGING DATA
Westcott 1988	Galah *Eolophus roseicapillus*	mainly seeds, some flowers, shoots, vegetable matter	Foraging: ~51 Inactive: ~32 Moving: ~8	51%
Pepper 1996	Glossy Black Cockatoo *Calyptorhynchus lathami halmaturinus*	*Allocasuarina* seeds	Mean over Winter & Summer for non-breeders: Foraging: 60 Alert: 34 Rest: 3 Preening: 2	60% (non-breeders)
Emison 1994	Long-Billed Corella *Cacatua tenuirostris*	seeds, nuts, corms, bulbs, roots, insects		83%
Noske 1980	Sulphur-Crested Cockatoo *Cacatua galerita*	seeds, fruit, berries, nuts, flowers, leaf buds, roots, insects	Average over 4 seasons: Forage: 38 Fly: 15 Rest/perch: 47	38%
MeanTotal:				**58%**

Table 3.4: The mean percentage of daylight hours spent in feeding and foraging behaviours by four populations of wild cockatoos, and details of the data on activity budgets found in the wild cockatoo literature where available. All data were collected during the Winter.

From the scanty data available, it also appears that, like the parrots, the wild cockatoos spent less time resting and in maintenance behaviour than the captive birds. In captivity, the mixed species group spent a mean of 11% of the day in maintenance behaviour (the Major Mitchells cockatoos spent 10%) and the Major Mitchells pair spent 17% whereas wild glossy black cockatoos (the only species for which maintenance data were found) are reported to spend 8% of the day in this activity by Clout (1989) and 4% by Pepper (1996). The only wild cockatoo species for which locomotion data were available was the sulphur-crested cockatoo which is recorded as spending 15% of the day flying (Noske, 1980) but this figure does not include time spent walking or climbing during foraging. The mixed species captive group spent a mean of 21% in locomotion (the Major Mitchells cockatoos spent 26%) and the pair of Major Mitchells cockatoos spent 8%. The latter value is thought to be so low, relative to their conspecifics in the mixed group, because of the much smaller dimensions of their enclosure which limited their flying activity, but they may also have been affected by being kept as a pair instead of in a larger social group, by the fact that the birds in the mixed group are both male whereas the other two birds are a true pair, or by the fact that the solitary pair were observed in Autumn and the mixed group was studied in Winter. Instead of locomotion, the pair spent more time than their conspecifics in the mixed group in maintenance and resting behaviours (see Table 3.5).

SPECIES	SOCIAL GROUP	WILD DIET	ACTIVITY BUDGET (%)	FEEDING & FORAGING DATA
Galah *Eolophus roseicapillus*	Mixed	mainly seeds, some flowers, shoots, roots, leaf buds, rhizomes, insects, larvae, fruits, nuts	Rest: 13 Alert: 33 Maintenance: 18 Locomotion: 20 Feeding & Foraging: 11 Other: 2	11%
Sulphur-Crested Cockatoo *Cacatua galerita*	Mixed	seeds, fruit, berries, nuts, flowers, leaf buds, roots, insects	Rest: 6 Alert: 28 Maintenance: 6 Locomotion: 21 Feeding & Foraging: 33 Other: 6	33%
Long-Billed Corella *Cacatua tenuirostris*	Mixed	seeds, nuts, corms, bulbs, roots, insects	Rest: 7 Alert: 31 Maintenance: 11 Locomotion: 18 Feeding & Foraging: 25 Other: 8	25%
Major Mitchell's Cockatoo *Cacatua leadbeateri*	Mixed	seeds, fruits, roots, bulbs, insect larvae	Rest: 5 Alert: 26 Maintenance: 10 Locomotion: 26 Feeding & Foraging: 24 Other: 9	24%
Major Mitchell's Cockatoo *Cacatua leadbeateri*	Pair	seeds, fruits, roots, bulbs, insect larvae	Rest: 13 Alert: 38 Maintenance: 17 Locomotion: 8 Feeding & Foraging: 21 Other: 3	21%
Mean Total:			**Rest: 9** **Alert: 31** **Maintenance: 12** **Locomotion: 15** **Feeding & Foraging: 23** **Other: 10**	**23%**

Table 3.5: The mean percentage of daylight hours spent in feeding and foraging behaviours by the Melbourne Zoo cockatoo groups during the Winter. Activity budgets are shown for each species, but activities performed for less than 1% of the day are classified as 'other'. The information on the wild diets of the birds is taken from a review by Higgins (1999).

There were few wild data on feeding and foraging available for Major Mitchells cockatoos, although some data from the wild were collated for the other three species studied in captivity (see Table 3.5). In the limited published information on the behaviour of Major Mitchells cockatoos in the wild they are reported as spending more than half the daylight hours foraging during the Winter (Rowley, 1991), more than double the time spent in feeding activities by the four conspecifics observed in captivity in this study (see Table 3.5). The galahs and long-billed corellas spent more than four times and three times as much time respectively foraging in the wild as they did in captivity.

It is interesting to see that the sulphur-crested cockatoos were the only species where the captive birds spent as much time in feeding and foraging activity as the birds in the population from which the wild data was collected (independent t-test: t=0.477, df=9, p=0.645. NS.) (see Tables 3.4 & 3.5). As is shown in Table 3.5, 33% of the day was spent in this activity by the captive pair, and further analysis indicated that a mean of 19% of the day (58% of the total time spent feeding and foraging) was spent foraging for and pecking at particles of food spread about the enclosure by the other birds as they ate food taken from the feeding trough. This food tended to be fresh fruit and vegetable matter as lumps of this were taken away from the trough in the beaks of the Major Mitchells cockatoos, who then perched on a branch in the enclosure and held the food in a foot while eating. The corellas were also observed carrying and eating lumps of corn cob in the same way. The seed, on the other hand, tended to be eaten directly from the feeding trough by all four species, rather than taken elsewhere in the enclosure.

Discussion

Galahs, long-billed corellas and sulphur-crested cockatoos all feed primarily at ground level in the wild (Higgins, 1999) but whereas galahs feed mainly on seed (Rowley, 1990) and the corellas feed on subterranean parts of plants as well as seeds (Emison, 1994) it is reported that sulphur-crested cockatoos will readily eat a variety of foods including fruits (Higgins, 1999). It seems probable, therefore, that the baseline environment in the mixed species enclosure was suitable for the sulphur-crested cockatoos to carry out their natural foraging behaviour in, and that they did so. It does not appear, however, that the other species were choosing to carry out similar behaviours to the same extent, perhaps because they do not tend to forage for fruit or vegetable matter on the ground in the wild.

In addition, it was observed that the captive sulphur-crested cockatoos were active for more of the day than the other cockatoo species studied. Unlike the other birds, they maintained high levels of activity , including foraging behaviours, during the middle of the day. This may have been a result of natural variation in the species, but it is also possible that it is related to the previous history of the individuals from which the data were collected. It is thought that the two sulphur-crested cockatoos, alone among the birds studied, were kept as pets before being donated to the zoo, although they were born in the wild. Animals kept as pets prior to their transfer to a zoo are more likely to exhibit atypical behaviours, as a result of their rearing environment (Kreger *et al.*, 1998). It was observed that both birds approached humans readily, begged for food and had a vocabulary of several words and, as their enclosure was located near the zoo restaurant and cafeteria, the middle of the day was a prime time for getting lunchtime scraps of food supplied (against zoo rules) by visitors to the zoo. It may be that the birds' innate behaviour patterns had been distorted as a result of these interaction with humans, so that they now foraged and fed throughout the midday period. In support of this theory, Fig. 3.5 shows that, despite considerable variation in the levels of interaction with humans shown by the sulphur-crested cockatoos, they perform this behaviour most frequently during the middle of the day when they would be expected, according to the data from wild conspecifics, to be spending most of their time resting or otherwise inactive.

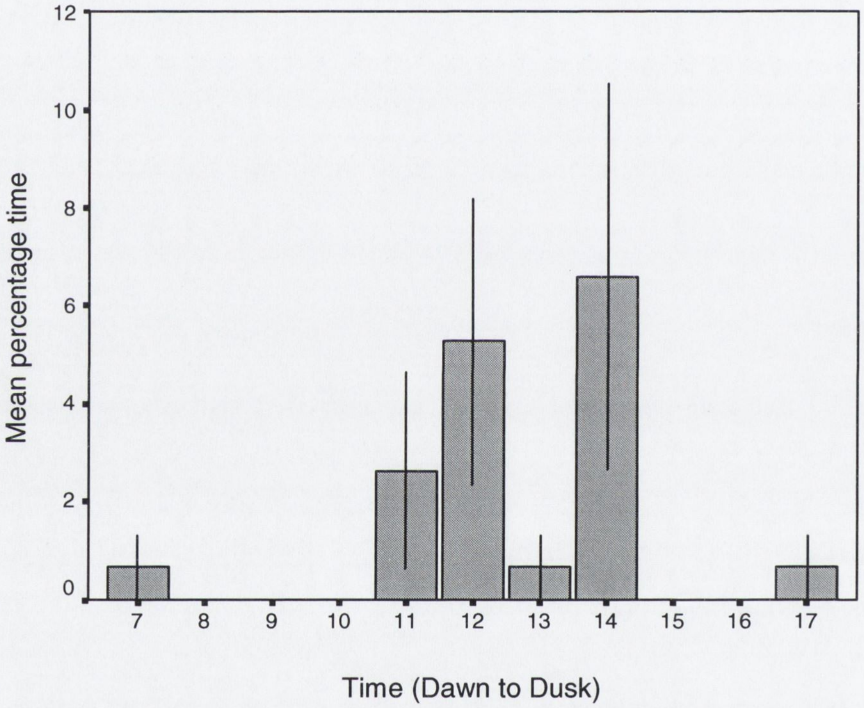


Fig. 3.5: The mean percentage time spent interacting with humans outside the aviary at different times of day by the pair of sulphur-crested cockatoos in the Melbourne Zoo Mixed Species Cockatoo Aviary (N=10).

3.1.3 Lories

It did not prove possible to find any literature containing data concerning the activity budgets of wild lories. In order to gain some information about the percentage of daylight hours spent feeding and foraging by these species, therefore, observations were made on the Royal Park wild lory group which visited Melbourne Zoo in order to use the nectar feeders provided in the zoo grounds (see section 2.6).

The ethogram detailed in section 3.1.1 was used for the studies on both the wild and captive lories.

3.1.3.1 Wild Lory Experiment

Methods

The three supplementary rocket feeders stationed within the zoo (see Plate 2.5 in Chapter 2) were kept supplied with artificial nectar mix throughout daylight hours. The nectar was the same as that fed to the captive lories housed within the zoo. Usually the feeders were only filled twice a day, but during the experiment, and for two weeks beforehand, they were monitored regularly and were refilled as necessary. Every hour, from dawn to dusk (07.00 – 18.00) a complete circuit of the zoo was walked (incorporating all the feeders, the known roosting sites of the lories and all blossoming trees) and the behaviour of each rainbow lory observed was noted. The classification of behaviours detailed in the parrot ethogram (Table 3.1) was followed throughout. Each circuit took about 40 minutes to walk and the study was carried out for 5 days in the August of Winter 2000. The mean number of lories seen feeding and foraging was calculated as a percentage of the total number of lories seen that day, in order to give an indication of the percentage of the day the flock spent in feeding behaviours within the zoo grounds.

Flocks of rainbow lories roosted in date palms growing in the zoo grounds. They left their roosts soon after dawn and while some flew out of the zoo across Royal Park, where they were seen feeding in flowering trees, others fed at the zoo feeding stations before flying towards the park. Throughout the day, except between the hours of 11 am to 2 pm when they tended to rest, birds were constantly arriving at and leaving the feeding stations.

Results

The lories spent a mean of 20% of daylight hours alert, 13% in maintenance behaviours, 49% in locomotion (37% flying, 12% other), 17% eating from the feeders and 1% foraging in trees within the zoo grounds.

These figures are based on the assumption that the numbers of birds observed, for example, feeding daily, as a proportion of the total number of birds observed, gives an accurate indication of the percentage of daylight hours spent feeding by individual lories in the population. This method of calculating activity budgets is widely used in studies of wild psittacines, for example Barclay (1976), Noske (1980), Jones (1983) and Westcott, 1988.

3.1.3.2 Observations on Captive Lories

Methods

The methods followed those outlined in section 3.1.1. After a three day acclimatisation period, the birds of the Melbourne Zoo Lory Group (see section 2.5) were observed in their unenriched baseline enclosures during the Autumn month of April 1999. They were scan-sampled 15 times every hour from dawn until dusk (07.00 – 18.00) for 5 days.

Qualitative Results

The captive birds tended to spend less time feeding from their prepared food than the wild lories did and less time moving around. The lories differed from the parrots and cockatoos studied in that the captive and wild groups appeared to spend about the same amount of time in maintenance behaviours such as preening (possible reasons for this will be discussed in Chapter 4).

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with caution).

The activity budgets calculated for the captive birds are shown in Table 3.6. There was no significant difference between the time spent feeding and foraging by the red lory pair, and that observed in the wild group (independent t-test: t=0.096, df=13, p=0.925). The yellow-backed chattering lories, however, spent significantly more time in these activities than the wild group (independent t-test: t=2.941, df=9.90, p=0.015). The wild lories were rarely observed feeding or foraging during the study, except from the supplementary nectar.

They were thought to forage daily in trees outside the zoo, however, so the 17% of the day they spent using the supplementary feeders may be an underestimate of the total time they spent in feeding and foraging activity. A comparison of the time spent feeding by the captive lories from their prepared food and that spent feeding from the supplementary nectar by the wild birds could be more illuminating as this excludes the time spent performing non-consummatory foraging behaviours by the captive birds as well as the time spent in consummatory foraging behaviours by the wild birds. When these comparisons were carried out, using independent t-tests, it is clear that the wild birds spent significantly more time feeding from the prepared food than either of the two species studied in captivity. The wild birds spent a mean of 17% of the day feeding but the red lories spent only 7% (t=4.872, df=13, p<0.001) and the chattering lories spent only 6% (t=7.348, df=13, p<0.001). A trend of greater foraging activity in the wild than in captivity appears to be present.

SPECIES	WILD DIET (very little known)	ACTIVITY BUDGET (%)	FEEDING & FORAGING DATA
Red Lory *Eos bornea*	nectar, pollen, flower fragments, insects	Rest: 1 Alert: 51 Maintenance: 11 Locomotion: 11 Feeding & Foraging: 18 Other: 8	18%
Yellow-Backed Chattering Lory *Lorius garrulus flavopalliatus*	nectar, pollen, other food available among flowering coconut palms	Alert: 45 Maintenance: 17 Locomotion: 10 Feeding & Foraging: 24 Other: 4	24%
Mean Total:		**Rest: 1** **Alert: 48** **Maintenance: 14** **Locomotion: 11** **Feeding & Foraging: 21** **Other: 6**	**21%**

Table 3.6: The mean percentage of daylight hours spent in feeding and foraging behaviours by the Melbourne Zoo lory group during the Autumn. Activity budgets are shown for each species, but activities performed for less than 1% of the day are classified as 'other'. The information on the wild diets of the birds is taken from a review by Forshaw (1973).

Discussion

The values calculated for the wild lories' activity budget do not take into account the time spent feeding from trees in Royal Park, nor the fact that the birds had effectively to 'queue' in order to use the supplementary feeders. The figures do, however, give an approximation of the minimum percentage of daylight hours spent in feeding behaviours by the Royal Park wild lory group. It is also possible that the levels of flying recorded may be disproportionately high as the birds were easiest to spot when they were in the air, and they flew regularly between the supplementary feeders and the trees a few kilometres away in Royal Park. Alternatively, it may be that spending a third of the day in flight is normal behaviour for nectar feeding birds particularly when, as in Royal Park, blossoming trees tend to be found singly, rather than in clumps.

Despite a lack of data in most areas, the results suggest that the lories probably followed the same pattern as that seen in the cockatoo and parrot groups, with the wild birds spending more time feeding and foraging. This difference between the wild and captive groups could be a result of variation between species, but, as both groups were eating the same nectar mix, it may indicate instead the need of wild lories for a higher intake of food than lories in captivity.

This result is particularly interesting as the reason for psittacines spending more time in foraging behaviours in the wild could be merely because it takes them longer than the captive birds to ingest the same amount of calories. The wild birds have to search for and process their food before consumption, whereas the captive birds can eat directly from a dish of prepared food and, hence, spend less time in feeding and foraging activities. The result may indicate, however, that the wild psittacines actually need to ingest more calories than their captive conspecifics, and hence need to spend longer periods foraging, partly because their calorific needs are higher. This seems probable, given that flight is an energetically expensive activity (Schmidt-Nielsen, 1984) the considerable distances flown by many wild psittacines (e.g. Rowley, 1990 & 1991; Carter, 1993; Emison, 1994) and the probable energy expenditure involved in searching for and manipulating food items in the wild (Magrath, 1983) compared with eating prepared food from a dish.

3.2 Further Discussion

When data on wild parrot and cockatoo activity budgets were compared with activity budgets from the captive psittacines at Melbourne Zoo it was found that there were several differences between the two groups. The wild birds spent more time in social interaction and locomotion than did the captive birds, and less time inactive. In particular, the wild psittacines spent significantly more time feeding and foraging (the active behaviours in which they all spent most time) than the captive birds. While opportunities for locomotion and social interaction are largely limited by enclosure size and collection management policies in a captive environment, enrichments that provide opportunities for foraging can be utilised in all types of husbandry set-ups. As a result of these considerations, and the possible advantages of enrichments designed to allow foraging behaviour discussed below and in Chapter 1, foraging behaviours were made the focus of this project.

The amount of time spent feeding and foraging daily (ingesting, looking for, manipulating or processing potential food items) was significantly greater for the wild parrots and cockatoos than for their respective captive groups. The extra time (a mean of 99 minutes a day for parrots and 211 minutes a day for cockatoos) was spent by the captive birds in inactivity or in preening and the performance of other maintenance behaviours (scratching, stretching, toe nibbling, feather shaking).

The time spent feeding from the supplementary feeders in the zoo by the Rainbow Lories was significantly greater than that spent feeding by the two lory species observed in captivity. Rainbow Lories are recorded as eating mainly nectar and pollen but also seeds, fruits, leaf buds, bark and insects (Higgins, 1999), and the birds in the study are presumed to have been feeding on these things daily in Royal Park, as well as utilising the supplementary feeders. This species is recorded in the literature as 'feeding throughout the daylight hours, particularly in the afternoon' (see Higgins, 1999). It seems probable, therefore, that, as was the case with the parrots and cockatoos studied, the wild lories spent significantly more time in feeding and foraging behaviours than their captive counterparts

This disparity in activity levels between the wild and captive psittacine populations is not unexpected. Several species of animals and birds have been found to show similarly lowered levels of activity in captivity (e.g. Chamove, 1989; Newberry, 1995). This can result in health problems such as obesity and hepatic lipidosis in psittacines (Bauck, 1998). Studies have also shown that birds in long-term captivity may lose significant amounts of pectoral muscle mass while expending energy on the growth of organs such as the liver (Warkentin and West, 1990). Environmental enrichment can be used to increase activity levels in captive animals and, hence, help to avoid such conditions. When such enrichments are implemented, other problems may also be avoided. For example, where enrichments result in increased activity levels in captive animals, it can be easier to spot when an animal is feeling unwell. Although they may show little other outward sign, they may abstain from vigorous activity and, hence, not use the enrichment devices as much as normal (Markowitz and Aday, 1998). In addition, it is thought that stereoptypic problems occur when the time used for an otherwise normal behaviour, such as grooming, may be increased to an inappropriate level (Bauck, 1998). Levels of preening and other maintenance behaviours were elevated in the captive parrot and cockatoo populations in this study, when compared with the wild data, so if the introduction of environmental enrichment leads to increased levels of other activities, that may correct any tendency to over-groom which could lead to the development of feather plucking stereotypies. The effects of enrichment on psittacine behaviour will be investigated in the following three chapters.

It is interesting to note that all the captive birds spent time engaged in foraging behaviour, such as substrate pecking, wood chewing and leaf manipulation, which did not as far as could be seen result in any consumption of food. For example, the parrot group spent a mean of 33 minutes in such activities daily, the cockatoo group 92 minutes and the lory group 73 minutes. The purpose served by this behaviour is unclear but may concern such things as beak maintenance in the case of the cockatoos, although the biology underlying wood chewing is not fully understood (Milam, 1999). This, however, does not explain all the non-consummatory foraging behaviour shown by the captive birds, for example both the lory species shredded dry leaves which they had pulled through the mesh of their enclosure roof, and the Scarlet-Chested Parrots frequently pecked at the sand substrate of their enclosure without, apparently, ingesting anything. These behaviours fulfil no obvious function and are not reported as occurring at significant levels in the activity budgets calculated for wild psittacines. One possible explanation for the expression of such behaviours in captive psittacines arises from frustration, thwarting or conflict of innate motivations (for review see McFarland, 1985). The inability to perform a particular behaviour in captivity may leave a void which may result in boredom, redirected behaviour, vacuum activities or stereotypies (Veasey *et al.*, 1996). Situations where animals are motivated to perform behaviours which have no functional application in a captive environment are well documented, as discussed in Chapter 1 (although it has been argued that the behaviours may be fulfilling in themselves (e.g. Wiepkema, 1985)). For example, intensively housed pigs will show nosing and rooting foraging behaviours in the absence of any floor covering (Van Putten, 1979), early weaned calves, lambs and piglets will commonly show sucking behaviour towards substitute objects (Hughes, 1989) and domestic hens will also perform pecking and scratching food searching behaviours when housed on a bare floor with no food or added substrate present for them to forage through (Bubier, 1996). Behaviours such as this, which animals are strongly motivated to perform have been described as ethological needs (e.g. Hughes, 1989) and the results from this study suggest that foraging behaviours in psittacines may fall into this category.

Another point to arise from the experiments described in this chapter comes from the comparison of wild and captive lory behaviour in section 3.1.3. The results of the study indicate that wild psittacines may forage for longer than their captive conspecifics because they have higher calorific needs. For example, wild passerine birds have been estimated to require 10-20% more energy than their caged conspecifics (Willson & Harmeson, 1973). Another possible reason is that it takes the wild birds longer to find and process their food (for example, in the wild, Glossy Black Cockatoos feed almost exclusively on the seeds of *Allocasurina* (drooping sheoak) trees, which they extract from unopened woody cones (Clout, 1989).This species is reported as spending at least 60% of daylight hours foraging during the Winter and the handling and manipulation of the cones takes up 94% of that time (Pepper, 1996).

It is probable that both the factors outlined above contribute to the difference seen in the time spent feeding and foraging by the wild and captive psittacines, but a third influence could also be important. It may be that the captive birds would spend the same amount of time foraging as their wild conspecifics if they were given opportunities to do so, but that such opportunities are not afforded them in their baseline enclosures. The experiments described in the next two chapters will test this theory by providing the birds with enrichment devices designed to allow the expression of wild-type feeding and foraging behaviours.

Chapter 4

The Effects of Daily Enrichment on Psittacine Activity Budgets

Introduction

These experiments were carried out in order to examine the effects of food-based enrichments on the activity budgets of a variety of psittacine species held in captivity. The baseline data referred to is that described and discussed in Chapter 3. The feeding and foraging sections of the activity budgets will be examined in particular detail in order to ascertain whether the provision of food-based enrichments results in captive psittacines increasing the proportion of the day they spend in feeding and foraging behaviours, bringing them closer to wild-type levels.

As discussed in Chapters 1 and 2, the environmental enrichment devices were selected with psittacine ecology in mind and were devised in order to provide wild-type foraging opportunities for the birds (see Table 2.7). For example, species that in the wild are reported as feeding on seed scattered on the ground, were provided with forage trays so that they could display the same behaviour in captivity. Throughout the experiments all the birds continued to be supplied with their usual *ad lib* daily diet in dishes, which meant that they did not need to eat from the enrichments in order to fulfil their nutritional requirements.

As in Chapter 3, the ethogram in Table 3.1 and the behaviour groupings described in Table 3.7 were used throughout.

4.1 Parrots

Methods

This study was carried out on the Melbourne Zoo parrot group (see section 2.2.1.1) during the Winter months of June and July in 2000. In each experiment, after a three day acclimatisation period to accustom the birds to the presence of the enrichments in their enclosure, all the parrots were scan-sampled 8 times during every hour from dawn until dusk (07.00 - 17.00) and their behaviour noted in the same way as was described in the previous chapter. This procedure was repeated each day for five days. By analysing and extrapolating from the information collected in the way described in Chapter 3, activity budgets were compiled, both for the entire parrot group and for each species.

During the baseline observations, no changes were made to the enclosures or to the usual daily husbandry regime and no enrichments were provided for the birds. In the three ensuing experiments the parrots were provided with their usual *ad lib* daily diet and various enrichment devices, designed to stimulate natural foraging activity, were also added to each enclosure (individual enrichment devices are described in more detail in Chapter 2):

- In Enrichment 1 a swinging fruit branch (see j) below), a forage tray (see a) below) and fresh endive leaves placed on the enclosure floor
- In Enrichment 2, a sprouted seed tray (see d) below) and a seeded branch (see c) below)
- In the Multiple Enrichment experiment, the following enrichments were used in each enclosure:

  a) a forage tray filled with sand (wood chip for the king parrots) with dry seed mixed into it; b) a suspended, open pine cone coated with dry seed mix stuck on using a non-toxic, water-soluble PVA glue; c) a wooden branch, suspended from the roof by a rope passing through it, and coated with dry seed mix stuck on using a non-toxic, water-soluble PVA glue; d) a tray filled with soil and planted with seed mix. The seeds were sprouted to a height of 5 cm before the tray was introduced into the enclosure; e) sprays of *Panicum* millet; f) a vertically suspended rope with fresh flowers threaded through it; g) a whole corn cob suspended from the side netting on a skewer; h) a block of dry seed (available in pet shops) suspended from a perch; i) fresh branches of eucalyptus browse; j) a wooden branch, suspended from the roof by a rope passing through it, with fresh fruit and vegetable pieces stuck onto nails protruding from the branch.

The types of fruit and vegetable used in the enrichments were: Apple, satsuma, passionfruit, grapes, broccoli, banana, sweet potato, pieces of corn cob and pear. All of the enrichments, with the exception of the flower ropes and the fresh browse, only contained food materials which were already present in the daily diet of the birds. They were replaced daily or when necessary (e.g. all the fruit and vegetables were replaced at least once a day; the browse was replaced when it wilted or was significantly chewed by the birds).

Qualitative Results

The provision of food-based enrichments resulted in the parrots showing a tendency to increase the amount of time they spent in active behaviours such as moving around and foraging, and reduce the amount of time they spent in less active behaviours such as preening and resting. In addition the birds tended to spend less time feeding from their dishes of prepared food when the foodstuffs were also provided to them in the form of enrichments.

The various parrot species studied showed a tendency to prefer particular enrichments based on the foods they supplied as well as the mode of presentation.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with caution).

All the enrichment experiments resulted in levels of foraging and locomotory behaviours significantly increased from the baseline (see Table 4.1). The amount of time the birds spent resting and in maintenance activities (primarily preening) were significantly reduced, suggesting that the baseline levels of those behaviours were unnecessarily high. The time the group spent feeding from the dishes of prepared food also decreased significantly when enrichment devices were present, presumably because the birds were eating food from the enrichments and so required less from the dishes.

Experiment	**Maintenance Activity**	**Locomotion**	**Feeding From Dish**	**Foraging**	**Feeding and Foraging**	**Rest**	**Medium Energy Activity**	**High Energy Activity**
Baseline	15	10	14	5	19	11	59	30
Enrichment 1	12*	14*	5*	18*	*23	8	54*	37*
Enrichment 2	9*	17*	7*	18*	*25	6*	51*	43*
Multiple Enrichments	10*	16*	4*	25*	*29	6*	50*	44*
RESULTS OF ONE-WAY ANOVA	F= 17.8 d.f.= 3 p< 0.001	F= 14.4 d.f.= 3 p< 0.001	F= 65.2 d.f.= 3 p<0.001	F= 62.5 d.f.= 3 p<0.001	F= 13.5 d.f.= 3 p<0.001	F=5.4 d.f.=3 p=0.001	F= 8.4 d.f.= 3 p<0.001	F= 24.5 d.f.= 3 p<0.001

* Significantly different from baseline (Bonferroni post hoc test; sig. at 0.05).

Table 4.1: Summary of the mean percentage time spent in different activities during daylight hours by the Melbourne Zoo parrot group during the Winter (N=80). Medium Energy Activity = maintenance activities and alert but inactive; High Energy Activity = locomotion, feeding and foraging.

The mean percentage time spent feeding and foraging by parrot species in the wild was calculated to be about 34% of daylight hours (see Chapter 3), varying between 25% and 40% in the species for which data were available. In the presence of enrichments, the captive species studied increased the time they spent in these activities, which brought the mean values were closer to those of wild parrots. In the Melbourne Zoo parrot group the mean time spent feeding and foraging varied between 23 and 36% of daylight hours when multiple enrichments were provided, depending on the species studied. A comparison of the data from the wild and the data from the captive parrots in the multiple enrichment experiment, indicated no significant difference in the level of feeding and foraging behaviours shown by the two groups (paired t-test: t=0.81, df=7, p=0.447. NS).

Although the increases in foraging behaviour by the whole parrot group were significant when enrichments were present, there were also some interesting differences between the five species studied. Fig. 4.1 indicates how each species' foraging levels changed as they were provided with different enrichments. They increased significantly from baseline levels for all the species during each enrichment experiment, but some species had distinct preferences for particular enrichment devices. For example, during Enrichment 2, no fruit-based enrichments were provided and the king parrots carried out significantly less foraging during this experiment than when enrichments containing fruit were present in Enrichment 1 (independent t-test: t=3.22, d.f.=12.96 p=0.007) or when multiple enrichments were provided (independent t-test: t=4.76, d.f.=12.87 p<0.001). This may be because birds of this species eat fruits and berries as well as seed in the wild, and so were more attracted to enrichment combinations which included those foods. Both the king and princess parrots also utilised the flower rope which was only provided in the multiple enrichment experiment, spending a mean of 6% of daylight hours (about 40 minutes a day) manipulating the blossoms. Again, flowers are a food documented as being eaten by both these species in the wild. The princess parrots showed a significant increase in foraging behaviour in the multiple enrichment experiment, compared with the levels they displayed in the other two enrichment experiments (independent t-tests: Enriched 1 v Multiple: t=2.12, df=18, p=0.048; Enriched 2 v Multiple: t=2.93, df=18, p=0.009). The magnitude of this increase was probably due to the presence of the flower rope which, as already mentioned, they used for a mean of 40 minutes a day. According to the literature on wild diets (see Table 3.3 in Chapter 3), flowers and nectar constitute a regular part of the food intake of princess parrots, although the pair studied were probably born in captivity and, therefore, were unlikely to have encountered fresh blossom prior to this study.

The mean levels of feeding and foraging behaviours exhibited by the parrots varied with species. For example, the scarlet-chested parrots increased their foraging level to between 25 and 28% during all the enrichment experiments and decreased the time they spent feeding from their dishes. This maintained the total time they spent feeding and foraging at the same level that had been seen in the baseline enclosure (see Table 4.2) regardless of the enrichment provided. The king parrots, on the other hand, used more than 30% of their time foraging when multiple enrichments were provided but only about 15% during Enrichment 2 (when, as mentioned earlier, no fruit was included in the enrichments). As with the other species apart from the scarlet-chested parrots, the mean total time the king parrots spent feeding (from their dishes) and foraging (from enrichments and other items) increased significantly in the presence of enrichments.

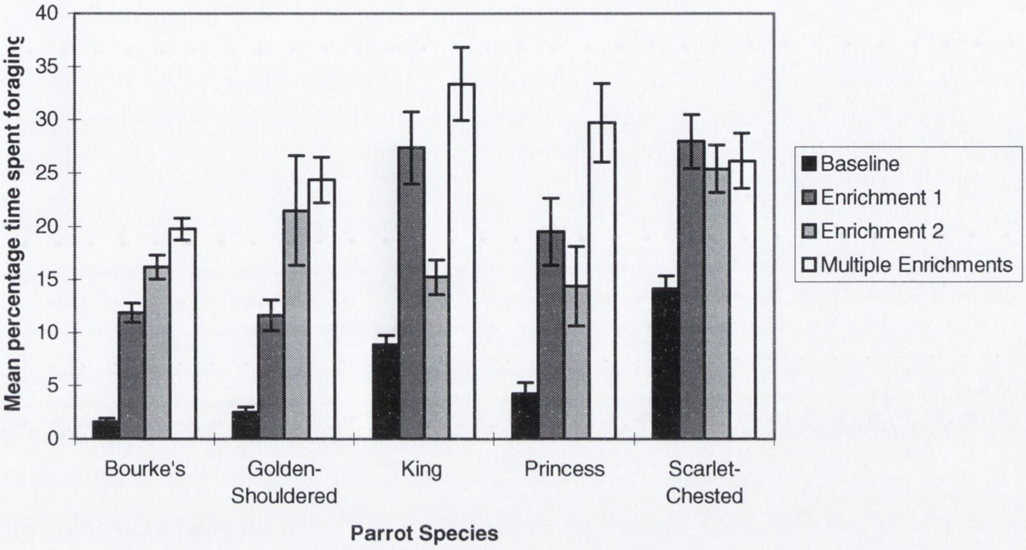


Fig. 4.1: The mean percentage time spent in foraging behaviours by the birds in the Melbourne Zoo parrot group in four enrichment experiments. (N=10 for all species except the scarlet-chested parrots (N=15) and Bourkes parrots (N=35)). All values were significantly different from baseline at the 0.001 significance level (1-way ANOVA followed by Bonferroni post hoc tests).

Experiment	Feeding & Foraging	Substrate Pecking
Baseline	30	9
Enrichment 1	35	5*
Enrichment 2	36	3*
Multiple Enrichments	33	3*

* Significantly different from baseline (independent t-test; sig. at 0.01).

Table 4.2: The mean percentage time spent feeding & foraging and pecking at their enclosure substrate by the Scarlet-Chested Parrots (N=15)

The scarlet-chested parrots, as mentioned in the previous chapter, showed unusually high mean levels of foraging in baseline conditions (14%) of which 9% involved pecking at the enclosure substrate. Table 4.2 shows how, in the presence of enrichments, the levels of that behaviour decreased significantly, although the levels of foraging increased significantly overall (see Fig. 4.1). It may be that the substrate pecking was a substitute behaviour, and that when they were provided with an opportunity to perform both the appetitive and consummatory components of foraging behaviour, they largely chose to do that in preference to the substrate pecking.

Discussion

It is clear that the provision of food-based enrichments resulted in the captive parrots significantly increasing the time they spend in high energy activities, particularly foraging, causing their daily activity budgets to approximate more closely to those of their wild conspecifics. The results suggest, however, that different species of parrot will show differing maximum levels of feeding and foraging activity in captivity in the presence of *ad lib.* food, and that such levels will only be seen when enrichments appropriate for the species are present. The seed-eating scarlet-chested parrots needed fewer types of enrichment to provide them with all the components of their usual diet than the king parrots, for example, who eat seed, fruit and flowers in the wild, and who were given fruit and seed in their prepared diet. The golden-shouldered parrots, however, which are primarily seed eaters, foraged less from the enrichments in Enrichment 1, than from those containing the same food components in Enrichment 2 or the multiple enrichment experiment. This suggested that they were influenced by the presentation of the enrichments, and it seems probable that both the presentation and the contents of enrichment devices can influence the motivation of the birds to interact with them. Species-specific preferences in that area will be investigated further in Chapter 5.

4.2 Cockatoos

4.2.1 Single Species Pair

Methods

The study was carried out on the Melbourne Zoo cockatoo pair (see section 2.2.1.2) in the Autumn months of April and May in 2000. In each experiment, after a three day acclimatisation period, the birds were scan-sampled 15 times during every hour from dawn to dusk (07.00 – 18.00) and their behaviour noted. This procedure was repeated each day for 5 days and activity budgets were calculated for the cockatoos in the same way as for the parrot species.

During the baseline observations, no changes were made to the enclosures (except for the removal of the fresh browse with which the birds were usually provided) or to the usual daily husbandry regime, and no enrichments were provided for the birds. In the two ensuing experiments the cockatoos were provided with their usual *ad lib* daily diet, and various enrichment devices, designed to stimulate natural foraging activity:

- In Enrichment 1: Large branches of fresh eucalyptus browse (see a) below) and a forage tray (see b) below)
- In the Multiple Enrichment experiment, the following enrichments were used: a) branches of fresh eucalyptus browse placed upright around perches in the enclosure; b) a forage tray filled with bark chips, with dry seed mix and nuts in their shells mixed in; c) fresh pine cones scattered on the floor; d) seed pods and cones from native Australian trees (e.g. *Hakia, Banksia, Eucalyptus*) scattered on the floor; e) a pinecone coated with dry seed mix using a non-toxic, water soluble PVA glue and suspended from a perch; f) a whole cob of corn suspended from the side netting of the enclosure on a skewer; g) a kebab of fruit and vegetable pieces threaded onto a length of wire, hooked onto the mesh wall of the enclosure above a fixed perch.

The types of fruit and vegetable used were: apple, satsuma, corn on the cob, green capsicum, celery, fennel root, carrot, sweet potato and button squash. Only the native seed pods, fresh pinecones and some of the varieties of nuts provided were not usually present in the birds' daily diet. All the enrichments were replaced daily, or when necessary, throughout the experiments.

Qualitative Results

When provided with food-based enrichments, the pair of Major Mitchells cockatoos showed a tendency to spend more time in active behaviours, such as moving around and foraging, and less time in less active behaviours such as resting. They also tended to spend less time feeding from the prepared foods in their dishes.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with caution).

The pair of Major Mitchells cockatoos responded to the presence of enrichments by significantly increasing the time they spent in locomotion and foraging, and significantly decreasing the time they spent eating from their prepared food (feeding) or in an inactive but alert state (Table 4.3). They also showed a decrease in the amount of time they spent in maintenance behaviours, but the decrease was only significant when the multiple enrichments were provided (see Table 4.3). The total mean percentage time which they spent feeding and foraging was the same (28%) in both enrichment experiments (see Fig. 4.5) which was significantly greater than their baseline levels (10%) despite a significant decrease in time spent feeding from their prepared food.

	Alert	Maintenance Activity	Locomotion	Feeding From Dish	Foraging	Feeding and Foraging	Medium Energy Activity	High Energy Activity
Baseline	38	17	8	10	10	21	59	29
Enrichment 1	32*	14	11*	4*	24*	28*	51*	39*
Multiple Enrichments	32*	10*	13*	2*	26*	28*	48*	41*
RESULTS OF ONE-WAY ANOVA	F=3.2 d.f.=2 p=0.06. NS	F= 7.3 d.f.= 2 p=0.003	F= 14.1 d.f.= 2 p< 0.001	F= 32.7 d.f.= 2 p<0.001	F= 23.3 d.f.= 2 p<0.001	F= 6.2 d.f.= 2 p=0.006	F= 15.0 d.f.= 2 p<0.001	F= 14.2 d.f.= 2 p<0.001

* Significantly different from baseline (Bonferroni post hoc test; sig. at 0.05).

Table 4.3: Summary of the mean percentage time spent in different activities during daylight hours by the Melbourne Zoo cockatoo pair during the Autumn (N=10). Medium Energy Activity = maintenance activities and alert but inactive; High Energy Activity = locomotion, feeding and foraging.

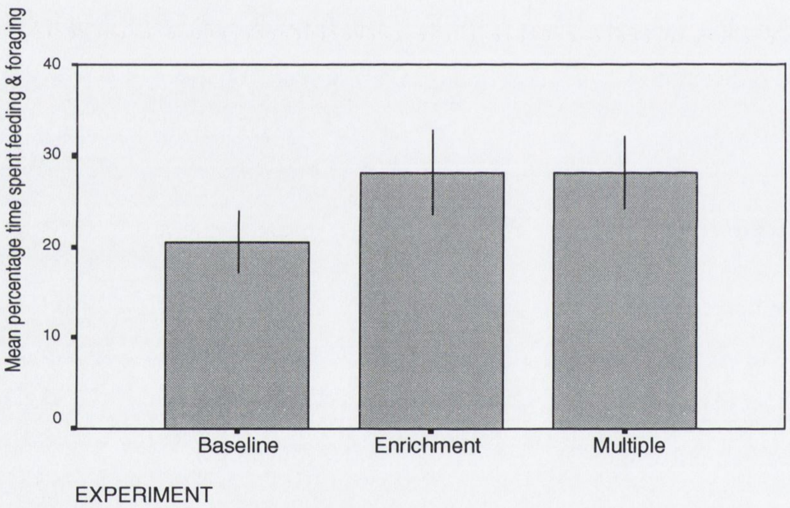


Fig. 4.5: The mean percentage time spent in feeding and foraging behaviours by the Melbourne Zoo cockatoo pair (N=10)

4.2.2 Mixed Species Aviary

Methods

The study was carried our on the Melbourne Zoo mixed species cockatoo group (see section 2.2.1.3) in the Winter month of August 2000. In each experiment, after a three day acclimatisation period, the birds were all scan-sampled 15 times during every hour from dawn until dusk (07.00 - 18.00) and their behaviour noted. This procedure was repeated each day for five days and activity budgets were calculated for the cockatoos in the same way as for the parrot species (see section 4.1).

During the baseline observations, no changes were made to the birds' regular daily husbandry regime except that the usual browse, which was replaced once a week, was removed from the enclosure and no enrichments were provided for the birds. In the two ensuing experiments the cockatoos were provided with their usual *ad lib* daily diet and various enrichment devices, designed to stimulate natural foraging activity. The large aviary in which the birds were housed (see Plate 2.3) made it possible to try out a wider range of enrichments than could be provided for the birds housed in smaller enclosures, such as the cockatoo pair, the lory group and the parrot group. The enrichment devices used were:

- In Enrichment 1 large branches of fresh eucalyptus browse (see j) below) and spiked fruit and vegetable pieces (see k) below) were added to the aviary, and the single feeding trough was replaced with 4 smaller feeding dishes, with the birds' usual amount of food divided between them. This set of enrichments consisted of devices which were suggested by one of the keepers usually in charge of the cockatoo aviary. It was made up of things which were easy for a keeper to provide daily (or replace when necessary, in the case of the browse) with the minimum of time and effort. As the exhibit housed a mixture of species it was thought that the provision of extra feeding dishes might reduce competition between the birds and allow them to forage in way which was less stressful than was possible when the food was provided in a single trough.

- In the Multiple Enrichment experiment, the 4 feeding dishes were left in place, and the following enrichments were also added to the enclosure: a) a forage tray filled with bark chips with dry seed mix and nuts in their shells mixed in; b) a log of wood coated with dry seed mix stuck on with non-toxic water soluble PVA glue; c) fresh pine cones scattered on the floor; d) dry seed mix sprouted to a height of 10cm in a tray of soil; e) seed pods and cones from native Australian trees (e.g. *Hakia, Banksia, Eucalyptus*) scattered on the floor; f) a pinecone coated with dry seed mix using a non-toxic, water soluble PVA glue and suspended from a perch; g) fresh *Banksia* flowers pushed stem first into the enclosure substrate; h) a whole cob of corn suspended from the side netting of the enclosure on a skewer; i) a block of dry seed (available in pet shops) suspended from a perch; j) large branches of fresh eucalyptus browse presented upright in containers of water; k) 6 inch, bullet-headed nails hammered into perches, with whole and half vegetables and fruits spiked on them.

The fresh produce used was: Green capsicum, passionfruit, broccoli, half cobs of corn (some with the husk left on), apple, pear, peanut squash, button squash, carrot, beetroot, sweet potato, orange and satsuma. Only the native seed pods, fresh pinecones and some of the varieties of nuts provided as enrichments were not usually present in the birds' diet. All the enrichments were replaced daily, or when necessary, throughout the experiments.

Qualitative Results

When provided with food-based enrichments, the birds in the cockatoo group showed a tendency to spend more time foraging and less time in inactive behaviours such as preening and resting in an alert state. Unlike the previous groups studied, they did not show any increase in the time they spent moving around their enclosure. The time they spent feeding from their prepared food increased when more dishes were provided for the birds to use, along with browse and spiked fruit and vegetables but decreased again when a greater variety of enrichments were provided along with the extra dishes.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with caution).

The cockatoo group, like the parrots and the Major Mitchells pair, significantly increased the mean percentage time they spent foraging and decreased the time they spent alert but inactive, or in maintenance behaviours (see Table 4.4) when enrichments were provided. Unlike the parrots and the Major Mitchells pair, the cockatoo group did not significantly alter the time they spent in locomotory activity, but even at baseline levels it was much higher than was shown by the cockatoo pair even in enriched surroundings (see Table 4.3).

	Alert	Maintenance Activity	Locomotion	Feeding From Dish	Foraging	Feeding and Foraging	Medium Energy Activity	High Energy Activity
Baseline	29	11	21	9	14	23	49	44
Enrichment 1	23*	7*	22	11*	24*	35*	39*	57*
Multiple Enrichments	20*	8*	22	7	30*	37*	38*	60*
RESULTS OF ONE-WAY ANOVA	F=20.8 d.f.=2 p<0.001	F= 7.3 d.f.= 2 p=0.003	F= 14.1 d.f.= 2 p< 0.001	F= 32.7 d.f.= 2 p<0.001	F= 23.3 d.f.= 2 p<0.001	F= 6.2 d.f.= 2 p=0.006	F= 15.0 d.f.= 2 p<0.001	F= 14.2 d.f.= 2 p<0.001

* Significantly different from baseline (Bonferroni post hoc test; sig. at 0.05).

Table 4.4: Summary of the mean percentage time spent in different activities during daylight hours by the Melbourne Zoo mixed species cockatoo group during the Winter (N=40). Medium Energy Activity = maintenance activities and alert but inactive; High Energy Activity = locomotion, feeding and foraging.

Another area in which the results from the cockatoo group differed from those of the parrots and the Major Mitchells pair, was the time the birds spent feeding from their dishes of prepared food. In Enrichment 1, when extra feeding dishes were provided, in addition to fresh browse and fresh fruit and vegetable pieces, the time spent using the dishes increased significantly from baseline levels. In the multiple enrichment experiment the extra dishes were still present but use of them decreased back down to baseline levels, as the birds spent even more time foraging from the enrichments.

All the cockatoo species significantly increased the time they spent foraging in both enrichment studies as well as the total time they spent in feeding and foraging behaviours (see Fig. 4.7 (feeding and foraging are plotted here, not just foraging, as the addition of the extra feeding bowls was, itself, an enrichment. The same was done for the single species pair in Fig. 4.5 for ease of comparison)). There was no significant difference between the total time spent feeding and foraging in the two enrichment experiments by any of the four species, although, like the parrots, the species differed in the maximum levels they exhibited (see Fig. 4.7). The increases in foraging behaviour during the multiple enrichment experiment, when compared with Enrichment 1, were countered by a reduction in the time spent feeding from the dishes. This was also the case for the group as a whole (see Table 4.4).

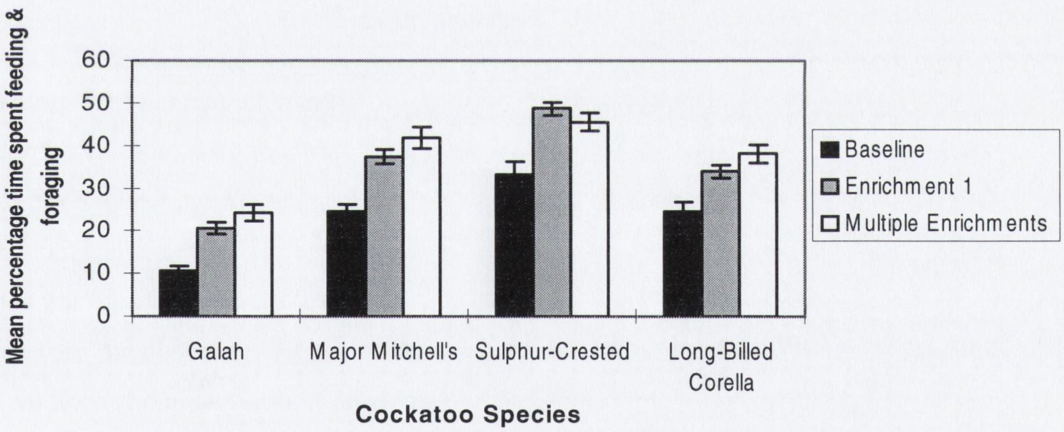


Fig. 4.7: The mean percentage time spent in feeding and foraging behaviours by the Melbourne Zoo mixed species cockatoo group (N=40). All values are significantly different from baseline at the 0.001 significance level (1-way ANOVA followed by Bonferroni post hoc tests).

Discussion

It seems that the use of multiple feeding dishes in a mixed species enclosure resulted in the birds spending longer using them. Although the birds may have been ingesting more food when the extra dishes were present, it could be that, when competition for the prepared food was reduced, they were more leisurely in their selection and processing of the food items, and so spent more time at the dishes than they had at the trough.

Unlike the parrots, when the cockatoos were enriched they still spent far less time in feeding and foraging behaviours than their wild conspecifics are reported to do (see Table 4.5). This was with the exception of the sulphur-crested cockatoos, who were apparently spending longer in these behaviours in captivity. It is difficult to be sure whether this is due to natural variance within this species, or whether the wild data is perhaps inaccurate in some way. It certainly seems strange that such a large cockatoo should spend such a comparatively small part of the day feeding in the wild.

Cockatoo Species	Feeding & Foraging (captive)	Feeding & Foraging (wild)
Galah	24	51
Major Mitchells	42	At least half the day
Sulphur-Crested	46	38
Long-Billed Corella	38	83

Table 4.5: The mean percentage of daylight hours spent feeding and foraging by the birds in the mixed species cockatoo group in the multiple enrichment experiment and their wild conspecifics in Winter (wild data taken from Table 3.4 and Rowley, 1991)

Cockatoos may usually spend longer foraging in the wild than in captivity in these experiments, whereas the parrots do not, because of the different diets of the two groups in the wild. The parrot species studied eat small grains, flowers and soft fruit, which cockatoos may also eat, but in the main, wild cockatoos feed on items which require a longer processing time. They extract seeds from hard seed pods and cones, as well as digging up roots and corms and digging insect larvae out of trees. Although the cockatoos were provided with seed pods and nuts in their shells in the multiple enrichment experiment, it almost certainly took the birds less effort to obtain food from most of their enrichments than it would take wild cockatoos to forage for their natural foods. In the wild studies examined, however, the sulphur-crested cockatoos were studied in grain producing areas and a lot of their foraging was from wheat and other cereal crops, which are probably as quick to process as the foods eaten by wild parrots. A second explanation, of course, is that the cockatoos were not provided with enrichments as appropriate and interesting to them as the parrots were, and so did not increase the time they spent foraging to the same level as their wild conspecifics.

It should be noted, however, that the degree to which the time spent feeding and foraging differed between the captive cockatoos in their baseline enclosure and the wild cockatoos, was much smaller than the difference in levels of feeding and foraging behaviour between the wild and captive parrots. It is possible that this is due to the different recording methods used in the wild studies. In much of the literature on wild cockatoo activity budgets, unlike the parrot literature, the studies are ambiguous about locomotory activity. Locomotion which occurred during foraging activity may have been counted as foraging during the wild studies. If that had been done with the captive cockatoos, their 'foraging' levels would have been higher, and their levels of locomotion lower, and their levels of feeding and foraging would be closer to those of their wild conspecifics.

4.3 Lories

Methods

The study was carried out on the Melbourne Zoo lory group (see section 2.5) in the Autumn months of April and May in 2000. In each experiment, after a three day acclimatisation period, the birds were scan-sampled 15 times during every hour from dawn to dusk (07.00 – 18.00) and their behaviour noted. This procedure was repeated each day for 5 days and activity budgets were calculated for the lories in the same way as for the parrot species (see section 4.1).

During the baseline observations, no changes were made to the enclosures (except for the removal of the fresh browse, with which they were provided every two weeks or so) or to the usual daily husbandry regime, and no enrichments were provided for the birds. In the three ensuing experiments the lories were provided with their usual daily diet (mainly nectar, but with some seed and fruit) and various enrichment devices, designed to stimulate natural foraging activity:

- In Enrichment 1, a flower rope (see e) below) and a whole corn cob (see b) below)
- In Enrichment 2, a seeded branch (see d) below) and branches of fresh browse (see f) below).
- In the Multiple Enrichment experiment, the following enrichments were used: a) an open pinecone coated with dry seed mix using a non-toxic, water soluble PVA glue and suspended from a perch; b) a whole cob of corn suspended from the side netting of the enclosure on a skewer; c) a kebab of fruit and vegetable pieces threaded onto a length of wire, hooked onto the mesh wall of the enclosure; d) a wooden branch, suspended from the roof by a rope passing through it, and coated with dry seed mix stuck on using a non-toxic, water-soluble PVA glue; e) a vertically suspended rope with fresh flowers threaded through it; f) fresh branches of eucalyptus browse; g) a block of wood with holes of

various sizes drilled in it, stuffed with dried fruit and seed mix; h) a wooden branch, suspended from the roof by a rope passing through it, with fresh fruit and vegetable pieces stuck onto nails protruding from the branch.

The types of fruit and vegetable used in the enrichments were: Apple, satsuma, passionfruit, grapes, broccoli, banana, pieces of corn cob and pear. All of the enrichments, with the exception of the flower ropes and the fresh browse, only contained food materials which were already present in the daily diet of the birds, although the fruit-based enrichments contained more types of fruit and vegetables than the birds would usually receive and they were given limited, rather than *ad lib*, seed mix in their daily diet. The enrichments were replaced daily or when necessary.

Qualitative Results

When provided with food-based enrichments. The birds in the lory group showed a tendency to spend more time in foraging behaviours, and less time in an alert but inactive state. There was no apparent change in the time they spent preening, nor in the time they spent feeding from their prepared food (which primarily consisted of an artificial nectar mix).

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with caution).

	Alert	Maintenance Activity	Locomotion	Feeding From Dish	Foraging	Feeding and Foraging	Medium Energy Activity	High Energy Activity
Baseline	32	14	11	7	15	21	61	32
Enrichment 1	18*	13	8	5	29*	34*	51*	46*
Enrichment 2	16*	16	9	8	20*	28*	47*	37
Multiple Enrichments	15*	13	9	5	31*	36*	44*	45*
RESULTS OF ONE-WAY ANOVA	F=42.8 d.f.=3 p<0.001	F= 0.9 d.f.= 3 p=0.5. NS	F= 2.1 d.f.= 3 p=0.1. NS	F= 4.7 d.f.= 3 p=0.005	F= 15.3 d.f.= 3 p<0.001	F= 13.5 d.f.= 3 p<0.001	F= 11.4 d.f.= 3 p<0.001	F= 13.0 d.f.= 3 p<0.001

* Significantly different from baseline (Bonferroni post hoc test; sig. at 0.05).

Table 4.6: Summary of the mean percentage time spent in different activities during daylight hours by the Melbourne Zoo lory group during the Autumn (N=20). Medium Energy Activity = maintenance activities and alert but inactive; High Energy Activity = locomotion, feeding and foraging.

The birds in the lory group significantly increased the mean percentage time they spent foraging and, hence, feeding and foraging, from baseline levels in the three enrichment experiments (see Table 4.6). They significantly decreased the time they spent alert but inactive, but, unlike the parrots and cockatoos, there was no decrease in the amount of time they spent in maintenance behaviours, or in feeding from their dishes. There was no significant change either, in the time the lories spent in locomotory activity.

The two species of lory both behaved in accordance with the levels of significance showed by the whole group in Table 4.6 (i.e. neither species showed any significant change in maintenance behaviour or feeding from their dishes, and both significantly increased the time they spent foraging). As the time they spent feeding from their prepared food did not change significantly when enrichments were present, but foraging increased (see Fig. 4.11), the total time spent feeding and foraging by each species increased significantly from baseline in each enrichment experiment.

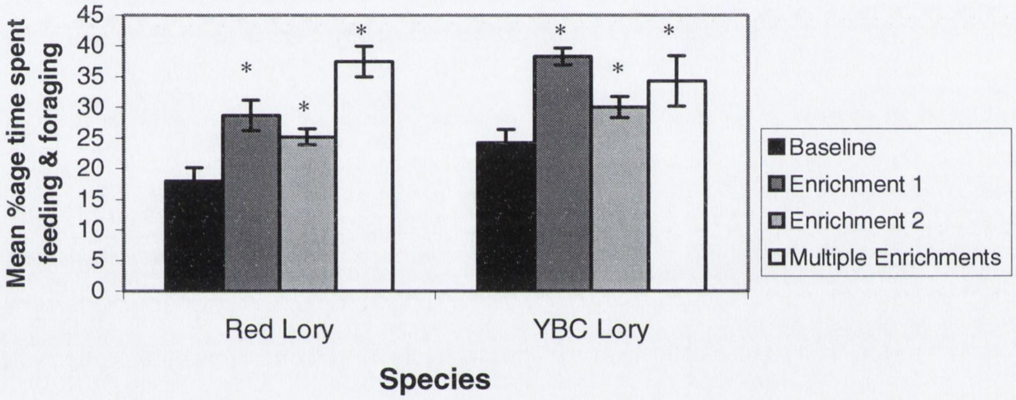


Fig. 4.11: The mean percentage time spent in foraging behaviours by the birds in the Melbourne Zoo lory group in three enrichment experiments. (N=10 for each species). All values are significantly different from baseline at the 0.05 significance level (1-way ANOVA followed by Bonferroni post hoc tests).

Species	Experiment	Leaf Manipulation
Red Lory	Baseline	8
	Enrichment 1	1*
	Enrichment 2	2*
	Multiple Enrichments	0.2*
Yellow-Backed Chattering Lory	Baseline	14
	Enrichment 1	0.5*
	Enrichment 2	1*
	Multiple Enrichments	0.5*

* Significantly different from baseline (Bonferroni post hoc test; sig. at 0.05).

Table 4.7: The mean percentage time spent manipulating fallen leaves from the roof of their aviaries by the birds in the Melbourne Zoo lory group in the Autumn (N=10 for each species).

As mentioned in Chapter 3, both species of lory, especially the chattering lories, displayed a behaviour during the study which involved pulling leaves fallen from nearby trees through the wire mesh roof of their aviary (see Plate 4.1). The birds would then hang upside down by one foot, holding a leaf in the other, and shred it into small pieces using their beaks. Table 4.7 shows that the time the birds spent in this behaviour decreased significantly when the birds were provided with environmental enrichments. It is likely, therefore, that the leaf shredding was a vacuum or substitute activity.

Plate 4.1: Red Lory pulling a fallen leaf through the wire mesh roof of its enclosure, preparatory to shredding it

Discussion

The birds in the lory group increased the mean percentage time they spent in foraging behaviour when enrichments were present and decreased the time they spent alert but inactive, but they differed from both the cockatoos and the parrots studied in other ways. The lories did not show any change in the time they spent in maintenance behaviours when they were provided with enrichments. When the time the lory group spent in these behaviours in the three enrichment experiments was compared with the time spent in them by the wild lories, there was no significant difference (paired t-test: t=0.53, df=3, p=0.635. NS). This indicates that the captive birds may not have been performing unnecessarily high levels of preening in their baseline enclosure, and so they did not decrease the time they spent in maintenance behaviours when they used more time foraging. Instead the lories reduced the time they spent in alert but inactive behaviour.

Another difference between the lories and the parrot and cockatoo groups was that the lories did not significantly decrease the time they spent feeding from their prepared food. Their main food was an artificial nectar mix, and it may be that they drank the same amount of that daily, whatever other foods were present. Alternatively, the lories could have been spending the same amount of time feeding, but could have been doing so more slowly, and, hence, ingesting less, in enriched surroundings. The former theory, however, is supported by the results put forward in Chapter 7. A pair of Yellow-Backed Chattering Lories, held at Dublin Zoo, were provided with enrichment devices and their food dishes were weighed in order to see if they ate more or less when food-based enrichments were present. The Dublin Zoo lories, unlike those in Melbourne Zoo, were given *ad lib* fruit, seeds and pulses daily, as well as a measured volume of artificial nectar mix. They drank most of their nectar daily, leaving only the dregs, but results showed a significant decrease in the mass of solid food which they ate from their dish when food-based enrichments were provided. It seems probable, therefore, that the species of lory studied in these experiments either have a minimum requirement for nectar, regardless of whether fruit and seed is also available, or they have such a strong preference for nectar as a food that they will drink whatever volume is provided for them (up to a physiologically limited maximum).

Unlike the parrots and cockatoos, the Melbourne Zoo lories did not receive *ad lib* seed and fruit in their feeding dishes. But the results from the Dublin Zoo study indicate that, if they had then they, like the other psittacines studied, would eat significantly less from their dishes when enrichments containing the same foods were provided.

4.4 Further Discussion

During the enrichment experiments all the birds studied continued to receive their regular diet in their feeding dishes. They were, as usual, given more food than they actually ate daily, so they always had some present in their dishes should they be hungry and could feed *ad lib* (with the exception of the lory species, which received limited amounts of seed). Thus, they had no need to use the enrichments in order to obtain nutrition; it was much less effort for them to eat the food from the dishes than for them to obtain the same food from the enrichment devices. Not only did the birds have to expend energy and time to obtain the food contained in the enrichments, but to use most of the devices, especially the suspended branches, they had to use wing and leg muscles in order to balance themselves. This applied particularly to the parrots and lories which used the seeded or fruit branch enrichments.

Despite the effort involved in using the enrichments, their presence resulted in levels of foraging behaviour significantly increased from the baseline for the parrots, cockatoos and lories, and a decrease in levels of more sedentary behaviours. Previous experiments have shown similar results, for example, a study was carried out on a female blue-eyed cockatoo (*Cacatua opthalmica*) which was showing severe feather picking behaviour. An environmental enrichment program resulted in a decrease in preening activity, while foraging behaviours increased significantly (King, 1992b). In another study, Coulton (1997) observed a set of psittacines consisting of thick-billed parrots *Rhynhopsitta pachyrhyncha*, green-winged macaws *Ara Chloroptera* and yellow-backed chattering lories. These birds spent significantly less time feeding from their dishes when provided with food-based enrichments (seeds and beans placed in holes drilled into pieces of wood, and the holes covered with starch paper).

Contrafreeloading (CFL) is a behavioural phenomenon whereby captive animals choose to work for food rather than eating identical, freely available food (e.g. Jensen, 1963). The authors of the Coulton paper suggested that CFL might be occurring, perhaps as a result of the psittacines sampling all the food supplies available to them in order to assess the benefits of switching from one to another, instead of just eating from their dishes. The results outlined in this chapter certainly indicate that psittacines will choose to spend time feeding from food-based enrichments, even in the presence of more easily available, prepared food, and thereby perform contrafreeloading behaviour. The results set out in Chapter 5 of this study, however, show that all the species observed showed definite preferences for particular enrichments, when several were provided. This does not support the idea that their contrafreeloading behaviour was a result of random food sampling by the birds (as suggested by Coulton *et al.*, 1997).

The results outlined in this chapter indicate that the birds studied show CFL behaviour, because they choose to spend time feeding from the enrichments. The experiments outlined in Chapters 7 and 8 investigate this area of behaviour further. Chapter 7 examines whether psittacines in captivity show CFL behaviour in regard to the mass of food which they choose to ingest from their dishes, as well as in regard to the time they spend in foraging activity, and from enrichment devices. Chapter 8 describes a set of experiments designed to investigate the causes of contrafreeloading in more detail.

It seems that, while all the psittacines decreased the time they spent in inactive behaviours when enrichments were provided, spending more time foraging instead, there were also some differences between the groups studied. Levels of locomotion increased from baseline in the parrot group and the single species cockatoo pair during all the enrichment experiments. No increase in locomotory activity was shown by the cockatoo group, or by the lory group, when they were provided with enrichments. The cockatoos in the mixed aviary all showed much higher levels of locomotion than the cockatoo pair, and it was thought likely that this was because of the limited space available to the pair in their enclosure, which restricted their movement. Once enrichments were provided, they moved more between enrichments and perches, thereby increasing their levels of locomotion. The lories, however, were kept in enclosures of similar size to the parrot group and cockatoo pair, and their baseline locomotion levels were similar to those of the parrot group, but they did not increase their level of locomotion when enrichments were provided. It may be that the differences seen in the parrots and cockatoos were primarily influenced by enclosure size, but that lories do not conform to the same pattern. Lories may need to be provided with stimuli other than enrichment devices in order to increase their levels of locomotion; in a larger enclosure, for example, they might move around more.

Another difference between the groups studied was that the lories did not decrease the time they spent feeding from their dishes when enrichments were present. As discussed in section 4.3, it is thought that this was mainly due to the birds receiving relatively low levels of seed and fruit in their prepared food. It also appears that, unsurprisingly, lories show a strong inclination to drink nectar, regardless of what other foods are provided.

The other way in which the lories differed from the other psittacines studied was that their levels of maintenance behaviour did not decrease when enrichments were provided. As discussed earlier, it seems to be the case that the lories were only performing the necessary levels of these behaviours, even in baseline enclosures, but that the other birds may have been displaying higher levels of maintenance behaviours than were needed to keep their skin and plumage in good condition. None of the results supported the finding of Coulton *et al.*(1997) described in Chapter 1, that psittacines increased the amount of time they spent in maintenance behaviours when they were provided with food-based enrichment devices. It is not clear whether the increase in preening observed by Coulton *et al.* occurred as a result of providing the birds with enrichment, but the results of this study suggest that that may be unlikely. Alternatively, it may be that the enrichment device used in the Coulton study (a length of wood with 50 holes drilled in it and one bean, one sunflower seed or three saffra seeds place in all or some of the holes, which were then covered with starch paper) was not sufficiently attractive to the species studied to result in the behaviour levels seen in the experiments outlined here. The birds only spent a mean of 3 - 4 % of their observation periods using the device, but why that should lead to a significant increase in preening levels is unclear.

The published literature on animal behaviour and the economics of choice, discussed in Chapter 1, describes how the choices made by captive animals can indicate the relative importance of the activities in which they choose to increase or decrease their levels of performance. The birds studied, had ten or eleven hours of daylight to fill with various behaviours. Some behaviours have necessary minimum levels, for example, the birds have to spent a certain amount of time feeding every day in order to ingest sufficient nutrients for their health and survival; the animal's demand for such behaviours may be called inelastic. Other behaviours such as resting may be less important and the time spent in them can vary considerably with no ill effects for the animal. The demand or need animals have to perform such behaviour can be termed elastic (review by Dawkins, 1990).

By comparing the activity budgets of the psittacines studied in baseline enclosures with their behaviour when enrichments were provided, the relative importance of various behaviours to the different birds can be assessed. When the enrichments were added to the enclosures, the birds were presented with a new set of choices about how to use their time. All the species studied chose to increase the time they spent in foraging behaviours although to differing, perhaps species-specific, maxima), so they had to decrease the time they spent in other behaviours in order to compensate. The parrots, cockatoos and lories all chose to decrease their levels of inactive behaviours, spending less time resting or in an alert but inactive state, and all, except the lories (for the reasons discussed above) spent less time feeding from their prepared food. Whereas the decrease in feeding was compensated for by the increase in foraging, so that the birds still ingested food, merely from a different source, the decrease in resting behaviours was replaced by a behaviour (foraging) with a completely different function. It appears, therefore, that psittacines in captivity exhibit an elastic demand for resting behaviours and that they will decrease their levels of such behaviours if they are provided with opportunities to forage instead.

Maintenance behaviours appear to be in elastic demand for all the groups studied except for the lories. This may indicate that these behaviours are of greater importance to the lories than to the other birds and that they are more inelastic in their demand for them. The reasons for this difference are unknown but may be related to the ecology of the birds in the wild state. Lories tend to roost in large groups in holes in trees (Forshaw, 1989; Higgins, 1999), so may be more susceptible to ectoparasites, meaning that preening would be of greater importance to them than to psittacines which roost in more open surroundings. Alternatively, as the lories predominantly feed on nectar and move through large clusters of blossom in order to feed, it may be that they have a greater need to preen than psittacines with other feeding strategies, in order to keep their feathers clean of nectar residue. More information on the behaviour of these birds in the wild is needed in order to test these theories.

A high degree of motivation for carrying out different activities can also be indicated by animals performing functionally inappropriate, or 'vacuum' behaviours (Vestergaard, 1980). The scarlet-chested parrots and both species of lory studied performed high levels of foraging behaviour in baseline conditions, despite the fact that they were not apparently gaining any food as a consequence. It is thought that such behaviours indicate the frustration of an ethological 'need' (Hughes & Duncan, 1988) as discussed in Chapter 3, and the results from this chapter, indicating that the birds decrease their vacuum behaviours significantly in favour of more productive foraging, support the idea that foraging is a highly motivated activity in psittacines. Although not all the birds studied showed such high levels of vacuum activities, the fact that they all chose to spend substantial lengths of time foraging from enrichment devices, when they could have eaten the same food from their dishes, suggests that, even in a relatively complex captive environment, psittacines do find the opportunity to exhibit foraging behaviour a strong stimulus.

In the baseline enclosures, the Major Mitchells pair spent significantly less time feeding and foraging than their conspecific pair in the mixed cockatoo aviary (independent t-test: t=2.162, df=18, p=0.044). Whether this difference was a result of the social or physical environment of the birds, or whether it resulted from normal behavioural variation within the species is not clear. It is worth noting in this context, however, that while the Major Mitchells cockatoos in the mixed aviary were bred at Melbourne Zoo, the pair housed separately came from an aviculturalist and were raised in hanging wire cages with no enrichment except wood for chewing. It may well be, therefore, that they showed less foraging behaviour (making less use of the enrichment devices) than their conspecifics as a result of that early environmental conditioning. Alternatively, it may be that this species, at least, is more active in a large enclosure, or in one with more than two cockatoos in it, where the competition intrinsic to a larger group may stimulate them to spend more time foraging. One of the difficulties encountered in zoo research is that the animals' early experience is often unknown and may involve a sub-standard environment if they were not bred in the zoo where they are studied as adults. Various experiments have established that the level of enrichment supplied in the early environment can have effects on the levels of exploratory and foraging behaviour shown later in life (e.g. Rozensweig, 1986; Wemelsfelder, 1997; Mendl, 1990), although the degree and type of effect varies from study to study and more research is needed in order to establish the effects of early enrichment on adult behaviour..

The activity budgets of the captive birds became more similar to what is known of wild psittacine behaviour, when they were provided with appropriate enrichment devices. It was difficult to assess the actual degree of species-specific behaviour which was seen in the captive environment, and to compare the wild and captive behaviours of any particular species, because of the paucity of wild data available, and the small size of the captive groups being studied, but the results certainly indicate some strong species-specific behaviour patterns. It is also interesting to note that the princess parrots foraged from a flower rope when it was unlikely that they had even seen blossom before. The lories were all captive bred and had definitely not had the opportunity to feed from flowers, prior to the enrichment experiments. These species displayed, apparently innate, wild type foraging behaviours, but further research is needed on both captive and wild birds in order to ascertain whether all captive psittacine species show similar species-specific patterns to their wild conspecifics, when they are kept in enriched environments.

Chapter 5

Foraging Preferences

Introduction

The two previous chapters have examined the behaviours of captive psittacines, with particular reference to feeding and foraging behaviours. Although species differences were analysed, the main thrust of the research concerned general patterns of behaviour which applied to parrots, cockatoos or lories. Wild psittacine species do, however, engage in foraging behaviours which are species-specific, and the birds' use of enrichments reported in Chapter 4 appeared to reflect this. For example, the king parrots showed their highest levels of foraging only when fruit based enrichments were provided as well as seed, but the Bourkes parrots only made use of seed-based enrichments. By discovering the foraging preferences of different psittacine species in captivity, therefore, each species can be provided with those enrichments to which it is most attracted and of which it makes most use. This is an approach recommended in the environmental enrichment literature, but one which has been underused to date (Mench, 1998).

The results from Chapter 4 indicated that it was during the multiple enrichment experiments that maximum observed levels of foraging behaviour were performed by all the psittacines studied. For some species, these levels were also at a maximum during other enrichment experiments; it depended on the enrichment devices that were provided. This showed that psittacines may only choose to be 'maximally' active when they are provided with their preferred, probably species-specific, enrichment devices.

As discussed in Chapter 1, it is thought that species-specific behaviours may be lost or modified in captivity if the animals are not given the opportunity to express them (Shepherdson, 1994; McClean, 1997). Learnt behaviours are lost from a population more rapidly than innate behaviours, which may be recovered after generations of absence if the correct environmental stimuli are recreated (May, 1991). It is important, therefore, to ascertain whether captive psittacines will perform wild-type species-specific foraging behaviours when the opportunity is provided, even if they have never encountered such a situation previously.

In order to look at some of these issues, the results of the multiple enrichment experiments described in Chapter 4 are examined in greater detail here, so that the preferences of the birds for different enrichment devices can be assessed. As the numbers of individuals of each species studied were low, it is possible that individual, rather than species-specific, preferences could be shown in the results. When the observed preferences of a species correspond to reported wild-type behaviours, however, it is more likely that the individuals studied are displaying behaviour normal for their species.

Methods

The methods and study groups used in the multiple enrichment experiments were described in detail in Chapter 4.

5.1 Parrots

Qualitative Results

The species golden-shouldered parrots, scarlet-chested parrots and Bourkes parrots tended to forage primarily from the seed-based enrichments, the princess parrots mainly used the seed and flower-based enrichments (as well as the seeded fruits such as passionfruit) and the king parrots foraged from the seed, flower and fruit-based enrichments, indicating a more generalist approach to feeding, consistent with descriptions of their ecology in the published literature.

The golden-shouldered parrots showed a tendency to prefer the seeded branch to the forage tray, whereas the scarlet-chested parrots tended to use the forage tray more. Both these enrichments contained the same seed mix but the branch was suspended in the air whereas the forage tray was on the floor of the aviary. The scarlet-chested parrots also foraged from the millet sprays provided near ground level. These results suggests that the positioning and type of enrichment provided can be as important to the birds as the food it contains.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with caution).

The golden-shouldered parrots spent most of their foraging time on the seeded branch during the experiment, although they also foraged from millet sprays, the forage tray and the flower rope (see Table 5.1). This preference for the seeded branch over the forage tray which contained the same seed mix (paired t-test: $N=10$, $t=9.85$, $df=9$, $p< 0.001$) is particularly interesting as, when the only other enrichments provided were a swinging fruit branch and endive leaves (for description of enrichments see section 4.1) the golden-shouldered parrots used the forage tray for a mean of 9% of the day, a significantly longer time than they spent using it in the multiple enrichment experiment (independent t-test: t=4.51, df=10.93, p=0.001).

	Golden-Shouldered Parrot	Scarlet-Chested Parrot	Bourkes Parrot	Princess Parrot	King Parrot
1	Seeded Branch 18% (119 mins.)	Millet 9% (59 mins.)	Seeded Branch 11% (73 mins.)	Forage Tray 9% (59 mins.)	Fruit Branch 13% (86 mins.)
2	Millet* 2% (13 mins.)	Forage Tray 6% (40 mins.)	Forage Tray* 7% (46 mins.)	Flower Rope 6% (40 mins.)	Flower Rope* 6% (40 mins.)
3	Forage Tray^ 2% (13 mins.)	Flower Rope^ 4% (26 mins.)	Millet*^ 1% (7 mins.)	Fruit Branch 5% (33 mins.)	Seeded Branch^ 5% (33 mins.)
4	Flower Rope 2% (13 mins.)	Sprouted Seeds 3% (20 mins.)	Fruit Branch*^ <1% (< 7 mins.)	Seed Block " 4% (26 mins.)	Seed Block 3% (20 mins.)

* Significantly different from the value immediately above; ^ significantly different from the value two above; " significantly different from the value three above. Paired samples t-test, significant at the 0.05 level)

Table 5.1: The top four preferences of each parrot species during the multiple enrichment experiment (the mean percentage and the mean number of minutes of the 11 hour day spent using each device is indicated).

The birds' preference for the seeded branch may be because, in the wild, the golden-shouldered parrots usually obtain their food from seedpods, grassheads or seed-bearing plants in understorey woodland (Garnett & Crowley, 1995), a process involving manipulation of the seeds in a way mimicked by tearing the seeds from the hanging branch. They only feed from dry fallen seed (such as that provided in the forage tray) when seeding plants aren't available. An alternative explanation is that the birds preferred to feed two metres from the ground, rather than at ground level. If this is the case, however, it is likely to be a captivity-induced preference; they are recorded as mainly feeding close to or on the ground in the wild (Garnett & Crowley, 1995).

The scarlet-chested parrots, on the other hand, feed mainly on the ground from fallen seed and grass heads in the wild and showed a strong preference for the ground level seed-based enrichments in this study (see Table 5.1). Their strongest preference was for the millet sprays but they also foraged from the forage tray, the sprouted seeds and the flower rope.

The Bourkes, like the golden-shouldered parrots, showed a significant preference for the seeded branch over their second preference, the forage tray (paired t-test: N=35, t=-4.10, df=34, p<0.001), although they also used the tray for a mean 7% of daylight hours (46 minutes a day). They spent some time using the millet sprays, but mainly limited their foraging to the seeded branch and forage tray and showed no interest in the enrichments which were not seed-based. These observations are mainly in accordance with the wild-type feeding behaviour described in the literature (see review by Higgins, 1999) where they are regarded as being entirely seed-eaters. This species lives in arid and semi-arid areas of Australia and, although they are thought to be primarily ground-level feeders, they are also known to forage in trees and their overall diet in the wild is poorly known. Their preference for the seeded branch over the forage tray may be influenced by the same considerations as affected the golden-shouldered parrots, with the preference being weaker as a result of living in more arid conditions, where dry seed on the ground is the only food source available to them for longer periods than those experienced by the golden-shouldered parrots.

Both the Australian king parrots and the princess parrots utilised the flower rope when it was provided, spending a mean 6% of daylight hours (about 40 minutes a day) manipulating the blossoms (see Table 5.1). Flowers are a food documented as being eaten by both these species in the wild, as well as the golden-shouldered parrots, but the scarlet-chested parrots also spent time foraging from the flower rope. In the available literature on their feeding habits in the wild, the scarlet-chested parrots are regarded exclusively as seed eaters (see review by Higgins, 1999). While their use of the flower enrichment could be a behaviour induced by captivity, it seems more likely that the data on their food preferences in the wild are incomplete and that they do regard flowers as a potential source of food.

The king parrots are cited as eating mainly seeds in the wild but also fruit, berries, flowers and nectar (see review by Higgins, 1999). This generalist approach to feeding was reflected in their enrichment preferences which covered seeds, fruit and flowers. At first glance, the fact that the most preferred enrichment was the fruit branch, rather than a seed-based enrichment, is surprising but this result does not, on closer inspection, contradict the information from the wild. One of the constituents of the fruit branch was fresh corn on the cob, and maize is one of the seeds from cultivated crops which king parrots eat in the wild state (Jenkins, 1971). As well as eating satsuma, apple, passionfruit, grapes and pear from the fruit branch, the king parrots ate broccoli florets (really a flower) and, as previously mentioned, corn on the cob (a seed). Likewise, princess parrots are described in the literature as eating mainly seeds but also flowers and leaves (Higgins, 1999) so their use of the fruit branch was initially surprising. They pecked a little at the apple and other fruits on the branch, as well as eating the broccoli florets, but their main preference was for the passionfruit. Although passionfruit are made up primarily of seeds, there is also a substantial amount of flesh present which the princess parrots also ate. Again, while this may be a captivity-induced behaviour, it is possible that this species may eat fruits or berries in the wild when the opportunity arises. It may be that this occurs only rarely or when the birds are camouflaged in fruiting trees, and, hence, has not been widely observed or recorded. The princess parrot may be a more generalist feeder than was previously thought.

5.2 Cockatoos

5.2.1 Single Species Pair

Qualitative Results

The Major Mitchell's pair foraged from fruit, seed and nut-based enrichments, but showed a tendency to prefer pecking at and stripping bark, branches and browse.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined in the text below should be treated with caution)

1	2	3	4	5	6
Bark & Branches 9% (59 mins.)	Browse 6% (40 mins.)	Nuts in Shells 5% (33 mins.)	Fruit Kebab^ 3% (20 mins.)	Forage Tray^ 1% (7 mins.)	Native Seedpods 1% (7 mins.)

* Significantly different from the value immediately to the left; ^ significantly different from the value two to the left.
Paired samples t-test, significant at p=0.05)

Table 5.2: The top 6 preferences of the pair of Major Mitchell's Cockatoos at Melbourne Zoo during the multiple enrichment (the mean percentage and the number of minutes of the 11 hour day spent using each device is indicated).

5.2.2 Mixed Species Aviary

Qualitative Results

The galahs foraged primarily on the fruit and vegetables provided and, along with the sulphur-crested cockatoos, showed a tendency to feed close to ground level in preference to eating the same foods on provided on higher perches. The corellas showed the same liking for fruit and vegetable-based enrichments as the other two species, but spent less time foraging from enrichments at ground level. The Major Mitchell's cockatoos, however, ate a wider range of the foods provided in the enrichments, at a greater variety of heights.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with caution)

	Galah	Sulphur Crested	Major Mitchell	Corella
1	Floor Food 8% (53 mins.)	Floor Food 19% (125 mins.)	Seed Block 10% (66 mins.)	Fruit & Veg. Pieces 11% (73 mins.)
2	Fruit & Veg. Pieces 3% (20 mins.)	Fruit & Veg. Pieces* 3% (20 mins.)	Fruit & Veg. Pieces 7% (46 mins.)	Floor Food* 5% (33 mins.)
3	Roof Beams 2% (13 mins.)	Banksia^ 2% (13 mins.)	Browse^ 6% (40 mins.)	Browse*^ 2% (13 mins.)
4	Substrate*^ 1% (7 mins.)	Sprouted Seeds 2% (13 mins.)	Nut In Shells^ 3% (20 mins.)	Roof Beams 2% (13 mins.)
5	Browse* 1% (7 mins.)	Wall 2% (13 mins.)	Sprouted Seeds 3% (20 mins.)	Substrate 1% (7 mins.)
6	Wall^ 1% (7 mins.)	Native Seed Pods 1% (7 mins.)	Forage Tray 2% (13 mins.)	Bark 1% (7 mins.)

* Significantly different from the value immediately above; ^ significantly different from the value two above. Paired samples t-test, significant at p=0.05)

Table 5.3: The top six preferences of each cockatoo species during the multiple enrichment experiment (the mean percentage and the number of minutes of the 11 hour day spent using each device is indicated).

The species in the mixed cockatoo aviary (see Table 5.3), like the parrots, mainly showed enrichment preferences in accordance with their recorded wild-type feeding behaviour (see Table 3.4). The galahs fed primarily from the fruit and from the corn cobs, although they preferred to pick up the pieces which fell to the enclosure floor, rather than feeding from a higher perch. They pecked at the joins of the enclosure's metal roof-support girders for an average of 13 minutes a day, possibly looking for insects, as well as spending a mean of 7 minutes a day manipulating the fresh eucalyptus browse. The sulphur-crested cockatoos also foraged mainly on the ground although they fed from the fruit and vegetables on the higher perches as well. They tore the fresh *Banksia* flowers apart in addition to pulling up the sprouted seeds and chewing at the native seed pods. These preferences are in accordance with the literature on wild-type feeding behaviour (see review by Higgins, 1999) which cites both galahs and sulphur-crested cockatoos as being primarily ground level feeders. In the study, these two species also spent some time each day pecking at the plaster wall of the enclosure (no significant change from baseline levels (ANOVA: F=1.66, df=2, p=0.20) possibly looking for extra minerals or performing beak cleaning or maintenance behaviour. Alternatively the plaster pecking may have been a stereotypic behaviour which was unaffected by the enrichment regime.

The long-billed corellas are regarded in the literature as primarily ground level feeders (see review by Higgins, 1999). In this experiment, however, they spent significantly more time foraging from the whole fruit and vegetables fixed to perches above ground level than they spent feeding from the same food that had fallen to the floor (see Table 5.3). They did appear to favour the lowest of the perches (20 cm from the floor) although they also fed from higher perches, but unfortunately data were not recorded on those variables. It may be that the performance of the appetitive behaviours involved in foraging from these enrichments was of more importance to the birds than the height above ground level at which the behaviour was performed. This species has a beak specialised for digging up and shredding bulbs and corms, and the processing of half corn cobs or squashes may utilise the same wild-type manipulative skills as they would use in more natural foraging behaviours.

Like the galahs the corellas spent time every day manipulating the iron girders that supported the enclosure roof. The corellas, however, pecked directly at the metal of the girders and of the roof itself. Interestingly, this may not be entirely a captivity-induced behaviour; birds of this species were observed in the wild pecking at the iron girders of a bridge spanning the Murray River in Echuca, Victoria in Autumn 2001 (pers. obs.).

Major Mitchell's cockatoos are reported to be generalist feeders in the wild and forage both at ground level and in shrubs and trees; they eat seed and fruit as well as roots, insect larvae and bulbs (see review by Higgins, 1999). The birds in the mixed aviary showed similar feeding habits in the enrichment experiment (see Table 5.3). They fed mainly from the seed block and fruit and vegetables, but also foraged on the fresh browse, the nuts in their shells, the sprouted seeds and the dry seed mix from the forage tray. The single-species pair, however, showed some different preferences (see Table 5.2). Their strongest preference was for pecking at bark and branches, mainly at their nesting log, as they were a breeding pair starting to nest-build (they laid eggs a few weeks later). Both pairs used the browse, nuts and forage tray, and the mixed aviary pair also manipulated the sprouted seeds, an enrichment that was not provided for the single species pair. The mixed aviary birds were provided with fruit and vegetables fixed on long nails, hammered into log and branch perches, but due to lack of space the single species pair were given fruit and vegetables on a wire kebab, suspended from the wire mesh of the enclosure wall instead. The birds in the mixed aviary spent more time foraging from their spiked fruit and vegetable pieces than their conspecifics spent eating from their kebab. This may be due to the presentation of the food; the kebab was less robust than the fruit on nails, and contained smaller pieces of food, so may have been less preferred as a foraging device by the cockatoos.

The most striking difference in preferences between the two pairs of Major Mitchells cockatoos is that, while the pair in the mixed aviary spent a mean 10% of their time foraging from the seed block, the other pair did not use either the seed block or the seed-coated pinecone. It may be that the difference between the pairs is due to natural variation within the species, but it seems odd that birds which eat seed from a dish daily should have a natural reluctance to forage for it when given the opportunity. It is more likely, perhaps, that the early environment of the single-species pair has made them less inclined than their conspecifics in the mixed aviary to examine novel objects. As discussed in the previous chapter (section 4.4), they were raised in a fairly barren environment, which may have caused them to show low levels of exploratory behaviour as adults. From comparison with what is known of the foraging behaviour of this species in the wild, it seems likely that the single-species pair may have been showing less species-typical behaviour than the pair in the mixed species aviary.

5.3 Lories

Qualitative Results

Both lory species showed a tendency to prefer the flower-based enrichments to the others, although they also foraged from fruit and seed-based enrichments.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined in the text below should be treated with caution)

	1	2	3	4	5	6
Red Lory	Flower Rope 11% (73 mins.)	Fruit Kebab 8% (53 mins.)	Fruit Branch 7% (46 mins.)	Corn Cob*^ 3% (20 mins.)	Seeded Branch^ 2% (13 mins.)	Wood Block*^ 1% (7 mins.)
Yellow-Backed Chattering Lory	Flower Rope 16% (106 mins.)	Fruit Branch* 3% (20 mins.)	Fruit Kebab^ 3% (20 mins.)	Seeded Branch* 2% (13 mins)	Browse* 2% (13 mins.)	Corn Cob* 2% (13 mins.)

* Significantly different from the value immediately to the left; ^ significantly different from the value two to the left.
Paired samples t-test, significant at p=0.05

Table 5.4: The top six preferences of each lory species during the multiple enrichment experiment (the mean percentage and the number of minutes of the 11 hour day spent using each device is indicated).

Both species of lory made most use of the flower and fruit enrichments although only the chattering lories spent significantly more time foraging from the flower rope than from the fruit branch or kebab (see Table 5.4). Both species also used the seed-based enrichments (including maize) and the chattering lories showed what may have been a species-specific tra in their liking for fresh browse. The birds were observed to strip off thin pieces of green bark and, apparently, lick the sappy wood beneath.

Generally, however, the two species showed similar preferences, and although little is known about their behaviour in the wild (see Chapter 3), their preferences do fit with what is known of the diet of wild rainbow lories, scaly lories and other Australian species. These birds are recorded as eating mainly nectar and pollen but also fruits, seeds, leaf buds, bark and, occasionally, insects in the wild (Utschick, 1989; see review Higgins, 1999). This may indicate, therefore, that lories tend to be less species-specific in their foraging preferences than other psittacines. Alternatively, it is, of course, possible that the foraging preferences shown by the captive birds were not wild-type choices, but were induced by captivity.

5.4 Discussion

The enrichment devices for use in the study were designed with the aim of increasing the levels of foraging behaviour shown by the captive psittacines. It was decided that preference should be given in the enrichment experiments to devices which would encourage expression of the whole complex of behaviours associated with feeding and acquiring food, as the satisfaction of both the appetitive and consummatory phases of these behaviours could be important to the birds (Mench, 1998).

The species-specific preferences for particular enrichments observed in this experiment indicated preferences not only in foodstuffs, but also in forms of food presentation (and, hence, the appetitive behaviours needed for foraging). For example, in the parrot group dry seed mix was presented in forage trays, in seed blocks, in the millet sprays (in part) and stuck to hanging branches, as well as being provided *ad lib* in a dish; different parrot species exhibited strong preferences for different forms of presentation. In the cockatoo group both the galahs and the sulphur-crested cockatoos fed from the fruit and vegetables presented in dishes and on long nails, but preferred to eat the pieces that fell to the floor. These examples suggest that it is the performance of the foraging activity, rather than merely the ingestion of the food, that is the main purpose of the behaviour.

As mentioned in the introduction to this chapter, it has been postulated that failure to provide a captive environment that is at least functionally equivalent of that of the wild (including supplying opportunities for species-specific behaviours such as foraging) will result in the loss of many natural behaviours in animal and bird species. The results of this study indicate that a variety of parrot and cockatoo species retained species-specific foraging behaviours in captivity, and performed them when appropriate opportunities were provided.

Both the sulphur-crested cockatoos, one galah and one of the long-billed corellas studied were definitely born in the wild; both golden-shouldered parrots, all the scarlet-chested parrots, one king parrot, one Bourkes parrot, one corella, both of the Major Mitchells cockatoos from the single-species aviary and all of the lories were born in captivity. The provenance of the other birds is unknown (all information from Melbourne Zoo records).

The golden-shouldered and scarlet-chested parrots were all captive bred, as were all the lories, and so were known not to have encountered the foraging opportunities provided by the enrichment devices previously. Their parents may, or may not, have been captive bred themselves, but it is difficult to see how they could have taught wild-type foraging techniques to their offspring, when there was no opportunity in their captive environment to express them. Despite this, the birds appeared to show species-specific behaviours and preferences which were in accordance with their wild-type ecology. For example, the golden-shouldered parrots preferred the seeded branch over the forage tray or millet sprays, whilst the scarlet-chested parrots preferred the seed-based enrichments that were provided at floor level. This may indicate that some wild-type psittacine foraging behaviours, at least, are innate and can be stimulated in a captive population by providing the birds with species-appropriate food-based enrichments. How long such behaviours will be retained in a population, if there are no opportunities for their expression, is unclear and is an area worthy of further research.

More research on psittacine feeding behaviours in the wild is also needed in order that conspecifics in captivity can be provided with appropriate dietary and behavioural choices as currently the information available is, at best, incomplete. For example, although some psittacine species are reported to eat invertebrates, they are rarely listed as eating larger creatures. Crimson rosellas (*Platycercus elegans*) like many psittacines, are reported to feed on seed, fruits, nuts, blossoms, buds and insects (Juniper & Parr, 1998; Higgins, 1999) but they have been observed taking and eating baby mice during the mating season by casual observers (Grant, 2000). The crimson rosella is a common species both in the wild and in captivity, yet this facet of their diet has been entirely missed in the reference books available for psittacine species. Without more information about wild behaviour and preferences, captive psittacines cannot be provided with a full range of species-specific opportunities.

Chapter 6

Spatial Use of Enclosures

Introduction

In Chapters 4 and 5 it was shown that a wide range of psittacines made use of food-based environmental enrichments when they were added to their enclosures. The enrichment devices were placed at various heights in each enclosure and at a variety of distances from the front wall, although never within 2m of any walls with a view of the public, in case this deterred the birds from approaching the enrichments. During the enrichment experiments, the birds used time that they had spent inactive or preening, during baseline observations, in foraging from the enrichment devices. It was thought that this enrichment use could result in the psittacines altering the spatial use they made of their enclosures. Alternatively it could be that the birds were fixed in their spatial use of their enclosures, and would only use enrichments that were in those areas that the birds would occupy anyway, even if unenriched. Research has indicated that the spatial distribution of food in a species' natural habitat can influence its preferred strategies for foraging in captivity (Roberts & Cunningham, 1986; Fernandes, 1996) but work by Nos and Camerino (1984) suggested that captive psittacines will often adapt their feeding strategies largely in accordance with the way in which their food is presented. For example, some parrot species which do not feed at ground level in the wild, will do so in captivity if the food is only available at that level, rather than carrying food to a higher perch before consuming it. These theories were tested in the experiment described in this chapter, which looked at psittacine behaviour in both basic and enriched environments to see if the birds displayed any preferences for enrichment devices based on where they were located in the aviary.

Methods

Height Category	Description
0	ground level
1	between 0 and 1metres from ground level
2	between 1 and 2 metres from ground level
3	between 2 and 3 metres from ground level
4	more than 3 metres from ground level

Table 6.1: Description of the height categories used throughout this study

This study is based on information collected during the experiments outlined in Chapter 8 carried out on the Healesville Sanctuary orange-bellied parrot group (see section 2.2.2.1). The behaviour of 16 orange-bellied parrots (groups A and B in the study described in Chapter 8), kept in pairs in identical enclosures, was monitored in their enclosures from 14.00 to 17.00 for two days. On the first day the birds were observed 8 times every hour in unenriched baseline enclosures, and on the second day they were provided with enrichments and observed again (see Chapter 8 for detailed methods). The height of each bird from the ground was noted, using the categories described in Table 6.1 and their behaviour recorded. The enrichments provided in each enclosure were:

- a forage tray filled with sand, with fine seed mix distributed through it, placed at ground level
- small planks of wood placed on the floor, with holes drilled in them and whole sprays of millet presented upright with their stalks in the holes
- a second forage tray was also provided in each enclosure at the same level as the birds' food was presented daily (slightly less than 1m from the ground).

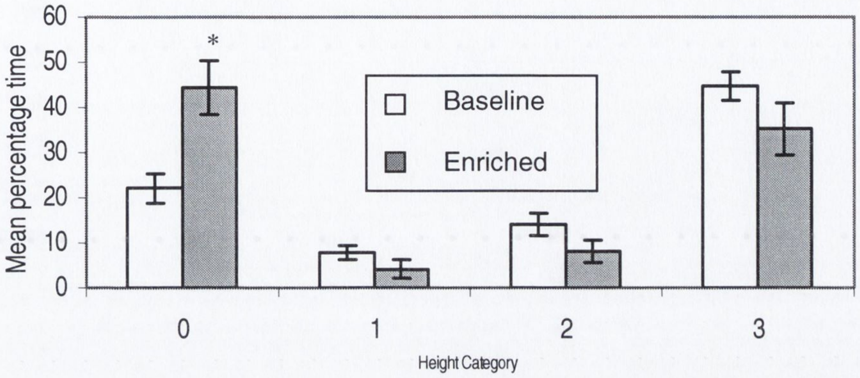
Qualitative Results

When provided with enrichments placed on the floor of the enclosure, as well as about 1 metre from the ground, the parrots tended to spend more time feeding from the lower devices.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with caution).

The parrots spent significantly less time using the high forage tray than the one at ground level (paired samples t-test: t=2.37, df=7, p=0.02) or the millet sprays (paired samples t-test: t=2.67, df=7, p=0.01) although both forage trays contained the same mix of seed in sand, and the millet was of the same variety as was included in the seed mix. In addition, the birds were all bred in captivity and used to eating their food from dishes placed almost 1m from the ground. The higher tray was about 50cm closer to the front of the enclosure than the lower tray but, given that the front of the enclosure was several metres away from the area walked through by the researcher and zoo keepers, it is unlikely that this would be enough to dissuade the birds from feeding at their usual position in the enclosure. That being the case, it appears that the parrots showed significant species-specific preferences for the positioning, as well as type, of enrichments. In the wild this species feed mainly at ground level (Smales, 2000) and these experiments indicated a significant preference for doing so in captivity also.



(* significantly different from baseline value at 0.05 level – One-way ANOVA followed by Bonferroni post hoc tests)

Fig. 6.3: Graph Showing the Mean Percentage Time spent at Different Heights From the Ground by the Healesville Sanctuary Orange-Bellied Parrot Group When They Were Provided With Environmental Enrichment Devices. (N=48)

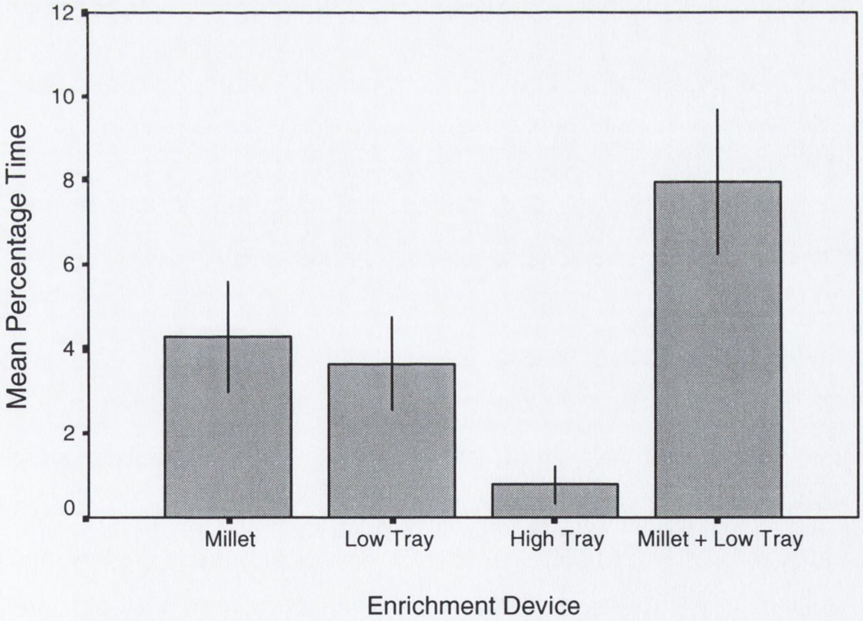


Fig. 6.4: The Mean Percentage Time Spent Using Different Enrichment Devices by the Healesville Sanctuary Orange-Bellied Parrot Group (N=48)

There was a significant increase in the time the birds spent at ground level when enrichments were provided (see Fig. 6.3). Although there was no significant change in the time spent at other levels, there was obviously a decrease in their summed values to compensate for the extra time spent on the ground. In order to investigate whether the birds were attracted to the floor by the enrichments presented there, or because they preferred to forage at that level, the birds' use of the different enrichment devices was analysed (see Fig. 6.4). As the high and low trays were identical in all but position, the results indicate that the birds' preference was to forage at ground level, given the opportunity to do so, although they also made use of the higher forage tray.

Discussion

The results from the experiment described here indicate that psittacines will use enrichments that allow the expression of species-specific foraging behaviours, whatever their location in their enclosure, if that is the only, or most preferred, enrichment available to them. This was also seen in the experiments outlined in Chapters 4 and 5 when, for example, the golden-shouldered parrots were observed feeding from a forage tray at ground level for a longer period of time daily when the seeded branch (their preferred enrichment) was not available. Psittacines do, however, show a preference for foraging at particular levels in the enclosure, and display high levels of foraging if both the type and location of the enrichment is in accordance with the wild-type ecology of the species under consideration. For example, the orange-bellied parrots foraged more from the low forage tray than from the high one, when given the choice. It would be interesting to carry out further research to see how long the birds would spend foraging from each tray if they were only provided with one at a time.

This study looked solely at the birds' use of vertical space. Having seen how psittacines approach and use the enrichment devices positioned around their enclosures at various levels, however, it seems probable that their use of horizontal space would increase in diversity if the enrichments were suitably placed. Further research would be needed in order to confirm or refute this idea with any certainty, however.

The results of these experiments indicated that food-based environmental enrichments do influence the spatial use of enclosures by captive psittacines. Enrichment devices may be placed in an aviary at a variety of appropriate heights and positions and thereby increase the usable foraging area of the enclosure. The birds, however, show species-specific preferences, both for particular enrichments and for their locations which indicates that the location of a food-based enrichment device in an enclosure may be critical to its degree of effectiveness in stimulating foraging behaviour.

Chapter 7

Dietary Intake

Introduction

The enrichment experiments described in Chapters 4 and 5 indicated that a variety of captive psittacine species chose to spend time eating from food-based enrichments rather than from their dishes of prepared food. The results did not, however, indicate whether the amount eaten by the birds changed when enrichments were present.

The study described in this chapter was designed to investigate the mass of food consumed daily by captive psittacines, both in the absence and presence of food-based enrichments. Most of the enrichments contained the same foods as were present in the prepared diet which the psittacines received daily. This meant that the birds could eat the same amounts of, for example, seed or fruit, whether enrichments were present or absent, but they could choose whether to obtain it from the enrichments as well as, or instead of, from their food dishes. Alternatively, the birds could eat more or less in total mass than usual when enrichments were present, or they could eat more of some dietary components and less of others. Either of the two latter scenarios could have serious implications for the health and husbandry of the enriched birds. As these studies used the enclosure as the experimental unit they are statistically more robust than the behavioural experiments outlined elsewhere in this thesis.

7.1 The Effects of Food-Based Enrichment on the Mass of Food Eaten From Prepared Diets

Methods

This experiment was carried out on the Dublin Zoo psittacine group (see 2.2.3.1) in the Winter month of November 2000. All of the birds in the group were given the same *ad lib* daily diet, made up of chopped fruit and vegetables, boiled egg, dry seed mix and sprouted pulses, placed in dishes in the indoor section of each enclosure, to which they had 24 hour access. The indoor enclosures were kept at an approximate temperature of 10-12°C throughout the experiment. One dish of food was put in each of the six enclosures except aviary 2, which was provided with two dishes, as two species were kept in that enclosure. The pair of lories were given 285ml of artificial nectar mix daily, in a separate feeder, in addition to their dish of food.

During this experiment all the food was weighed before being put in the feeding dishes in the birds' enclosures. All the pieces of food and seed husk remaining 24 hours later were collected and weighed again. In order to facilitate this, the floors of the indoor enclosures were lined with newspaper, instead of wood chip, for the duration of the experiment. The collected food remnants were divided into seed, egg, pulses and fruit and vegetables before being weighed. It should be noted that the seed husks tended to absorb water from the fresh foods and to get coated in small particles of egg and fruit, especially in the baseline experiment where more food was eaten from, and therefore mixed up in, the dishes. Consequently, the mass of seed eaten by the birds was almost certainly underestimated in the results. The weighing and sorting procedures were carried out for five days when the birds were in their baseline enclosures, and during that time they were given no other foods or enrichment.

Aviary	Species	Enrichment Devices
1	Orange-Winged Amazon Parrot (x2)	Fruit and vegetable pieces on long nails, forage tray, seeded branch
2	Blue-Crowned Conure (x5) Military Macaw (x2)	Seeded branch, millet sprays, fruit and vegetable pieces on long nails, forage tray
3	Moluccan Cockatoo (x1)	Fruit and vegetable pieces on long nails, forage tray
4	Yellow-Backed Chattering Lory (x2)	Fruit and vegetable pieces on long nails, millet sprays, seeded branch
5	Citroen-Crested Cockatoo (x2)	Fruit and vegetable pieces on long nails, forage tray
6	Moluccan Cockatoo (x1)	Fruit and vegetable pieces on long nails, forage tray

Table 7.1: The enrichment devices provided in each aviary for the Dublin Zoo psittacine group during the dietary intake experiment. The number of individuals of each species, housed in each aviary, are indicated in brackets. See section 2.3.1 for more detailed descriptions of the enrichment devices.

In the second phase of the experiment, the birds were provided with species-specific enrichments in their outdoor enclosures for four days to accustom all the birds to using them (see Table 7.1). The enrichments incorporated food items that were present in the prepared dishes of food which the birds received daily, and the devices selected for each aviary were designed to allow the performance of wild-type foraging behaviours by the psittacines being studied. The food weighing and sorting procedures were then repeated for another five days. During that time, the enrichments were all replaced daily or as necessary. It was not possible to measure the mass lost from the food as a result of evaporation in this experiment. It was assumed to be consistent in both the baseline and enriched enclosures, but the calculated masses of foods ingested should be regarded as for comparative purposes only. The mass of food eaten from their dishes by the birds in each aviary was compared for baseline and enriched conditions.

Qualitative Results

All the birds studied showed a clear tendency to eat less of their prepared food when food-based enrichments were also provided in their enclosures.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with a degree of caution).

The birds in all the aviaries showed a significant decrease in the total mass of food they ingested from their dishes of prepared food when enrichments were provided (see Fig. 7.1). The lories continued to drink the same volume of nectar (285ml) daily.

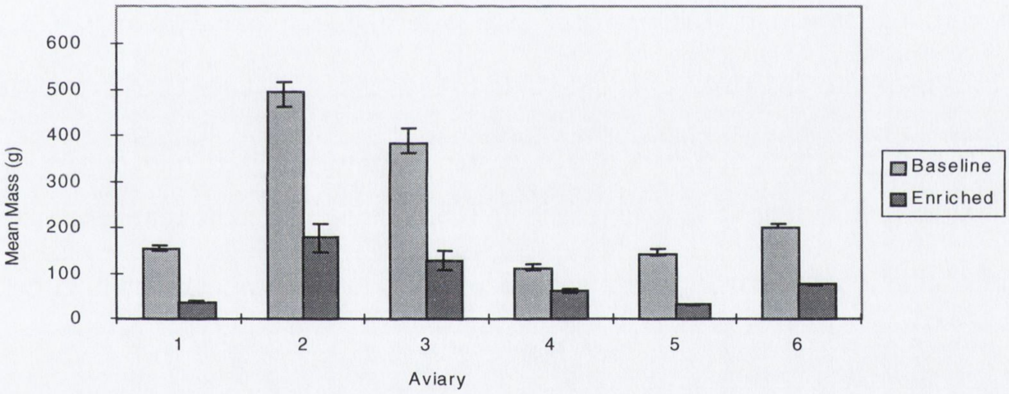


Fig. 7.1: The total mean mass (g) of food eaten daily from their prepared diet, provided in feeding dishes, by the Dublin Zoo Psittacine Group, both in unenriched (baseline) and enriched enclosures. The differences between the amounts eaten in the different conditions, for each aviary, were all significant at the 0.02 level (one-way ANOVA). See Table 7.1 for details of the birds in each aviary. N=5.

There were significant decreases in the mass of fruit and vegetables, the mass of pulses and the mass of boiled egg eaten by the whole group, and also by the birds in each aviary (see Fig. 7.2) with two exceptions: The lories (aviary 4) did not show a significant decrease in the amount of pulses they ingested when provided with enrichments (baseline mean = 10.6g, enriched mean = 4.4g; ANOVA: df=1, F=0.98, p=0.35. NS) and the second solitary Moluccan cockatoo (aviary 6) showed no significant decrease in the mass of egg he ate (baseline mean = 18.6g, enriched mean = 12.4g; ANOVA: df=1, F=2.6, p=0.15. NS). The reasons for these two results are not known, but it may be that the lories had a stronger preference for pulses than the other species studied while the Moluccan cockatoo may have been demonstrating an individual preference for boiled egg. Neither egg nor pulses were incorporated into the enrichment devices, so could only be eaten from the prepared dishes of food.

The results indicated that only the amazon parrots (aviary 1) showed a significant decrease in the amount of seed they ate from their dishes when enrichments were provided (baseline mean = 13.4g, enriched mean = 4.6g; ANOVA: df=1, F=5.6, p=0.045). That the birds in the other aviaries, and the group as a whole, didn't show a significant decrease in the amount of seed they ate is probably primarily due to the problems with sorting and weighing the seed remnants outlined in the methods section. The orange-winged amazons tended to mix up their food in their dishes less than the birds in the other aviaries (pers. obs.) so the results pertaining to their seed intake may be more accurate than those from the other aviaries.

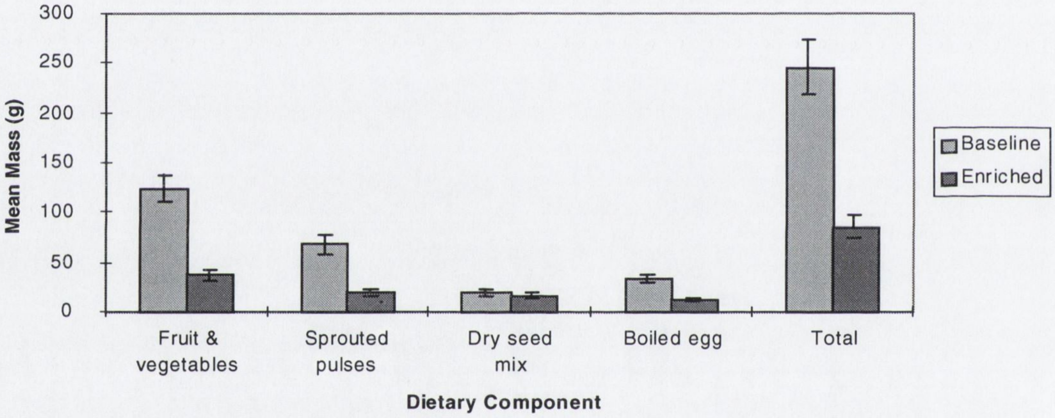


Fig. 7.2: The mean mass (g) of their prepared diet eaten from feeding dishes daily by the Dublin Zoo Psittacine Group, both in unenriched and enriched enclosures. There was no significant change in the amount of dry seed mix eaten in the two enclosure types (see explanation in 'Methods'), but the changes in the other food categories shown were all significant at the 0.01 level (one-way ANOVA). N=5.

7.2 The Mass of Food Ingested From Environmental Enrichments

Although the indoor aviaries at Dublin Zoo were suitable for presenting the prepared food in dishes, they were not large enough to contain the enrichment devices, which were all placed in the outdoor enclosures. These outside areas, however, were not suitable for carrying out experiments to assess the mass eaten from the various enrichment devices, as they had virtually no protection from the rain. As the mass of the enrichments would increase if they got damp, it would not be possible to measure accurately the amount eaten by the birds. In addition, the coarse, deep litter substrate in the outside enclosures would make it difficult to collect bits of food from the enrichments that had dropped onto the ground. This being the case, it was decided to look at the amount of food ingested from enrichment devices using a group of psittacines in Melbourne Zoo, Australia.

The enclosures at Melbourne Zoo were outdoor aviaries with large covered areas where the enrichments could be placed, and there was very little rainfall during the two weeks of the experiment. There were problems assessing the amount of prepared food eaten by the birds, however, as five of the seven aviaries had mice infestations, and the mice fed from the birds' food dishes, although there was no evidence of them feeding from the enrichments.

Methods

This study was carried out on the Melbourne Zoo psittacine group (see 2.2.1.6) in the Spring month of October 2001. The methods followed those of the Dublin Zoo study described above, but in this experiment, the enrichment devices as well as the prepared food were weighed daily, in addition to any food that had fallen from the enrichments onto the aviary floor. The enrichments placed in the seven enclosures are shown in Table 9.2 and were selected to provide species-specific foraging opportunities, based on descriptions of the birds' wild-type behaviour.

Aviary	Species	Enrichment Devices
1	Golden-Shouldered Parrot (x2)	Forage tray, seeded branch
2	Monk Parakeet (x5)	Flower rope, fruit and vegetable pieces on long nails, seeded pinecone
3	Australian King Parrot (x2)	Flower rope, swinging fruit branch, swinging seeded branch
4	Plum-Headed Parrot (x2)	Flower rope, swinging fruit branch, swinging seeded branch
5	Cloncurry Ringneck Parrot (x4)	Flower rope, forage tray
6	Galah (x2) Red-Tailed Black Cockatoo (x2)	Forage tray, fruit and vegetable pieces on long nails, seeded cone
7	Major Mitchell's Cockatoo (x2)	Fruit and vegetable pieces on long nails, seeded cone

Table 7.2: The enrichment devices provided in each aviary for the Melbourne Zoo psittacine group during the dietary intake experiment. The number of individuals of each species are indicated in brackets. See section 2.3.1 for more detailed descriptions of the enrichment devices.

The birds were given two dishes of prepared food daily; one of chopped fruit and vegetables and one of seed and nuts (the golden-shouldered parrots were the only species not to receive nuts in their diet). Keeping the fresh and dry foods separate in this way made it much easier to measure the mass of each than in the Dublin Zoo study, where the two were, of necessity, mixed together and had to be separated before weighing. All the dishes contained *ad lib* fresh food or seed mix, as well as a fixed number of peanuts in their shells for the parrots, and peanuts and walnuts in their shells for the cockatoos. The size of the chopped pieces of fruit and vegetable varied with the species, but were consistent for each, with the golden-shouldered parrots, for example, receiving much smaller pieces than the Major Mitchells cockatoos.

The temperature in the aviaries fluctuated according to the prevalent weather conditions (the ambient temperature during the experiment varied between 17 and 31°C during daylight hours), and the size of the pieces of fresh food was variable between aviaries, so it was not possible to calculate accurately the levels of evaporation of moisture from the enrichments or the prepared food. Preliminary studies, however, indicated that 100g of fruit and vegetables lost between 11 and 28g of moisture over a 24 hour period, in an aviary protected from direct wind and rain, and kept at a temperature of 20-30°C, depending on the size of the food pieces and the types of fruit and vegetables used. It should be noted, therefore, that, as in the study carried out at Dublin Zoo, when 'amount eaten' or 'ingested' is referred to in the text, the values quoted actually include mass lost through evaporation as well as, in this experiment, the mass of any pieces of food not collected from the floor, or those eaten by any pest species which got into the enclosures, both for the prepared food and for the enrichment devices. The results, therefore, should only be regarded as accurate for the purpose of comparisons within the group, not for assessing the exact mass of food eaten in each aviary.

In order to estimate the amount of material eaten from the flower rope enrichment, two control ropes were set up in spare aviaries and weighed and replaced daily. It was discovered that over a 24 hour period, the ropes each lost between 63 and 72g (mean = 69g) through evaporation. This mean mass was subtracted from the total decrease in the mass of the ropes over a 24 hour period in the aviaries which were provided with that enrichment. This gave an approximate value for the mass ingested and / or shredded beyond retrieval by the birds in those aviaries.

With two exceptions, the enrichment devices contained only those foods that were present in the daily diet of the species being examined. The exceptions to this were the flower ropes, and also that the cockatoos were provided with more varieties, and greater numbers, of nuts in their forage trays than they would usually receive.

7.2.1 Mass of Food Eaten From Enrichments and Feeding Dishes

Qualitative Results

The results revealed a tendency for the birds to ingest a greater total mass of food daily when food-based enrichments were provided as well as their usual prepared diet.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with a degree of caution).

It can be seen from Fig. 7.3 that the birds in all the aviaries except aviary 2 ate a significantly greater total mass of food daily (mass of prepared food eaten from feeding dishes + mass of food eaten from enrichment devices) when food-based enrichments were present, than when they were absent. This result was not significant for the aviary housing the monks parrakeets (aviary 2), but this was thought to be a consequence of the sparrow predation on the seed in their feeding dish being higher in the baseline experiment than when enrichments were present.

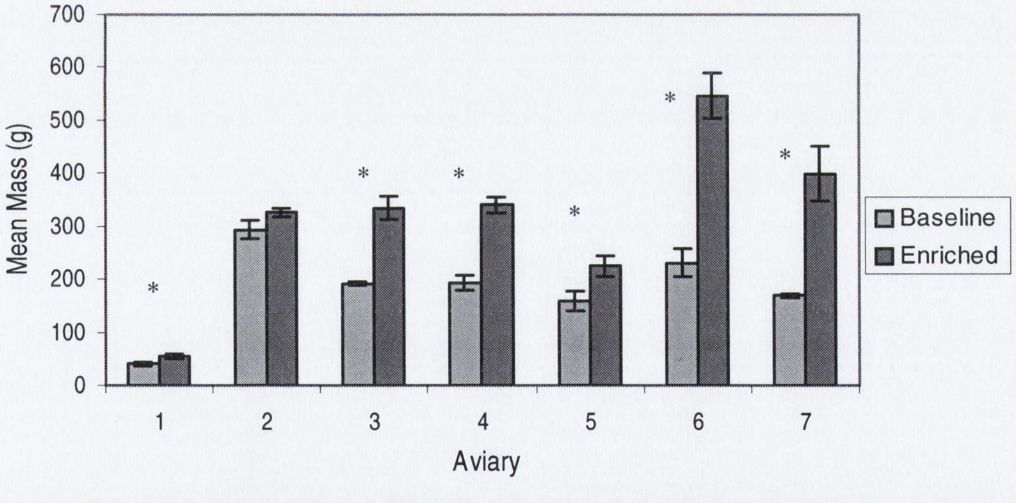


Fig. 7.3: The total mean mass of food (g) eaten daily by the Melbourne Zoo psittacine group, both from feeding dishes, and from enrichment devices (where provided). Results are shown from unenriched and enriched enclosures; a significant difference between the two at the 0.05 level (one-way ANOVA) is indicated by *. See Table 7.2 for details of the birds in each aviary. N=5.

After the study was completed it transpired that, unfortunately, aviary 2 had had a small hole in its exterior mesh through which house sparrows entered the enclosure to eat seed from the prepared dish. Even more unfortunately, this hole had been wired up on the first day of the enriched section of the experiment, trapping one sparrow in the enclosure, and keeping the rest outside, unable to eat their usual quota of seed. It is likely, therefore, that had the conditions in the baseline experiment been identical to those in the enrichment experiment, the birds in aviary 2 would have showed a significant increase in the total amount of food eaten when enrichments were present. This theory is supported by data indicating that the total amount of fresh food eaten by the monks parakeets did increase significantly in enriched conditions (see Fig. 7.5) while the total mass of seed and nuts that was eaten apparently decreased when enrichments were present (see Fig. 7.4). The sparrows were only seen feeding from the seed dish, never that containing fresh food, but monks parakeets are regarded as more generalist feeders, eating fruit, seeds, blossom and insects in the wild (Forshaw, 1989) and eating fresh food as well as dry seed mix in captivity.

Fig. 7.4 shows that the birds in all the aviaries except aviary 2 (see explanation above) showed a significant increase in the total mass of seeds and nuts which they ate once enrichments were provided. There was also a significant increase in the mass of fresh food eaten in the presence of enrichments in all the aviaries except aviary 1 and aviary 5 (see Fig. 7.5). These were the only two aviaries which were not provided with any fruit or vegetable enrichments. The Conclurry ringneck parrots in aviary 5 were, however, provided with a flower rope. There was no significant difference in the mean amount of fruit and vegetables they ate from their prepared dish, whether enrichments were present or absent (baseline = 131g, enriched = 148g; one-way ANOVA: df=1, F=0.69, p=0.431. NS). They consumed a mean of 20g from the flower rope daily (SE Mean = 1.3) but as a result of the amount of variation in the mass of fresh food which they ate (SE Mean: Baseline=12.6, enriched=15.9) that was not enough to provide a significant increase in the overall amount of fresh food eaten.

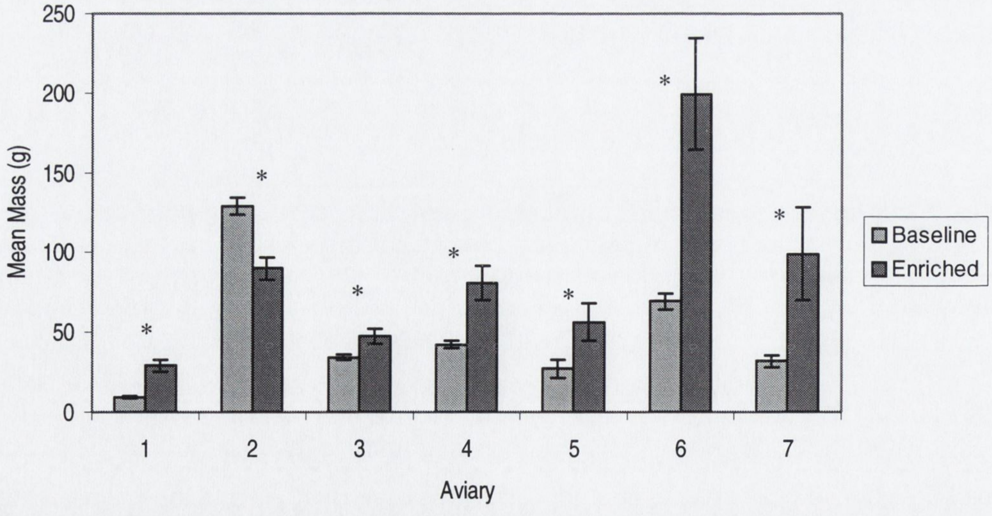


Fig. 7.4: The total mean mass of dry seed and nuts (g) eaten daily by the Melbourne Zoo psittacine group, both from feeding dishes, and from enrichment devices (where provided). Results are shown from both unenriched and enriched enclosures; a significant difference between the two at the 0.05 level (One-Way ANOVA) is indicated by *. N=5.

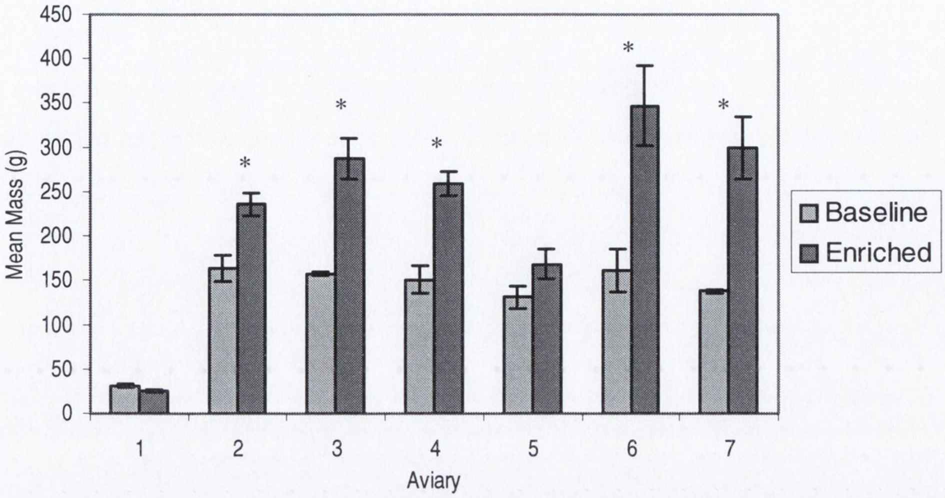


Fig. 7.5: The total mean mass of fresh fruit and vegetables (g) eaten daily by the Melbourne Zoo psittacine group, both from feeding dishes, and from enrichment devices (where provided). Results are shown from both unenriched and enriched enclosures; a significant difference between the two at the 0.05 level (one-way ANOVA) is indicated by *. N=5.

The pair of golden-shouldered parrots in aviary 1 were not provided with any enrichments containing fresh food and there was no significant difference in the mass of fresh food they ate from their feeding dish in the baseline and enriched conditions (baseline = 31g, enriched = 26g; independent t-test: t=2.20, df=8, p=0.059. NS). Without eating more from their dish than usual, they could not increase the amount of fresh food that they ate daily once their enclosure was enriched.

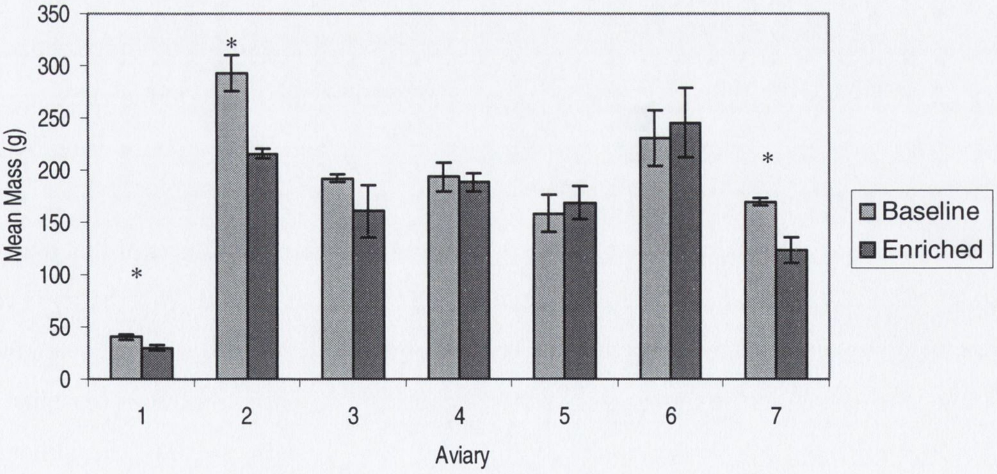


Fig. 7.6: The total mean mass of food (g) eaten daily by the Melbourne Zoo psittacine group from their feeding dishes both in unenriched and enriched enclosures. * indicates a significant difference between the two results at the 0.05 level (one-way ANOVA). N=5.

The psittacines in all the aviaries studied at Dublin Zoo (section 7.1) showed a significant decrease in the mass of food they ate from their prepared diet when they were provided with food-based enrichments. The birds in only three of the seven Melbourne Zoo aviaries showed a significant decrease in the mass of food that they ate from their dishes in enriched conditions. There was no significant change in the amount eaten by the birds in the other four aviaries (see Fig. 7.6).

Discussion

The four aviaries which showed no significant difference in the amount eaten from their feeding dishes (3, 4, 5 & 6) all had high levels of mouse infestation, as did aviary 2, despite the rodent control measures carried out regularly at the zoo, and droppings were found in the food dishes every morning. There was no evidence of the mice eating from the enrichment devices, possibly because they only went to the usual food dishes, and were not aware of the enrichment devices, or because the duration of the experiment was not long enough for the mice to overcome an aversion to novel objects appearing in an otherwise familiar environment. Such neophobia has been shown to be especially strong in rodent populations which experience intensive trapping and poisoning programmes (Brigham & Sibly, 1999).

It is possible, therefore, that the birds in the four infested aviaries did in fact show the same behaviour as those in the other three. If that were the case, then they would leave more food in their dishes when enrichments were also provided, so there would be more of the mice's preferred fruits, vegetables, seeds, nuts etc left in the dishes at night, which was the time during which the rodents were most active. This could result in the mice actually eating a greater mass of food from the dishes when enrichments were added to the enclosure, than they had in the baseline study, thereby covering up any decrease in the amount eaten by the birds.

Aviary 2 also had a degree of mouse infestation, but the effects of that may had been outweighed by the unequal sparrow predation on the prepared seed. This theory is supported by the fact that, as in the other four infested aviaries, the mass of fresh food eaten from the dish in aviary 2 did not show a significant decrease in enriched conditions (baseline mean = 164g, enriched mean = 132g; one-way ANOVA: df=1, F=4.38, p=0.07. NS), although the parrots were feeding regularly from the fruit and vegetable based enrichments (pers. obs.).

Alternatively, the rodent activity may not have affected the results significantly. It could be that the Dublin psittacines were merely showing a significant preference for eating in their outside rather than their inside enclosures, or that captive psittacines behave differently in the southern hemisphere than in the northern hemisphere, or that the birds held at the two institutions had different species-specific responses to enrichment, and that the birds in aviaries 1 and 7 at Melbourne Zoo may have been the ones behaving in an atypical manner for psittacines for that reason. The latter explanation seems unlikely, given the consistency of the behavioural responses to food-based enrichments of all the psittacine species studied (see Chapters 4 & 5).

In order to test which of the other theories is more likely to be correct, an experiment was designed to be carried out on eight separately housed pairs of orange-bellied parrots kept in the Healesville Sanctuary, Melbourne, Australia (see section 7.3).

7.2.2 Proportions of Fresh and Dry Foods Ingested

Qualitative Results

When provided with food-based enrichments which included both the fresh and dry components of the birds' prepared diet, the psittacines showed a tendency to eat approximately the same proportions of the two food categories (fresh and dry), as a percentage of their total daily food intake, as they did in unenriched enclosures when they were feeding solely form their dishes of prepared food.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with a degree of caution).

It was found that most of the birds (and possibly any rodents sharing their food) ate the same proportions of fresh food (fruit, vegetables, flowers) and dry food (seed mix and nuts) as a percentage of the total mass they consumed daily, whether enrichments were present or absent (see Table 7.3). The exceptions to this were the golden-shouldered parrots in aviary 1 and the monks parakeets in aviary 2.

The golden-shouldered parrots, when provided only with seed-based enrichments, decreased the proportion of fresh food they ate but increased the proportion of seed they consumed. They decreased the mass of both fresh and dry foods that they ate from their feeding dishes equally when the enrichments were present (mean decrease in fresh food = 5.6; mean decrease in seeds = 5.0. Paired samples t-test: t=0.65, df=4, p=0.553. NS) although the decrease in the mass of fresh food they ate was not significant, but then could only feed from seed-based enrichments to make up the rest of their diet.

Aviary		Fresh Food (%)	Dry Food (%)
1	**Baseline**	77	23
	Enriched	48	53
	Statistics	F=142.4, df=8, p<0.001	F=142.4, df=8, p<0.001
2	**Baseline**	56	44
	Enriched	72	28
	Statistics	F=25.6, df=8, p=0.001	25.6, df=8, p=0.001
3	**Baseline**	82	18
	Enriched	86	14
	Statistics	t=4.0, df=8, p=0.081. NS	t=4.0, df=8, p=0.081. NS
4	**Baseline**	77	23
	Enriched	76	24
	Statistics	F=0.1, df=8, p=0.772. NS	F=0.1, df=8, p=0.772. NS
5	**Baseline**	82	18
	Enriched	75	25
	Statistics	F=3.5, df=8, p=0.100. NS	F=3.5, df=8, p=0.100. NS
6	**Baseline**	68	32
	Enriched	63	37
	Statistics	F=0.7, df=8, p=0.417. NS	F=0.7, df=8, p=0.417. NS
7	**Baseline**	81	19
	Enriched	77	23
	Statistics	F=0.6, df=8, p=0.450. NS	F=0.6, df=8, p=0.450. NS

Table 7.3: The mean mass of fresh food (fruit and vegetables) and dry food (seed mix and nuts), shown as a percentage of the total mass of food eaten daily, that was consumed by the Melbourne Zoo psittacine group. The mean percentages from the baseline and enriched aviaries were compared using a one-way ANOVA. N=5.

Discussion

The only constituent of the fresh food that the golden-shouldered parrots were observed to eat was chopped green leaves (endive), which was unsurprising as they are primarily seed-eaters in the wild (Higgins, 1999). The reason for their behaviour differing from that of most of the other psittacines observed in this experiment is unclear. With hindsight, however, it would have been interesting to have provided endive leaves in aviary 1 as part of the parrots' forage tray enrichment. Results from the study would then have indicated whether the birds would have chosen to keep the proportions of fresh and dry foods which they ate constant, in the baseline and enriched enclosure, if they had been given the opportunity to forage for their fresh food of preference from an enrichment device. It may be, however, that this, primarily seed eating, species would consume only a certain amount of fresh food daily, regardless of its mode of presentation.

The monks parakeets appeared to decrease the proportion of seed and nuts that they consumed when provided with an enriched enclosure, and increased the proportion of fresh foods. It is probable that this result is another artefact arising from the unequal sparrow predation on the seed dish in aviary 2 across the baseline and enriched studies.

The results from this experiment are intriguing, but further research is needed to confirm whether captive psittacines really do choose to eat the same proportions of fresh and dry foods daily, whether they feed only from prepared food in dishes or also from food-based enrichments.

7.3 Orange-Bellied Parrots

This experiment was incorporated into the study described more fully in Chapter 8. The aims were to ascertain whether there was a) a significant decrease in the mass of food the birds ate from their food dishes in the presence of food-based enrichments and b) a significant increase in the total mass of food consumed by the birds when food-based enrichments were provided. As with the birds studied at Melbourne Zoo, the aviaries were not divided into different areas, so the enrichments could be placed in the enclosure with the prepared food. There were, moreover, no rodent or sparrow infestations in these aviaries.

Methods

The study group consisted of 16 birds from the orange-bellied parrot group, housed in pairs at the Healesville Sanctuary in Melbourne, Australia (see 2.2.2.1) and studied during the Spring month of October 2001. Their usual diet for the breeding season (the birds were starting to show courtship behaviour during the study) was provided in two bowls daily, with one (the 'mixed bowl') containing 5-10 sunflower seeds per bird, some chopped greens, small amounts of fly pupae (~4g), fresh apple (~4g) and fresh corn on the cob (~30g). The other bowl (the 'seed bowl') contained *ad lib* fine seed mix containing canary seed (*Phalaris canariensis*) and three varieties of *Panicum* millet (common, white and Japanese).

During the study the food dishes were weighed in each enclosure at 14.00, and were weighed again when they were removed at the same time on the next day. This procedure was first carried out when the birds were kept in unenriched enclosures, then enrichments were added to each aviary on the second day of the study and the measurements were repeated. The enrichments were weighed at the same time as the food dishes.

The enrichment devices provided were a) two forage trays filled with sand, with fine seed mix distributed through them, one placed at ground level and one about 1m from the ground, at the same level as the birds' feeding dishes were positioned; b) small planks of wood placed on the floor, with holes drilled in them and whole sprays of common *Panicum* millet presented upright with their stalks in the holes.

It should be noted that, as with the other experiments described in this chapter, decreases in the mass of the food dishes and enrichments over the experimental period were nominally ascribed to the birds having ingested that amount of food. These values were for purposes of comparison between the experimental groups and should not be regarded as representing the actual dietary intake of the birds, as some of the seed and sand may have been flung around the enclosure floor during foraging. The mass lost due to the evaporation of water from the food and from the enrichment devices was, however, taken into account in an approximate manner in the results. Control experiments set up in an empty aviary, identical to the experimental aviaries, were used to measure the mass of water lost from the birds' prepared food and enrichments, due to evaporative processes, during the experiment (see Table 7.4). These values were subtracted from the mass lost from the foods and enrichments on each day. The moisture loss from the enrichments was thought to be almost entirely due to evaporation of water from the slightly damp sand which was used as a substrate in the forage trays.

	Decrease in Total Mass Of Enrichments (g)	Decrease in Total Mass of Food in Dishes (g)
DAY 1	NA (no enrichments present)	8
DAY2	6	7

Table 7.4: The mass lost from the prepared food and food-based enrichments in an aviary, identical to those housing Healesville Sanctuary orange-bellied parrot group, due to evaporation, over a 24 hr period.

Qualitative Results

The orange-bellied parrots showed a clear tendency to increase the mass of food they consumed daily when provided with food-based enrichments. This was despite the fact that they tended to eat less of their prepared foods than they had done in an unenriched environment.

Quantitative Results

(Due to inescapable non-independence of some of the data (see Ch. 2.4) the statistical analyses outlined below should be treated with a degree of caution).

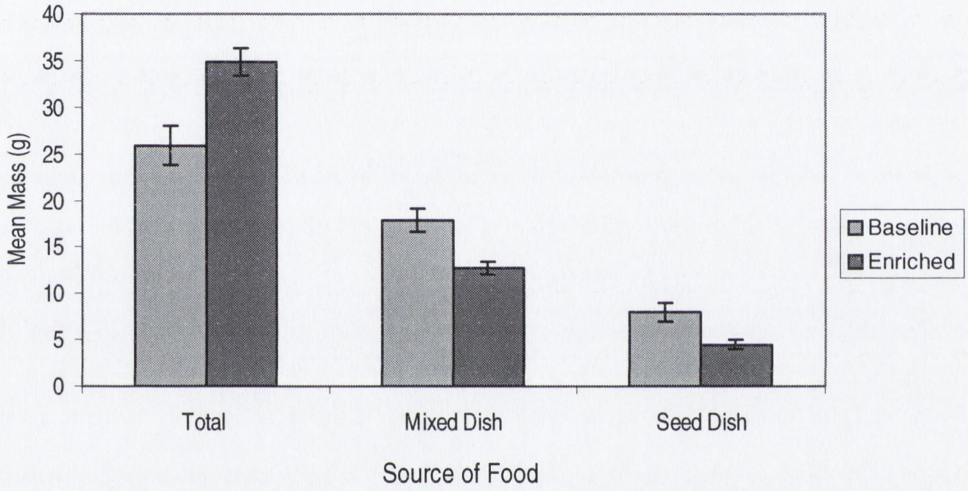


Fig. 7.7: The mean mass of fresh and dry food eaten from their feeding dishes, and the total mass of food eaten from both feeding dishes and enrichments, by the Healesville orange-bellied parrot group during a 24 hour period in both baseline and enriched enclosures (N=8). The differences between results from the two days were all significant at the 0.05 level (independent t-tests).

Measurements of the total mass of prepared food eaten by the birds over 24 hours showed that the 8 pairs studied in baseline conditions on day 1, and in enriched conditions on day 2, ate significantly less both from their dishes of fresh food and their dishes of seed when they were provided with seed-based enrichments (see Fig. 7.7).

7.4 Climate and Environmental Parameter Effects

Temperature, humidity, wind speed and light intensity were monitored hourly in the location of the study aviaries from dawn until dusk throughout all the experiments described above, except for the orange-bellied parrot study, where the readings were taken four times daily. The readings from the baseline experiments were compared with those from the periods when the birds were provided with enrichments, using independent sample t-tests. There were no significant differences at the 0.05 level in any of the experiments, for any of the parameters tested, with one exception: The mean humidity rose from 56% in the Dublin Zoo baseline study to 68% during the enriched experiment (t=2.87, df=8, p=0.021). The birds consumed less food from the dishes in their indoor enclosures, therefore, when the humidity was higher outside. However, the orange-bellied parrots behaved in the same way as the psittacines in Dublin, although there was no increase in humidity in their aviaries. It seems unlikely, therefore, that the change in humidity levels had a significant effect on the Dublin Zoo results.

7.5 Further Discussion

This study was designed in order to investigate the effects of food-based enrichments on the dietary intake of captive psittacines. The experiment carried out at Dublin Zoo indicated that the birds ate significantly less food from their feeding dishes when enrichments were provided for them, than when they were not. Most of the study group decreased the amount they ate of pulses, boiled egg and fruit & vegetables and, possibly, seed mix, as well as their total daily intake of food from their dishes. The seed mix could not be weighed accurately on retrieval from the enclosures as it absorbed moisture from the fresh foods and became coated with particles of fruit and egg.

The experiment performed at Melbourne Zoo indicated that the total mass of food eaten daily by the psittacines (from feeding bowls and enrichments) increased in enriched conditions. The birds provided with enrichment devices containing fruit and vegetables, as well as seed, increased the total amounts of fresh and dry foods that they ate daily. Those species provided mainly or solely with seed-based enrichments, containing no fruit and vegetables, only increased the total amount of dry food which they consumed each day. An interesting possibility indicated by the results of the Melbourne Zoo experiment was that the birds provided with both fresh and dry foods in their enrichment devices ingested approximately the same proportions of fresh and dry foods in the total daily diet, whether the enrichments were present or absent.

Whether the birds at Melbourne Zoo decreased the amount of food they ate from their feeding dishes when enrichments were provided was unclear, due to the presence of sparrow and rodent infestations in the aviaries. The feeding behaviour of these pest species may have affected the results of the experiment.

The experiment using the orange-bellied parrots was designed, therefore, in order to clarify further the results of the studies carried out in Dublin and Melbourne zoos on two points: Whether the mass of food which the birds ate from their feeding dishes decreased when enrichments were provided, and whether the total mass of food they ate daily increased.

It is possible that orange-bellied parrots are unrepresentative of psittacines generally, either in their behavioural responses to enrichment, or in their dietary responses. There is nothing in their recorded ecology to suggest this, however (Forshaw, 1989; Higgins, 1999) and they are closely related to scarlet-chested parrots, which were studied as part of the Melbourne Zoo parrot group (see Chapters 4 & 5) and may be expected to behave similarly. The scarlet-chested parrots altered their behaviour, in response to food-based enrichments, in accordance with the other species of parrots studied. It is likely, therefore, that the orange-bellied parrots were a suitable species to study, along with the birds from Dublin and Melbourne zoos, in order to investigate the general responses of psittacines to environmental enrichment.

The results from the orange-bellied parrot study indicated that the total mass of food eaten from their feeding dishes daily by the birds decreased when enrichments were provided. This agreed with the results from Dublin Zoo and indicated that the divergent results from Melbourne Zoo were probably atypical. They are likely to have been affected by the presence of rodent populations in most of the enclosures housing that study group.

Contrafreeloading has been mentioned in previous chapters. The results of these experiments on diet indicated that the psittacines studied not only reduced the time they spent feeding from their food dishes in the presence of food-based enrichments, but also reduced the mass of food they consumed from those dishes. It is clear, therefore, that the birds studied displayed contrafreeloading behaviour when they were provided with appropriate enrichment devices. In other words, they chose to spend extra time and effort feeding from the enrichments, when they could have eaten the same foods from their feeding dishes. Contrafreeloading in psittacines is investigated in more detail in Chapter 8.

The data collected from the orange-bellied parrots, pertaining to the total mass of food eaten by the birds daily in the presence of food-based enrichments, supported the result indicated by the Melbourne Zoo study. Although all but one of the aviaries at Melbourne Zoo gave results indicating a significant increase in the total mass of food eaten by the birds, it was possible that the results from the mouse-infested aviaries at least, could have been significantly compromised by the effects of the infestation. The orange-bellied parrots, however, also showed a significant increase in the total mass of food which they consumed when enrichments were present. This indicated that psittacines show a tendency to increase their food intake when they are provided with food-based enrichments as well as their usual food. It should be noted that, given the variation in weight loss through evaporation from the enrichments, and the possibility that not all of the shredded food bits or seed husks were collected from the enclosures for weighing, the contention that psittacines will eat a greater mass of food in enriched conditions needs further testing before it can be stated unequivocally. The results of this study do, however, indicate that this is at least a possible, and more likely a probable, consequence of providing psittacines with food-based enrichments, as well as their usual food.

This finding is supported by the results of a study by Smith *et al.* (1989). The authors looked at the effects of feeding a group of 10 captive lion-tailed macaques (*macaca silensis*) either chopped fruit and vegetables, or the same foods in their whole form. They too found that the members of the study group consumed a significantly greater mass of food when the fruit and vegetables were not chopped (a mean increase from 306g to 395g per individual). The time the macaques spent in feeding and foraging behaviours also increased significantly.

Another result to arise from the study was that the orange-bellied parrots ate significantly less from their mixed dish in the presence of enrichments, despite the fact that the enrichments did not contain any food of the types provided in that dish (see Fig. 7.7). This indicated that the provision of food based enrichments could alter the relative amounts of different food types ingested by psittacines. This was also seen in the results from Dublin Zoo (see section 7.1) where all of the birds except for the yellow-backed chattering lories showed a significant decrease in the mass of sprouted pulses they ate from their prepared food, even though there were no pulses in any of the enrichment devices. Likewise, all the birds except the solitary Moluccan cockatoo in aviary 6 showed a significant decrease in the mass of boiled egg which they consumed.

Further, more detailed, research would need to be carried out in order to ascertain whether the birds were getting the same levels of essential nutrients from their diet when it included food-based enrichments, as when they ate only from their prepared food. It is clear that the amounts of different foods which are ingested by captive psittacines may alter when enrichments are provided, particularly if the enrichments do not contain all of the types of food present in the usual diet. There is a possibility, therefore, that the birds' diet could become unbalanced in the presence of enrichments, and that their health could be affected by a lack of one nutrient, or a surfeit of another.

There may also be health implications to be considered if captive psittacines increase their total food intake in the presence of food-based enrichments and *ad lib.* food in dishes. Obesity can be a problem in some species of captive psittacines, with inactivity and high levels of fat intake being the principle causative factors (Bauck, 1995). Serious consequences, such as hepatic lipidosis, have been linked to such obesity (e.g. Rosskopf & Woerpel, 1991; Murphy, 1992).

It is certainly the case that, when provided with enrichments, the psittacines monitored in this study ingested a greater mass of relatively calorific foods, such as seeds and nuts, than they had done in their baseline enclosures. It is also the case, however, that all the psittacines whose behaviour in the presence of enrichments was recorded (see Chapter 4) increased their levels of activities such as foraging and, in the Melbourne Zoo parrot group and the Melbourne Zoo cockatoo pair, locomotion. The birds studied also decreased the amount of time they spent in inactive behaviours. Magrath & Lill (1983) ranked psittacine behaviours according to the amount of energy expended in each, as multiples of the species' basal metabolic rate, as follows: Roosting – 1 (King, 1974); resting – 1.5 (Aschoff & Pohl, 1970); alert but inactive – 1.9 (Orians, 1961); maintenance – 2.3 (Magrath & Lill, 1983); climbing – 2.8 (Kontogiannis, 1968); foraging – 3 (Custer & Pitelka, 1972); flying – 13.7 (Kendeigh *et al.*, 1977). Although the actual values were estimates, it is clear that replacing inactive behaviours with foraging and locomotion would entail the expenditure of extra energy. The exact energy content of the dietary components was not calculated in this study, but the question of whether the captive psittacines do actually increase their net intake of energy in enriched surroundings would be an interesting and useful area for further research. It would also be interesting to carry out more detailed studies in order to see what proportion of their food the birds would choose to work for, if all the components of their diet were provided in both their enrichment devices and in their feeding dishes.

Chapter 8

Contrafreeloading

Introduction

In previous chapters results indicated that psittacines, given the opportunity, chose to feed from food based enrichment devices instead of eating the same food only from feeding dishes. This was despite the fact that the food took more effort and time to obtain from the enrichments. Choosing to work for food or other rewards, rather than obtain them from a free source, is known as contrafreeloading (e.g. Jensen, 1963).

There are many documented examples of captive animals and birds choosing to perform contrafreeloading behaviour. For example, hungry laboratory rats preferred to use a long route with many blind alleys to reach food rather than a short direct route (Hebb and Mahut, 1955). They also bar-pressed for food rather than eat identical food from a bowl in the same cage (Carter and Berkowitz, 1970). Similarly, pigeons (*Columba* sp.) and domestic fowl preferred to peck a key to obtain grain rather than eat freely-available grain (Duncan and Hughes, 1972) while European starlings (*Sturnus vulgaris*) preferred to search in holes for mealworms, rather than eat them from a dish in a more cost-effective manner (Inglis and Fergusson, 1986). Humans too, both children and adults, have shown contrafreeloading behaviour when tested (e.g. Singh, 1970; Tarte, 1981).

The evidence of contrafreeloading detailed in the earlier chapters of this study is particularly interesting as, in contrast to the laboratory-based experiments described above, there were several novel, food-based enrichments added to each enclosure during the enrichment experiments. The psittacines studied in Australia were species-specific in their use of these, ignoring some of them completely, whilst spending considerable lengths of time manipulating others. The presence of a new food source was not necessarily enough in itself to interest the birds when they had the choice between several such food-based enrichments as well as their usual *ad lib* diet. In addition, the baseline environments of the parrots, lories and the pair of Major Mitchells cockatoos were relatively complex; each enclosure contained at least one conspecific, living grasses and shrubs, perches at several heights, a water pool, rocks, logs and a variety of substrate materials. The main cockatoo enclosure was socially more complex, containing two birds of each of four species, but structurally less complex than the other enclosures in the study. Although it was furnished with many perches of a mixture of sizes, positioned at various heights, a water pool, and a deep layer of sand as the floor substrate, it contained no living plants. Taken altogether, however, the data indicate that both in a fairly simple and a relatively complex (although unchanging and, therefore, predictable) environment, the opportunity to exhibit species-specific foraging behaviours through contrafreeloading was a strong stimulus for the psittacines studied.

The causes of contrafreeloading are as yet unknown, although several theories have been put forward to explain the phenomenon. It is of particular interest to both psychologists and ethologists, as it appears to contradict theories (e.g. optimal foraging theory (Stephens & Krebs, 1986) and learning and motivation theory (Mackintosh, 1974)) which predict that animals will maximise the ratio of reward to effort, or cost, of their behaviour. In an effort to reconcile contrafreeloading with the framework of such theories, attempts have been made to identify the reward to the animals of choosing to work for food. Recent explanations have invoked the idea of information primacy (Inglis & Ferguson (1986); Forkman (1991, 1993); Inglis *et al*, (2001)) which postulates that the animal is working for information, as well as food. It is argued that it is advantageous for animals living in changing environments to update regularly their estimates of the location and content of a, currently sub-optimal, food source because, in the longer term, it may become the optimal place to feed. Contrafreeloading, therefore, would be an adaptive behaviour in the wild state, under conditions of sufficient food availability (it has been shown to decrease in frequency under conditions of food deprivation in captivity (e.g. Inglis & Ferguson, 1986)).

One of the difficulties with the information primacy approach, lies in identifying the type of information being gathered by the contrafreeloading animals. Inglis (1987) found that wild-caught starlings chose to feed from a variable food source (mealworms were hidden in holes, behind opaque plastic flaps, but some holes contained no food) rather than from a dish of visible and easily obtainable mealworms, which had minimum uncertainty associated with it as a source of food. He maintained that there was more for the birds to learn about the variable food source, although he did not specify exactly what, and that it may have been in search of that information that they performed contrafreeloading behaviour. Inglis *et al.* (2001) argue that information collected in this manner can be used at a later time when the less variable food source disappears or has been reduced in profitability. In this way, it can enhance fitness by increasing the chances of the animals obtaining adequate amounts of food in the future.

Bean *et al.* (1999) tested the information primacy theory by assessing the information acquired by wild-caught starlings which performed contrafreeloading behaviour when they were provided with several dishes of food mixed with sand in varying proportions. When the researchers removed the dish containing most food, they found that the performance of contrafreeloading behaviour significantly improved the chances that the starlings would choose to feed from the second most profitable source without further inspection of the dishes. However, lowering levels of contrafreeloading behaviour by depriving the birds of food for longer, prior to the experiment, did not result in a corresponding decrease in information gain. In other words, no correlation was shown between the time spent contrafreeloading and the amount of information gained about their environment by the birds.

Although contrafreeloading behaviour may enable birds to weigh up accurately the relative profitability of different food sources, that does not explain why captive psittacines continually perform this behaviour when provided with food based enrichments, replenished regularly, and the same food *ad lib* in feeding dishes. The experiment outlined in this chapter was designed to test the information primacy hypothesis as a possible explanation of the birds' behaviour. It examined whether information gained from contrafreeloading improved the foraging performance of enriched orange-bellied parrots once their usual food dishes were removed. Their performance was compared with that of conspecifics who had not had the same opportunities to gather information about the enrichment devices prior to the food removal.

Methods

The study group consisted of the orange-bellied parrot group (see 2.2.2.1) housed at the Healesville Sanctuary in Melbourne, Australia and studied during the Spring month of October 2001. The group consisted of 30 birds, housed in pairs. Their usual diet for the breeding season (the birds were starting to show nesting behaviour during the study) was provided in two bowls in each aviary, with one (the 'mixed bowl') containing 5-10 sunflower seeds per bird, some chopped greens, approximately 4g of fly pupae, 4g fresh apple and 30g of fresh corn on the cob. The other bowl (the 'seed bowl') contained *ad lib* fine seed mix containing 30% canary seed (*Phalaris canariensis*), 30% white millet (*Panicum* sp.), 20% common millet (*Panicum* sp.) and 20% Japanese millet (*Panicum* sp.). The feeding dishes were emptied and replenished with fresh food at 8.00 every morning.

The enrichments devices intended for use in the main study were first tested on one pair of parrots in order to see if the birds made use of them at all. The devices provided were a) a forage tray filled with sand, with fine seed mix distributed through it, placed at ground level and b) a small plank of wood placed on the floor, with holes drilled in it and five whole sprays of common *Panicum* millet presented upright with their stalks in the holes. The test pair of parrots used both enrichment devices but were not included in the next stages of the study as they were no longer naïve in regard to the enrichments. The devices used in the main experiment were the two already described and a second forage tray that was also provided in each enclosure, at the same level as the birds' food was usually presented (about 1m from the ground) in case the birds preferred to forage at that height.

The 28 naïve birds were divided into four groups, with four pairs of birds in each of groups A and B, and three pairs of birds in groups C and D. The groups were all within auditory and vocal range of each other, and some birds could see into small areas of the enclosures occupied by the parrots in other groups. Table 8.1 shows the treatments applied to each group over the four days of the experiment.

All the food dishes were weighed at 14.00 and 17.00 on days 1 and 2, and the enrichments were also weighed at those times on all the days that they were provided for the birds. In this way the amount of food eaten during the 3 hour experimental period could be calculated. Enrichments were added to the enclosures at 14.00 on the appropriate day (see Table 8.1); the food dishes were removed from all the aviaries between 14.00 and 17.00 on days 3 and 4.

	DAY	FOOD ITEMS PROVIDED
GROUP A	**1**	Usual food only (baseline)
	2	Enrichments + usual food
	3	Enrichments left in from previous day & food dishes removed
	4	New enrichments in & food dishes removed
GROUP B	**1**	Usual food only (baseline)
	2	Enrichments + usual food
	3	Pre-used enrichments in & food dishes removed
	4	New enrichments in & food dishes removed
GROUP C	**1**	Usual food only (baseline)
	2	Usual food only (baseline)
	3	Enrichments in & food dishes removed
	4	New enrichments in & food dishes removed
GROUP D	**1**	Usual food only (baseline)
	2	Usual food only (baseline)
	3	Pre-used enrichments in & food dishes removed
	4	New enrichments in & food dishes removed

Table 8.1: The treatments carried out on four groups of orange-bellied parrots at the Healesville Sanctuary over the four days of the experiment. The enrichments used were those described in the text.

The levels of feeding and foraging behaviour shown by the birds were recorded from 14.00 to 17.00 on each of the four days. Observations were made 8 times an hour, using scan-sampling, and the behaviour of the birds in each aviary noted. The results were converted to percentages of the total period of time between 14.00 and 17.00 (following the assumption, as in previous chapters, that the observations gave an accurate indication of the proportion of time spent in each behaviour by the birds during each hour of the observation period). The results from each group as well as from unenriched and enriched enclosures, were compared. In addition, the time it took for a bird from each aviary to approach the enrichments once the food was removed on day 3 (the latency period) was recorded. These measurements were intended to indicate not only where the birds are getting their food intake from, but also how much time they were taking to get the ingested mass of food from the enrichments, and whether that was affected by their previous experience of the devices.

The baseline observations indicated how the groups behaved in the absence of enrichments. Groups C and D had two days of baseline observations (see Table 8.1) allowing their behaviour to be compared with that of the Group A and B birds once they were enriched on day 2. This was in order to examine the possibility that the enriched birds altered their behaviour as a result of influences outside the experimental parameters.

Group A birds were able to examine the enrichments on day 2 and so could know in advance exactly how much food was left in them, and how to feed from them, when the feeding dishes were removed from the enclosures on day 3. The Group B birds were provided with a less predictable food source in the form of their enrichments. They could examine the devices on day 2 and learn how to use them, but could not know in advance know how much food was present on the enrichments on day 3 as the enrichments were exchanged for 'pre-used' enrichments of the same types, with different amounts of food removed. (Initially, it had been planned to exchange the enrichments between the pairs in the groups receiving 'pre-used' enrichments but, due to fears of disease transmission, the enrichments were artificially 'pre-used' by hand instead. A few grammes of seed were removed from the enrichments, the seeds were de-husked, and the husks returned to the enrichment devices. The substrate in the forage tray was also 'pecked' with the beak-sized tip of a pen). On day 4 all four groups received freshly prepared enrichment devices, their food was removed and their use of the enrichments compared.

Groups C and D were naïve concerning the enrichments until they saw them on day 3, when the birds in Group C received new enrichments and those in Group D were given pre-used versions in order to see whether 'pre-use' affected the birds' foraging efficiency. As in Chapter 7, it should be noted that, throughout these experiments, decreases in the mass of the food dishes and enrichments over the experimental period are only nominally ascribed to the birds having ingested the relevant amount of food. These values are for purposes of comparison between the experimental groups and should not be regarded as the actual dietary intake of the birds. It is possible, for example, that some of the food may have been flung around the enclosure floor during foraging and not collected for weighing. Some food could thereby have been inadvertently included in the mass of food assumed to have been eaten by the birds. The approximate mass lost due to the evaporation of water from the food and from the enrichments was taken into account in the results, however. A control set of food dishes and enrichments were set up in an empty aviary and weighed at the same times as those placed in the aviaries occupied by the parrots. The masses lost from the food and enrichments due to evaporative processes, between 14.00 and 17.00, are shown in Table 8.2. The masses shown were deducted from the amount that had been lost during the experimental period from the feeding dishes or enrichments on the appropriate days of the study.

	Decrease in Total Mass of Enrichments (g)	Decrease in Total Mass of Food in Dishes (g)
DAY 1	NA	2
DAY2	5	3
DAY 3	1	NA
DAY 4	1	NA

Table 8.2: The mass of water (g) lost by evaporation from a set of food dishes and food-based enrichments during the period 14.00-17.00, in an unoccupied orange-bellied parrot aviary at Healesville Sanctuary. Readings are shown for each of the four days for which experiments were carried out on the parrots in the surrounding aviaries.

The possible effects of climatic parameters such as temperature and humidity were not considered in this study, as they were consistent for each group of birds. The study conclusions were based on comparisons between the groups of birds, rather than absolute values and, therefore, were unaffected by climatic influences.

Results

8.1 Contrafreeloading

In order to ascertain whether contrafreeloading occurred when the orange-bellied parrots were provided with three seed-based enrichments, as well as freely available food, groups A and B were examined on days 1 and 2 to see whether the birds chose to eat from their feeding dishes or from the enrichments.

8.1.1 Mass of Food Ingested

The amount of food eaten from the dishes between 14.00 and 17.00 by each pair of birds in groups A and B on day 1 was compared with that consumed by the same birds, during the same period on day 2, when the enrichments were added to their enclosures. There was a statistically significant decrease in the mass of food consumed from the feeding dishes once the enrichments were present (mean mass per aviary = 3.38g on day 1 and 0.63g on day 2; independent t-test (2-tailed): t=3.26, df=10, p=0.008).

In order to investigate this change further, and to ensure that the perceived decrease was not due to any change in the birds' behaviour on that day caused by some uncontrolled-for factor, the amounts eaten by groups A and B on the first two days of the experiment were compared with those eaten by groups C and D (unenriched until day 3). There was no significant difference between the amount eaten from the food dishes on day 1 by groups A and B and that eaten by groups C and D. Groups A and B ate a mean 4.4g per aviary of food from their dishes, while groups C and D ate a mean 4.5g (independent t-test: t=0.22, df=12, p=0.83. NS). On day 2, however, when groups A and B were enriched, the birds in groups C and D ate significantly more food from their feeding dishes than those birds from A and B. Groups A and B ate a mean of 8.0g of seed from the enrichment devices and 2.6g of food from their dishes, while groups C and D ate a significantly greater mean of 6.2g from their dishes (independent t-test: t=3.65, df=12, p=0.003). The results show, therefore, that the parrots in groups A and B ate significantly less from their food dishes, once they were provided with enrichments, than their unenriched conspecifics. This indicated that the enriched birds were displaying contrafreeloading behaviour.

While the mass of food groups A and B ate from their dishes decreased significantly in the presence of the enrichments, the mass eaten by the birds in groups C and D actually increased significantly on day 2, compared to day 1 (independent t-test: t=2.60, df=10, p=0.027). This may have been due to some unmeasured variable that affected all the parrots, but was outweighed by the influence of the enrichments on group A and B birds. Alternatively, the extra feeding and foraging activity shown by the enriched birds may have influenced the behaviour of their unenriched conspecifics, causing them to feed more than usual.

It should be noted here that the birds in groups A and B did not show any preference between the two forage trays on day 2. There was no difference at all in the mass of seed eaten from each one (paired samples t-test: t=0, df=15, p=1.00), indicating that when the food dishes were also present (1m from the ground) the birds used the high and low forage trays equally. When the food dishes were absent on day 4, there was significantly more seed eaten by the birds from the low tray than from the high one (paired samples t-test: t=2.31, df=13, p=0.038). It seems from these results, that the orange-bellied parrots may have had a preference for feeding at ground level but that they would feed at a higher level (1m from the ground) if their full range of food was located there.

8.1.2 Time Spent Feeding

The mean percentage time spent feeding from the dishes between 14.00 and 17.00 by groups A and B was calculated and was seen to decrease significantly on day 2: (Mean on day 1 = 8%, on day 2 = 4%. Independent t-test: t=2.06, df=93.8, p=0.043).

It should be noted, however, that a significant decrease in the time spent feeding from their dishes was also seen in the birds of groups C and D, although they remained unenriched on day 2: Mean on day 1 =17% and on day 2 = 8% (independent t-test: t=3.03, df=70, p=0.003). This is surprising when looked at in conjunction with the significant increase in the mass of food eaten by these birds on day 2 compared with day 1. It appears that the unenriched birds increased their feeding rate on day 2. They also showed a tendency to display higher levels of foraging behaviour elsewhere in their enclosures on day 2, although the increase was not significant (mean percentage time spent in foraging behaviour was 7% on day 1 and 12% on day 2. Independent t-test: t=1.9, df=65, p=0.056. NS). The unexpectedly increased levels of feeding and foraging behaviours shown by the unenriched birds may have been a result of social facilitation if they were influenced by the behaviour of their enriched conspecifics.

8.2 Effects of Prior Experience on Feeding Behaviours

8.2.1 Mass of Food Ingested

On day 3 of the experiment, all four groups were provided with enrichment devices, and their food dishes removed, at 14.00. Group A birds were left with their enrichments from the previous day, group C received new enrichments, and those given to groups B and D were 'pre-used' with seed husks added to the forage trays and the amount of seed available from each device altered. While the birds in groups A and B had had 24 hours to become accustomed to the enrichments, those in groups C and D had never been exposed to them before. A comparison of the mass of seed eaten from the enrichments by each group was carried out to see if previous knowledge of the devices affected the mass of food ingested from them.

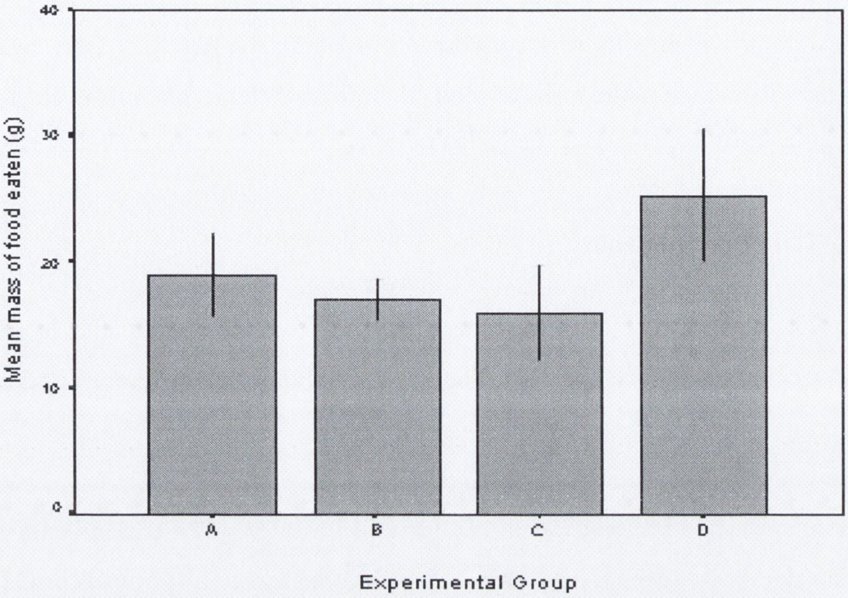


Fig. 8.1: The mean mass of food (g) eaten from the enrichment devices by each pair of birds in the orange-bellied parrot group between 14.00 and 17.00 on day 3 of the experiment. The only food available to the birds was seed from 2 forage trays and 5 sprays of millet (see methods section for more detailed descriptions). For groups A & B, N=4; for C & D, N=3.

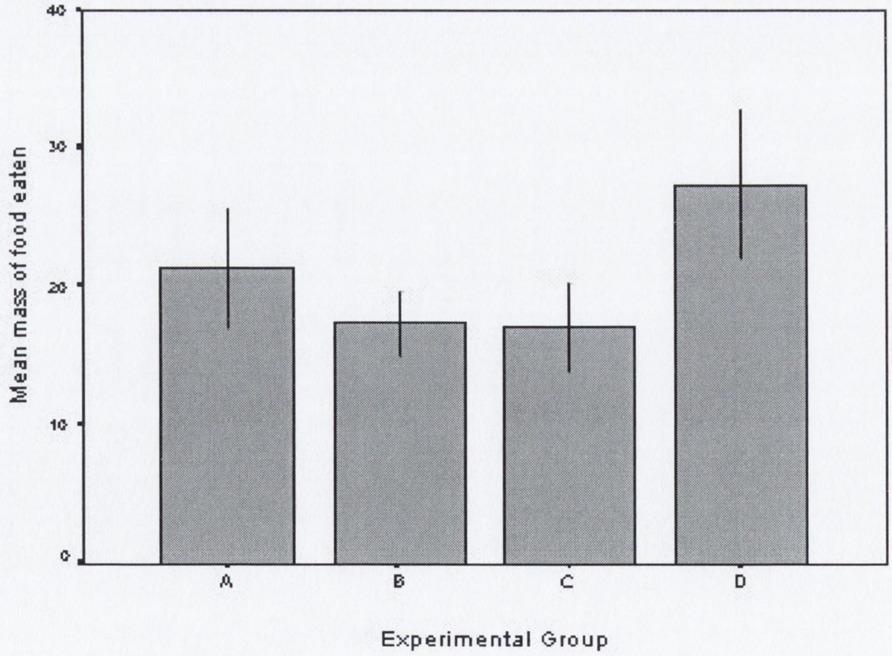


Fig. 8.2: The mean mass of food (g) eaten from the enrichment devices by each group of birds in the orange-bellied parrot group between 14.00 and 17.00 on day 4 of the experiment. The only food available to the birds was seed from 2 forage trays and 5 sprays of millet (see methods section for more detailed descriptions). For groups A & B, N=4; for C & D, N=3.

There was no significant difference in the amounts of seed taken from the enrichment devices by the four experimental groups on day 3 (see Fig. 8.1) (one-way ANOVA: df=3. F=1.32, p=0.321). The same tests were carried out on the results from day 4 when all four groups were provided with fresh enrichments at 14.00 (see Fig. 8.2). Once again there was no significant difference in the mass of seed taken from the enrichments by each group of birds (one-way ANOVA: df=3, F=1.34, p=0.316. NS).

8.2.2 Time Spent Feeding

The mean percentage times spent foraging from the enrichments by each group on day 3 were compared (see Fig. 8.3). There was no significant difference in the mean time spent foraging by any of the groups (one-way ANOVA: df=3, F=1.33, p=0.270). On day 4, however, significant differences were apparent (one-way ANOVA: df=3, F=5.40, p=0.002). Bonferroni post-hoc tests indicated that the time spent using the enrichments was significantly lower for the group A birds than for group D, although not for groups B or C (see Fig. 8.4) (mean of group A = 5.21 minutes; group D = 12.27 minutes; SEM=1.85, p=0.002).

In order to investigate these variations further, the foraging efficiency of each group was calculated for both day 3 and day 4 in order to ascertain whether prior experience altered the mass of seed obtained from the enrichments per unit time.

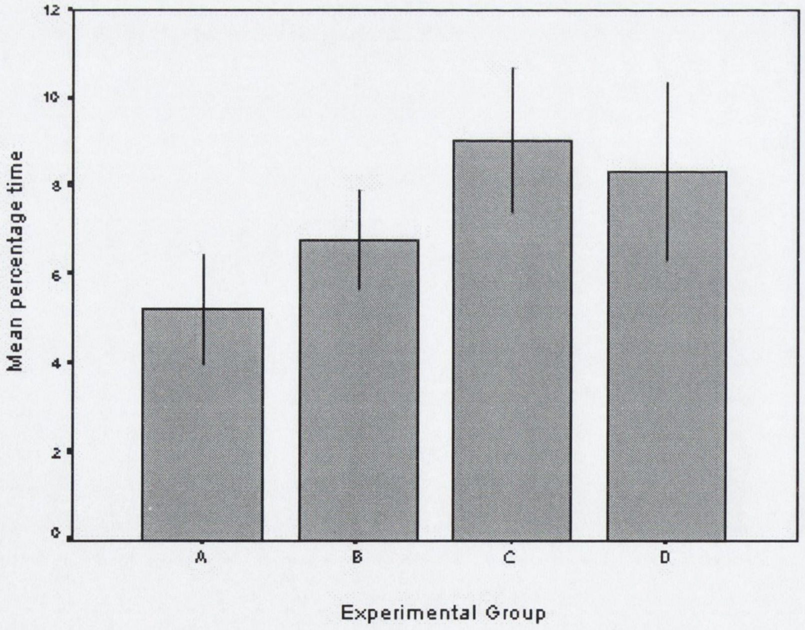


Fig. 8.3: The mean percentage time spent foraging from enrichment devices by each group of birds in the orange-bellied parrot group between 14.00 and 17.00 on day 3 of the experiment. The only food available to the birds was seed from 2 forage trays and 5 sprays of millet (see methods section for more detailed descriptions). For groups A & B, N=8; for C & D, N=6.

When the mean mass of food eaten between 14.00 and 17.00 on day 3 was divided by the time spent using the enrichments by the birds in each enclosure, there was no significant difference in the rate of feeding (g/hr) between any of the four groups (one-way ANOVA: df=3, F=1.59, p=0.254. NS). The same was the case of day 4 (one-way ANOVA: df=3, F=1.37, p=0.132. NS).

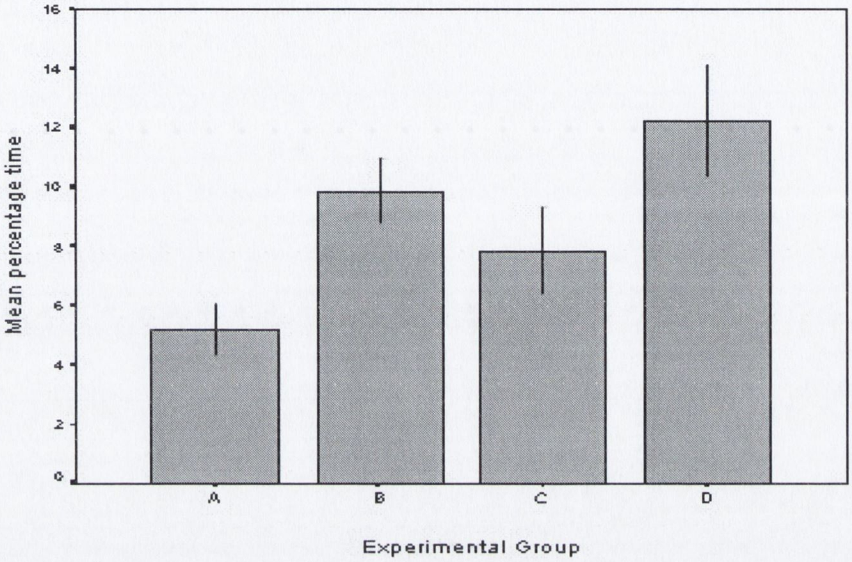


Fig. 8.4: The mean percentage time spent foraging from enrichment devices by each group of birds in the orange-bellied parrot group between 14.00 and 17.00 on day 4 of the experiment. The only food available to the birds was seed from 2 forage trays and 5 sprays of millet (see methods section for more detailed descriptions). For groups A & B, N=8; for C & D, N=6.

There was no significant difference in foraging efficiency between the four experimental groups on day 3 or day 4. It seems, therefore, that the differences in time spent using the enrichments on day 4 did not indicate that the group A birds were more efficient in their use of the enrichments, compared with birds from group D, merely that they spent less time using the enrichments during the observation period.

That conclusion is supported by the results of analysis of the time spent feeding by the birds on day 1, when none of the enclosures were provided with enrichment devices. There was no significant difference in the time spent in foraging behaviour (feeding behaviour performed away from their dishes) by any of the groups (one-way ANOVA: df=3, F=1.39, p=0.252. NS) but one-way ANOVA followed by Bonferroni post hoc analysis indicated that group A birds spent significantly less time feeding from their dishes than those in group D between 14.00 and 17.00 on day 1 (one-way ANOVA: df=3, F=3.77, p=0.014; mean of group A = 6.77 minutes; group D = 18.06 minutes, SEM=4.02, p=0.037). There was no significant difference in the mean percentage time spent feeding from their dishes between any other pair of groups. It appears, therefore, that the birds in group D spent more time feeding, on average, than those in group A, regardless of whether enrichments were provided or not.

8.2.2 Latency of Approach to Enrichments

The length of time that it took the birds to approach any of the enrichment devices after 14.00 on day 3 was monitored. In order to put equal numbers of birds in each group for the purposes of comparison, one pair of birds (one aviary) was randomly selected and removed from groups A and B when the latency data were analysed. This left three aviaries (three pairs of birds) in each of the four experimental groups and the time it took the first bird from each aviary to approach and peck at an enrichment device was recorded to the nearest minute. The results are shown in Fig. 8.5).

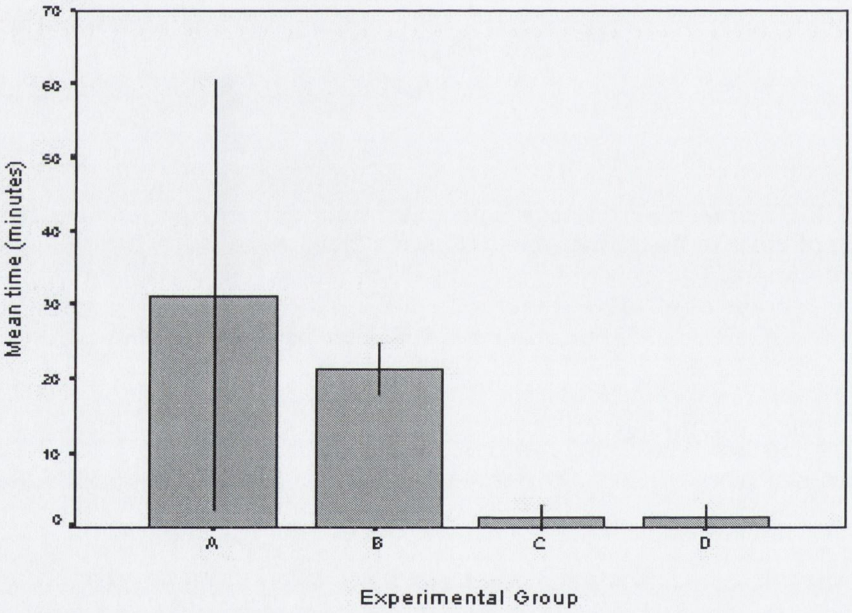


Fig. 8.5: The mean time (minutes) taken to approach the enrichments by each pair of birds observed in the orange-bellied parrot group on day 3 of the experiment from 14.00. New enrichments were added to all the enclosures at that time, except for those in Group A which retained the enrichment devices placed in the aviaries 24 hours previously (see methods section for more detailed descriptions). N=3 for all groups.

Independent t-tests showed a significant difference in the mean latency period only between groups B and C (t=5.3, df=4, p=0.006) and groups B and D (t=5.3, df=4, p=0.006). It should be noted that the values from group A were 4, 30 and 60 minutes, with the pair of parrots in one aviary taking an unusually long time (60 minutes) to approach the enrichments and increasing the mean latency of that group accordingly. It does appear, however, that it may have been the birds from the naïve groups (C and D) that were generally quickest to approach the enrichments, rather than the birds which already had experience of them.

Discussion

The orange-bellied parrots, like the psittacines studied in previous chapters, displayed contrafreeloading behaviour when they were provided with food based enrichments as well as the same food *ad lib* in feeding dishes. Although they showed a preference for feeding at ground level, they also fed from both food dishes and enrichments that were placed 1m from the floor.

According to the precepts of information primacy theory, the contrafreeloading behaviour of the parrots should have enabled them to gather information about the enrichment devices, which would be advantageous to them should their usual source of food (in this case, the feeding dishes) run out or become depleted. On day 3 of the experiment the feeding dishes were removed from all the enclosures and the birds were provided with food-based enrichment devices. Those given to birds in groups B and D were 'pre-used' so that the amount of food available in them and its distribution was not known to the parrots. Groups C and D had never been given enrichments before, whereas the birds in groups A and B had been using them for the previous two days. If the contrafreeloading behaviour of the parrots in groups A and B had provided them with useful information about the enrichments, it would be expected that the group A birds would forage most efficiently from them, group B would be the next most efficient, then groups C and D. If the pre-used condition of the enrichments itself affected the foraging efficiency of the birds, then group A would be more efficient than group B and group C would be more efficient than group D.

The results of the experiment did not conform to that pattern, either in the mass of food eaten by the birds, the amount of time they spent using the enrichments, or their rate of feeding. There was only one significant difference between the groups in any of these categories on days 3 or 4. That difference was between groups A and D, in the time they spent using the enrichments on day 4. This was due to the birds in group D feeding more than those in group A during that observation period, although not at a significantly different rate.

This experiment, therefore, did not support the predictions of the information primacy theory. The results do not, of course, in any way disprove the theory; there are several possible reasons why the experiment may have failed to provide evidence for it, even if the information primacy theory is the correct explanation of contrafreeloading behaviour. For example, the orange-bellied parrots may have used information gathered during use of enrichments to improve their foraging ability, but the effect may have been too small to show significance in the results. This could have been due to the ease and speed with which the birds could assess the distribution and amount of food present in the enrichment devices. The clarity of the results may also have been compromised by the low numbers of birds studied, and the variation in levels of behaviour shown by individuals.

There was some indication in the results that the latency of approach was shorter in the enrichment naïve groups. This may be due to the birds showing investigative behaviour of novel objects in their environment, although is possible that small sample sizes compromised the results of the latency experiment. However all the naïve pairs of parrots, unlike all but one of those with previous experience of the enrichment devices, approached their enrichments within 5 minutes of their introduction.

The validity of the results as a test of the information primacy theory also depended on whether the benefits of the information gathering process were identified correctly. The information primacy theory has been criticised in the past for failing to define the information supposedly gained from contrafreeloading (Kacelnik, 1987). This study was based on the assumption that the benefits would be indicated in greater foraging efficiency by the birds. That assumption may, of course, have been incorrect. Alternatively, the benefits may be in improved foraging efficiency, but they may only be significant in conditions of greater stress or need; for example, in an environment where food availability fluctuated unpredictably over a long period of time.

Another assumption made in this study was that it required more effort from the parrots to forage from enrichments than from their bowl of dry seed. This was not tested during the experiment, and it may be that the effort required to use the enrichments was too low to make contrafreeloading a significant influence on the results. This seems unlikely, given the extra searching and manipulation needed for the parrots to process the food from the enrichments, but it a point worthy of consideration in future research on the subject. With enrichments designed to elicit wild-type foraging behaviour, the birds are performing feeding behaviours for which their species has developed high levels of efficiency. This may be in contrast to the behaviours involved in feeding from their dishes.

If the results of the experiment are correct, they may support another explanation of contrafreeloading, rather than the information primacy theory. Hendrick (1943) and White (1959), for example, argued that efficient manipulation of the environment, using innate or learned skills, is reinforcing in its own right. Inglis & Ferguson (1986) and Inglis (1987) although proposing the information primacy theory as an explanation for contrafreeloading, agree that White's approach is worthy of further investigation.

Species-specific food-gathering behaviours, in particular, have been shown to be self-reinforcing in this way (Kacelnik, 1987; Gardener & Gardener, 1988). Singh and Query (1971) explained their observations of contrafreeloading behaviour in humans (Singh, 1970, 1972; Singh & Query, 1971) in terms of White's (1959) theory, which maintained that behaviour is primarily directed to controlling and modifying the environment. The ability to control the environment is regarded as a crucial survival trait (e.g. Kavanau, 1967; Bean *et al.*, 1999) and its importance for animal welfare in captivity has also been much discussed (see Chapter 1). It may be argued that it is the gathering of information about an environment by an animal that gives it control, by creating a reliable cognitive model of its surroundings (Inglis *et al.*, 1997). It is also the case, however, that the performance of searching and appetitive behaviours can establish and reinforce the connection between behaviour and its consequences (e.g. Misslin & Cigrang, 1986) in itself a knowledge vital for survival in the wild state and good health in a captive environment (Shepherdson, 1994). It could also be argued that birds which regularly exercise a range of foraging skills in the wild, could forage more efficiently than less practised conspecifics at times when food was scarce.

The contrafreeloading behaviour exhibited by psittacines in the presence of food-based enrichments as well as *ad lib.* food in dishes, may be explained by the birds having a strong motivation to perform species-specific searching and appetitive behaviours, especially when such behaviour is reinforced by food 'rewards'. They may also gather potentially useful information about the food source in the process (e.g. Valone & Giraldeau, 1993) but that does not mean that information gathering is the purpose of contrafreeloading behaviour (Bean *et al.*, 1999). Indeed, it is a behaviour that may be beneficial in several different ways, but the information gathering aspect may be of only limited use in enriched captive environments such as those described in this study. In such environments, the performance of functional appetitive behaviours may be of importance to the birds, although an assessment of the distribution and amount of food available from the enrichments may be of limited, if any, benefit to them.

The information primacy theory was also investigated by Kacelnik and Marsh (2002). They used European starlings in no-choice trials, where the birds flew sixteen 1 metre flights (high effort) or four 1 metre flights (low effort) to turn off a lamp and gain access to differently coloured keys, which they pecked to obtain identical food rewards. The researchers found that when they then gave the starlings access to both coloured keys without expending any effort, the majority preferred the colour of key which had been linked to 'high effort' in the no-choice trails. These results did not support the information primacy theory, although the authors cannot reject it completely because in nature, heavier loads may be associated with greater information gains.

From the results of the experiments described in previous chapters, it appears that the levels of contrafreeloading behaviour exhibited by psittacines may vary with species and with the type of enrichment device provided. It would be interesting to conduct further experiments in which levels of contrafreeloading behaviour were monitored while psittacines were provided with different enrichment devices, all containing equal, visible amounts of food but requiring different skills to remove that food. If the birds performed more contrafreeloading behaviour in the presence of species-specific enrichment devices, that could support the idea that gathering information about the state of the food supply was of secondary importance to the performance of foraging behaviours. Another area for further research would be to investigate whether levels of contrafreeloading can be used as a reliable indicator of motivation or preference in captive psittacines.

Another question to arise out of the orange-bellied parrot experiment was the role that social facilitation may have played in their behaviour. As discussed in Chapter 1, the presence of conspecifics performing a particular behaviour can influence an individual to carry out the same behaviour. For example, Keeling & Hurnik (1996) found that domestic chickens increased their rate of pecking for food when placed within sight and sound of a conspecific which increased its feeding rate as a result of having been previously deprived of food.

On day 2 of the orange-bellied parrot experiment, the birds in groups C and D ate a significantly greater mass of food than on day 1, but they spent less time doing it, so must have increased their rate of feeding considerably, possibly by decreasing the time they spent in appetitive behaviours. In reducing their feeding time they acted in the same way as the enriched birds, who spent less time feeding from their dishes than usual as, in addition, they were also foraging from food-based enrichments. The birds in groups C and D also showed a tendency to increase the time they spent in other foraging behaviours (although this increase was not significant; $p=0.056$) despite being unenriched. These changes in the behaviour of the unenriched parrots may have been in response to vocal, or perhaps visual, cues from the birds in the enriched aviaries.

The changes in the behaviour of both the enriched and unenriched groups, seen when enrichments were added to some aviaries could, of course, have been due to some factor unrelated to the experiment. However, the enriched birds responded behaviourally to the enrichments in the same ways as the Melbourne Zoo parrot group (including a species closely related to the orange-bellied parrot, the scarlet-chested parrot). It seems more likely, therefore, that the behaviour of the enriched parrots was influencing that of the unenriched birds.

Chapter 9

Final Discussion

Comparisons of the captive behaviour observed in basic aviaries in this study with what is known of psittacine behaviour in the wild, indicated that the captive environment resulted in significantly lower levels of activity and higher levels of sedentary behaviours. This is consistent with the results of research carried out on several mammalian species (e.g. Chamove, 1989; Newberry, 1995) and, as discussed in Chapter 1, may indicate that standard zoo aviaries are not optimal environments for psittacine birds to be kept in.

When they were provided with enrichments designed to allow the expression of wild-type foraging behaviours, the captive psittacines altered their activity budgets, causing them to approximate more closely to those of wild birds. These results suggest that psittacines are strongly motivated to forage for food, and that captive environments which do not allow psittacines to perform functional appetitive behaviours, are preventing the birds from fulfilling a behavioural need or requirement. Further support was given to this contention by the observations of food-related vacuum and displacement activities in the birds studied, such as substrate pecking by the scarlet-chested parrots and leaf shredding by the lory species, which decreased when enrichments were provided. In addition, the birds sustained their use of the enrichments for several weeks without any decrease in interest. Indeed, the zookeepers in charge of the cockatoos and lories at Melbourne Zoo continued to provide the same enrichment devices for their charges daily after the experimental period had ended, and the birds appeared to be using them with undiminished vigour after several months had passed (pers. obs.). This is contrary to the results of several enrichment studies which have found that the interest of captive animals in an enrichment device decreases over time. For example, Plowman & Knowles (2001) presented two captive Sumatran tigers (*Panthera tigris* sp.) with eight different enrichment devices, and found that an average gap of three weeks was necessary between presentations of an enrichment in order to maintain the interest of the animals. It is certainly easier to provide captive psittacines with wild-type foraging opportunities than it is to provide large carnivores like tigers with opportunities to hunt and kill their natural prey in captivity, but further research is needed in order to ascertain whether it is the inappropriateness or limitations of an enrichment device that leads to habituation, or whether some taxonomic groups are just more prone to habituate to enrichment than others.

Findings by Altman (1998) suggest that animated and functional activity by captive animals held in zoos elicit the most visitor interest in their behaviour. This, in turn, facilitates visitor learning. Behaviour with no obvious function, in particular stereotypical activity, was found to hold visitor attention significantly less well. One of the effects of enrichment identified in this study was to reduce the amount of time the birds spent inactive during the day. As a result, they were active for more of the time and were more likely to be seen performing foraging or locomotory behaviours by visitors to the zoo. The regular provision of appropriate food-based enrichments to zoo-held psittacines, therefore, is likely to increase visitor interest in those exhibits and to improve opportunities for educating those visitors about the behaviour, ecology and rarity of the birds.

When enriched, all the psittacines studied increased the total amount of time they spent feeding and foraging, and decreased the time they spent in more sedentary behaviours. This is in accordance with results published from other enrichment experiments carried out on parrots (e.g. Reed & Price, 2000). Levels of locomotion increased in the parrot group and single species cockatoo pair, but not in the cockatoo group which was held in a very large aviary (see Plate 2.3) or in the lories. The mixed species group of cockatoos were thought to maintain high levels of locomotory behaviours as a result of being housed in a very spacious aviary with plenty of opportunity for both intra and inter-specific interactions. The lories seemed to maintain high levels of locomotion despite the relatively small size of their enclosure. Lories were also the only species in the study which did not decrease the amount of time they spent on maintenance behaviours in the presence of enrichments. Reasons for this are discussed in Chapter 4, and are thought to be associated with the natural ecology of the birds. These results indicate that environmental enrichment is particularly important for parrots and cockatoos kept in small enclosures (i.e. in standard aviaries where there is insufficient space for sustained flight by the birds). The provision of enrichments in such enclosures resulted in significantly increased levels of locomotion by the birds in this study, and such activity is likely to result in improved muscular and cardiovascular tone and reduce the likelihood of obesity.

In the terminology of consumer economics, captive psittacines appear to exhibit an elastic demand for resting behaviours and, excepting lories, for maintenance behaviours. They reduced the time they spent in those activities, in order to spend more time feeding and foraging, when they were provided with enrichments. This supports the suggestion that the psittacines were strongly motivated to carry out those behaviours (e.g. foraging) even though they were not necessary for the survival of the birds. Further research is need to see whether enrichment experiments can always be used to indicate the species-specific behavioural priorities of psittacines in this way. Such a finding would have important implications for future research, as enrichment experiments are much less time-consuming to carry out than, for example, comparisons of activity budgets on days of different length. In addition they are not complicated by the seasonal differences which usually attend the latter method of identifying the relative importance of various behaviours to the birds.

The decrease in levels of maintenance behaviours performed by the parrots and cockatoos in enriched enclosures (Chapter 4) accorded with the results of enrichment studies examining over-preening in psittacines (King, 1992b; van Hoek & King, 1997) rather than the study by Coulton *et al.* (1997) where parrot and lory species were all reported to increase their levels of preening when enriched (see section 1.4.5). In the latter study, the enrichment devices used may not have been responsible for the change in preening levels (the researchers believed that changes in the weather may have been responsible for other alterations in the birds' behaviour during the enrichment period). Alternatively, the birds may indeed have preened more during the observation periods, but not in total during the enrichment experiment. Observations were only taken over 3-4 hours a day, rather than encompassing the whole period for which the birds were active.

It may be the case that over-preening can lead to feather plucking behaviour in captive psittacines. If so, then the provision of enrichment which reduces preening behaviour could prevent the initiation of such stereotypies. Whether an absence of opportunity to perform foraging behaviours could affect the welfare of captive psittacines, which had no history of feather plucking or other serious stereotypies, was not examined in this study. Research indicates, however, that high levels of lethargy, the frustration of innate motivations and lack of control over the environment can all have serious and negative effects on captive animals (e.g. Wiepkema *et al.*, 1983; Wiepkema & Koolhaas, 1993; Shepherdson, 1994).

The results of the multiple enrichment experiments outlined in Chapter 5 indicated that it was not solely the opportunity to exert more control over their environment that influenced the psittacines' response to the enrichment devices, although it may well have played a part. As discussed in Chapter 1, most enrichment devices provide a level of control over their environment to captive animals, and restore the link between the performance of a behaviour and its consequences. The opportunity to exert such control has been shown to be a powerful motivator for animals in captivity (see section 1.2.1) but the psittacines studied here showed specific preferences for particular forms of enrichment over others. This was despite the fact that all, if used, would have increased the birds' control over their environment, providing a functional link between foraging behaviours and the ingestion of food. The results suggested that the birds were most strongly motivated to perform species-specific behaviours, although most of them would use less species-appropriate enrichment devices in the absence of their preferred items (see Chapters 4 & 5). Results from this study also indicated that psittacines in captivity prefer to feed from certain positions in their enclosures (e.g. at particular heights from the ground), but that many will use other areas if they do not have the opportunity to feed or forage in their preferred positions (see Chapter 6).

It is clear that both the type and the location of the enrichment device in an enclosure are important in maximising the birds' use of the enrichments. The factors determining preferences appear to be primarily species-specific and may best be calculated from observations of wild-type behaviour. For example, Australian king parrots were found to forage more from enrichments that contained fruit, rather than just seed, and galahs and sulphur-crested cockatoos foraged at ground level in preference to eating the same foods from higher perches. These observations are in accordance with what is known about the species' foraging behaviours in the wild.

It has been proposed that providing captive animals with the environmental resources that they are most motivated to interact with can be an effective means of improving their welfare (e.g. Dawkins, 1983, 1990). The results of this study indicate that captive psittacines are strongly motivated to interact with food-based enrichment devices, especially those that are designed and positioned in such a way as to allow them to exhibit species-specific foraging behaviours. This has implications for the husbandry of psittacines in captivity as it indicates that enrichments should be provided for the birds which are designed to allow them to express the natural appetitive behaviours of their species.

With the exception of the pair of Major Mitchells cockatoos (which had been reared in a fairly barren environment) none of the psittacines studied showed any discernible neophobia towards their enrichment devices after a three day acclimatisation period. Further studies on neophobia in both captive and wild psittacines would be necessary in order to ascertain how, and to what degree, neophobic reactions are affected by the captive environment and how that could affect any captive-reared birds that are released into the wild. Research on a variety of species (see section 1.2.2) has indicated that a degree of novelty and unpredictability is important for the welfare of captive animals. It follows, therefore, that despite the apparent non-habituation of psittacines to food-based enrichment devices, some variation in the enrichments provided for the birds is likely to be beneficial.

When they were given food-based enrichments, the psittacines in the study decreased the mass of food which they ate from their feeding bowls, but increased their total intake of food by eating from the enrichment devices. Further experiments are needed to confirm this as there were problems with pest infestations in the study aviaries, which may have compromised the results. However, should they prove to be correct, studies of energy use also need to be carried out in order to see how the increase in consumption in enriched conditions affects both the nutrient intake and the calorific budgets of the birds. It may be that the increased levels of activity observed in enriched psittacines would compensate for their increased calorific intake but, if not, then food-based enrichments could contribute towards long-term health problems such as obesity, unless carefully rationed.

During the enrichment experiments, all the birds studied, with the exception of the Melbourne Zoo lory species, decreased the time spent feeding from their bowls when food-based enrichments were provided. It is thought that the lories behaved differently because their usual prepared diet provided only limited amounts of fruit and seed along with nectar and mealworms (which were not provided in the enrichment devices). Hence, they may have eaten the food provided in their bowls as well as using the enrichments. Alternatively, they may have eaten less food from their bowl, but taken longer than usual to do so. The lories of the same species studied at Dublin Zoo (which received *ad lib* fruit and seed in their daily diet), certainly decreased the mass of food they ate from their feeding bowl significantly when they were provided with similar enrichments.

The reduction in the time the captive psittacines spent eating from their bowls of prepared food when food-based enrichments were present indicated that they were performing contrafreeloading (CFL) behaviour. Further experiments were carried out to examine its possible causes using orange-bellied parrots (Chapter 8) and to investigate the information primacy hypothesis (Inglis & Ferguson, 1986) which postulates that contrafreeloading behaviours are carried out primarily in order to gain information about the feeding resources.

The results of this study did not support the information primacy theory, although neither did they demonstrate conclusively that the orange-bellied parrots do not gain useful information from their performance of contrafreeloading behaviour. Birds which were experienced in using the enrichment devices did not gain any perceptible advantage in foraging ability over naïve birds. It was also observed that the psittacines studied in the multiple enrichment experiments (Chapters 4 and 5) did not all use every enrichment device with which they were provided, and used some more than others in the performance of CFL behaviour. This did not appear to be related to the complexity of the device, and so suggests that CFL is unlikely to be motivated purely by the search for information.

Although contrafreeloading has apparently not been observed in the wild, the information primacy hypothesis is based on the idea of animals gaining a selective advantage in the wild state by accruing information about their environment during the performance of CFL behaviour. There may, however, be several aspects of behaviour (exploration, motivation to perform species-specific behaviours, exploitative sampling) which result in information gathering, but did not necessarily evolve primarily for that purpose. For example, surplus killing has been recorded in the wild (e.g of hens by foxes, or of prey animals by felids (see section 1.2.3). While such behaviour does not constitute contrafreeloading, as the predators do not always feed from their surplus kills, the animals involved, despite being able to feed to satiation from their first prey items, kill more, thereby using up extra energy, and perhaps risking injury to themselves. In these cases it is appears that the performance of predatory behaviour is itself strongly motivated, and it may be that CFL behaviours are similarly motivated by an innate inclination to perform species-specific behaviours associated with obtaining food. It has been proposed that efficient manipulation of the environment, especially in species-specific ways, is reinforcing in its own right (e.g White, 1949; Gardener & Gardener, 1988).

Another explanation for CFL behaviour is related to issues of control. As experiments on contrafreeloading behaviour are carried out in captive environments, it may be that the opportunity to reinforce the link between behaviour and consequences, achieved through manipulation of the environment (the enrichment devices in this study) is the motivating factor which stimulates the performance of CFL behaviour. As mentioned previously, and discussed in Chapter 1, control over their environment can be of great importance to animals in captivity (e.g. Misslin & Cigrang, 1986; Shepherdson, 1994; Carlstead, 1996).

Keeping psittacines in large groups has been advocated as a means of improving their reproduction in captivity, increasing levels of social behaviour, improving health (as a side-effect of groups needing to be kept in large enclosures with more room in which to fly) and creating more attractive and educational exhibits for zoo visitors (King, 2000). Keeping psittacines in mixed-gender groups allows free mate choice to occur between the birds, and this has been facilitated by some zoos and researchers. For example, Millam (1990) showed that forced pairings in cockatiels (*Nymphicus hollandicus*) resulted in fewer successful matings and lower egg fertility than were found in established free-choice pairings, and five pairs of military macaws kept at Antwerp Zoo all bred successfully, only after they were allowed to choose their own mates from a mixed-gender flock (King, 2000). It may well be, therefore, that keeping psittacines in small flocks, rather than pairs, will meet the needs and priorities of both zoos and researchers, as the latter will be aided by more individuals being available to take part in a study. Other species too may benefit from such an approach. Free-choice of their mate was found to improve the breeding success in captivity of, for example, American kestrels (*Falco sparvarius*), domestic pigeons (*Columba livia*) and Californian condors (*Gymnogyps californianus*) (Curio, 1996). When social species are kept in groups, however, social facilitation may occur and compromise the validity of any behavioural research conducted. The only way of avoiding such influences would be to keep each study animal in isolation. In this study, for example, such an approach would mean providing environmental enrichment for the birds and simultaneously introducing social deprivation. Not only would such methodology impact negatively on the welfare of the animals, but the results would provide no information that could be applied practically to captive or wild conspecifics which lived in groups. The results of this study, therefore, should be regarded as applying to small social groups of psittacines where social facilitation may be occurring. The results of this study indicate, however, that despite such limitations valid conclusions may be drawn from the results of experiments carried out on psittacines held in zoos.

If the birds used in the study were representative of zoo-held psittacines generally, then the results of this research have a wider significance than for the individual birds and species which featured in the experiments. Although the sample sizes in the study were small, the use of several different species in different locations went some way towards both ameliorating the problem and broadening the applicability of the results. Captive psittacines may show different levels of response to enrichments, depending on the social or species make-up of the holding group. The precise effects of different groupings were not examined in this study, but the responses to enrichments shown by psittacines were examined in twenty-two species and several different social combinations (e.g. single-species pairs, single-species flocks, mixed-species flocks). There was a high level of consistency of response between all the groups studied, and that was an important factor in assessing the validity of the experiments' conclusions. The dietary studies conducted in Chapters 7 and 8 used the aviary, rather than the individual bird, as the experimental unit, thereby substantially improving the robustness of the experiments by increasing the independence of the data points. The results of these experiments supported those of the previous studies where the data points lacked independence, indicating that the conclusions of those experiments are likely to be indicative of real behavioural effects. In particular, the experiments described in Chapter 8 were carried out on several groups of birds of the same species. This design gave results which were statistically stronger than those in other chapters, where the experiments described used fewer birds of each species. The effects of enrichment described in Chapter 8, however, were qualitatively the same as those observed in the other experiments, thereby supporting their findings.

These experiments looked at the effects of enrichment applied over relatively short periods of time. Research into the longer-term effects of food-based, species-specific enrichments, including effects on lifetime reproductive success, is needed in order to consolidate the validity of the results from the short-term studies. Another possible area for future research would be to look at the behaviour of captive psittacines when all their food is provided by way of enrichment devices. It would be interesting to see if the birds would obtain a sufficiently balanced diet by such means, and also to compare their activity budgets with those of their wild conspecifics, to see how closely the two approximate when the captive psittacines are required to forage for all their food.

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